CHAPTER 3 - BEHAVIOUR OF _PTEROPUS GIGANTEUS_

3.1 INTRODUCTION

The activity patterns of animals reflect the important environmental and ecological processes, which govern their lives. Survival in a fluctuating environment requires the successful evolution of strategies, which synchronise the daily and seasonal activities with the availability of critical resources. This is especially important in higher latitudes where environmental periodicities may be unpredictable and seasonal variability is large.

Bats are quintessential refugee animals. They spend well over half of their life time in a day-roost to rest, digest food, interact socially, sometimes to mate and care for their young. Despite the extreme importance of the roosting phase in the lives of bats (Kunz, 1982; Kunz and Fenton, 2003) relatively little is known about their day roosting behaviour. Time budgets in day roost have been described for microchiropterans like _Myotis lucifugus_ (Burnett and August, 1981), _Carollia perspicillata_ (Fleming, 1988), _Desmodus rotundus_ (Wilkinson, 1986) and _Pipistrellus subflavus_ (Winchell and Kunz, 1996). Among megachiropterans, diurnal time budget has been described in species like _Pteropus poliocephalus_ (Nelson, 1965a) and _Cynopterus sphinx_ (Balasingh et al., 1995).

Many sightings of 'diurnally active' bats refer to activity within the arboreal roosts, or movements between roost sites (Lekagul and Mcneeley, 1977), which could be responses to disturbance. In some instances it may refer to the prolonged foraging activity (Brooke, 2001).
Many investigators (Dann and Aschoff, 1975; Winchell and Kunz, 1996) have made systematic field studies on timing of activity of birds and animals including bats. Consequently, it has been concluded that the patterns of activity phasing can be attributed to the effectiveness and variations in both photoperiod and duration of twilight (Laufens, 1973).

Organisms enhance their fitness by aligning their activities to environmental factors such as light-dark cycles, temperature etc. As a result, many bodily phenomena oscillate rhythmically and keep pace with geophysical order. Light-dark cycles are presumably the main entraining agent or ‘zeitgeber’ in cueing a variety of behaviorally timed phenomena (Aschoff et al., 1982). In animals, the seasonal changes in phase relationship between the driving oscillation and the driven oscillation can easily be monitored by recording the locomotor activity in laboratory and in natural conditions.

The day-roost period may occasionally be interrupted by bouts of spontaneous activity, including self-grooming (Nelson, 1965a; Wickler and Seibt, 1976; Burnett and August, 1981), allogrooming (Bradbury, 1977a), copulation (McCracken and Bradbury, 1981), and flight. Burnett and August (1981) directly quantified the day-roosting activity of bats in a maternity roost of Myotis lucifugus. The timing of some roost activities may be influenced as much by the environment as it is by endogenous factors. The diurnal roosting budgets consist of various activity periods, a few are obtained to be periods with greater activity, a few with lesser activity and some with lull activity (Winchell and Kunz, 1993).
Most of the studies on seasonal changes in timing of daily activity in bats in relation to natural light-dark cycle are centred around temperate species in which these studies had to be carried out mostly during summer when the animals were out of hibernation.

Since bats, among mammals are strongly nocturnal and generally depend upon auditory rather than visual stimuli for navigation they were of particular interest for determining the effectiveness of the daily light cycles as an activity synchronizer. Furthermore, their preference for roosting in caves and dimly lit buildings, provided opportunities for studying ‘environmental testing behaviour’ and for demonstrating the ecological value of daily flight rhythms (Bateman and Vaughan, 1974).

Owing to the fact that a close correlation exists between sunset and emergence time, a few studies have ruled out other possible influences. Several authors have suggested that factors such as weather and the quantity of insects may regularly influence flight time and flight activity during foraging but convincing evidence is lacking (Lunde and Harestad, 1986). Studies by several authors lead to the conclusion for other bats, that sunset time is the major factor determining the time of emergence and only occasionally when unusual conditions prevail (e.g. Heavy rain or wind, high temperature etc) this pattern is modified greatly (Erkert, 1982).

Many species of bats leave the roost somewhat earlier or later in relation to sunset in certain seasons (for e.g. in the spring and fall) thereby implying a differential sensitivity to light at different seasons, an adaptation to colder climates
(Nyholm, 1957). On the other hand, some species leave later in relation to sunset in spring and fall and several temperate species exhibit this pattern of emergence (Twente, 1955; Church, 1957). There is a third category of bats, which leave about relatively the same time in relation to sunset throughout the year. The subtropical bats exhibit similar behaviour. Such behaviours are distributed in the lower latitudes where the timings of sunset do not vary markedly. (Gaisler, 1963b).

The study on the activity pattern and behavioural attributes of *P. giganteus* in southern part of Tamil Nadu, India is very low. Hence, a study was made on the diurnal roosting pattern, pre-emergence, emergence and returning behaviour, mother young relationship, activity periods, interaction between male and female bats, roosting hierarchy and post-return activity.

### 3.2 STUDY AREA

The study on the behaviour of *Pteropus giganteus* was done at Srivaikundam. The roosting place was situated on the banks of river Thamiraparani and Srivaikundam anaicut (Plate 4). The area is surrounded by agricultural fields, banana plantations and encircled by numerous trees of *Ficus religiosa*, *F. benghalensis*, *Azadirachta indica*, *Ceiba pentandra*, *Borassus flabellifer* and *Bassia latifolia*. Several fruit orchards of *Mangifera indica*, *Achras sapota* and *Psidium guajava* are also found around this roosting place, hence this area provides plenty of food resources to bats. Three other roosting sites of *P. giganteus* namely, Eral, Athur, and Murrapanadu are also found to be nearer to this roost. The area has a mean temperature of 32°C, which ranges from 21.10°C to 40.7°C during the seasons of the year and with a mean average rainfall of 525mm. The humidity
ranged from 32% to 96.8% and a wind velocity of 2.17Km/hr to 22.2Km/hr was observed in the roosting site during the study period.

3.3 METHODOLOGY

Diurnal roosting budget of *P. giganteus* was studied during May 2003 to April 2004 at Srivaikundam, Tuticorin district. The activity pattern in the diurnal roost, interaction between the conspecific in the day-roost, pre-emergence, emergence and returning behaviour and post-return behaviour and roosting hierarchy were studied.

Diurnal activity budgets of bats were studied throughout the year at weekly intervals. A total of 52 observations were made during the study period. Behaviour delineator was studied as described by Burnett and August (1981) and Winchell and Kunz (1993). To study the emergence and returning activities, observation was started before sunset and continued from emergence of first bat to the return of all bats to the roost (dusk to dawn observation). The pre-emergence activity, one hour before the emergence of first bat, was estimated by observing the various behaviours of bats for every fifteen minutes. The returning and post-return behaviour, for ninety minutes, after the return of the bats, were studied for every ten minutes. The emergence pattern of *Pteropus giganteus* was estimated by evening dispersal counts. The bats were observed visually with the help of two field assistants, who stood at different vantage points to observe and count the bats. The time of the first and the last bat emergence was recorded, and bats emerging at different time intervals were counted using handy bat counter. On each observation, the number of individuals
emerging in every successive 5-minute interval was counted and the peak emergence time was determined.

During the observation period, environmental parameters like temperature and humidity around the roost site was measured using thermo-hygrometer (Barigo, Germany), and the light intensity during the emergence and returning of the bats was measured using lux meter (Lutron LX-101 – Lux meter) with the photo sensor directly facing the zenith. The behavioural observations were done using binocular (Super Zenith, 12 x 50, Field 5°). Sunset and sunrise timings were obtained from the tables of the Indian Ephemeris Nautical Almanac published by the Director of Observatories, Calcutta and were adjusted for longitude, latitude and Indian Standard time. In order to find out the possible effects of lunar periodicity upon activity rhythms of bats, observations were scheduled to coincide with phases of lunar cycles (full moon, new moon, first and last quarters). The behaviour attributes were also made periodically in the nearby roosts. Behavioural activities at the diurnal roosting sites were estimated by the percentage of bats involved in various activities in selected branches of the roosting trees in a stipulated time of every fifteen minutes.

Timings of the onset and end of activity were compared with the period of sunset and sunrise over the season. Seasonal variations of timings of onset and end of activity were used to calculate the phase angle difference and activity time of bats following the method of Daan and Aschoff (1975).

Seasonal variations of onset and end of activity permitted to calculate following parameters.
Activity time (in hours) = ‘onset’ to ‘end’ of activity
Resting time (in hours) = ‘end’ to ‘onset’ of activity

Phase angle difference (in minutes)

\[ \Psi - \text{Onset} (\Psi_o) = \text{between sunset and onset of activity} \]
\[ \Psi - \text{End} (\Psi_e) = \text{between sunrise and end of activity} \]
\[ \Psi - \text{Midpoint} (\Psi_m) = \frac{1}{2} (\Psi - \text{onset} + \Psi - \text{end}) \]

According to Aschoff (1965, 1969), a third measure of the phase angle difference between the activity rhythm and the entraining light dark cycles are \( \Psi \) midpoint (\( \Psi_m \)) i.e. the time interval between the midpoint of activity and midpoint of dark time. The seasonal course of \( \Psi_m \) showed relatively lesser variations compared to \( \Psi_o \) and \( \Psi_e \).

The night activity patterns of the bats in their diurnal roosting sites and foraging haunts were observed using red filtered torchlight (860nm), as it gives least disturbance to the bats. Bats were captured using nets (Plate 5 – Fig 2) (mesh size having diameter of 12 inches) for studying the behavioural attributes in captive rearing chamber. The captured bats were selected depending on their sex, reproductive status and morphological measurements, tagged with beaded necklaces (Isaac et al., 2003) and introduced into the captive rearing chamber. The behaviour attribute of \( P. \ giganteus \) was also observed in the seminaturalistic condition in a cage (4 x 2 x 3 metres) and also in a captive rearing chamber (designed by Lubee
foundation, USA) in the Zoology Research Centre, St. John's College, Palayamkottai. Bats in the captive rearing chamber were fed with locally available fruits and leaves that are preferred by *P. giganteus*. Multivitamin and calcium syrups were given to bats both by oral feeding and through coated fruits.

### 3.3.1 Description of the rearing chamber

Observation and experiments in captivity were carried out in a specially designed octagonal chamber (Plate 5 - Fig 1), fitted with a glass cubicle to facilitate observation. This glass cubicle was fitted in a manner that each and every corner of the chamber could be seen clearly, which helped to observe the activities of the bats. Water was provided *ad libitum*.

Wooden poles fitted with aluminium wires were attached on the roofs of the observation chamber to facilitate roosting of bats. The floor of the chamber was covered with sand for easy removal of the bolus and guano that fell on the floor. The activities of the bats were observed using red-filtered torchlight and the observation chamber was also illuminated with red light (860nm) to facilitate easy observation at night. Since, sunlight diffused into the chamber through glass windows during daytime, the animals were subjected to natural day and night cycle, during study period.

### 3.4 RESULTS

Study on the behaviour of *P. giganteus* was conducted during the year May 2003 to April 2004 at Srivaikundam, a breeding roost of *P. giganteus* situated in the banks of river Thamiraparani (Plate 4). Behaviour was also observed in
Fig 1 - Diagrammatic representation of observation chamber

Fig 2 - Mistnet capture of *P. giganteus*

Fig 3 - Bats in captive chamber

Fig 4 - Bat in rearing cage

Fig 5 - Behaviour of *P. giganteus* in the day roost
seminaturalistic condition in the Research lab of St. John's College, Palayamkottai, south India (Plate 5 – Fig 3). Observation in the captivity was done in two different chambers. A total of 6 individuals, which includes 4 adult females and 1 subadult and one adult male bat were introduced into the captive rearing chamber. Apart from this, 3 individuals of *P. giganteus* that includes two adult female and one adult male was introduced into a rearing cage for observations (Plate 5 – fig 4). Behavioural delineators were observed regularly in the naturalistic and seminaturalistic conditions at regular intervals throughout the study period.

3.4.1 Roosting hierarchy of *Pteropus giganteus*

*P. giganteus* was observed to have a profound character of roosting hierarchy in its diurnal roost. It was observed to form two types of roosting camps (i) the breeding camp and (ii) the non-breeding camp. In non-breeding camps usually the males and subadult females along with juveniles were found to be more in number. In non-breeding camps the male bats usually occupied and roosted in the territory (outer and top) region of the trees, subadult females in the mid and top crown regions of the trees and juveniles roosted in the lower branches of the trees. In breeding camps, the adult male and female bats along with few subadults and juveniles of both sexes could be seen. During the pre-breeding season in breeding camps, adult bats were observed to roost in the top regions and also in the peripheral regions of trees, subadults roosted in the peripheral and core regions of the trees, juveniles roosted in the lower branches of trees and adult females roosted in the core regions and also in the top of the trees.
In certain camps, where more than one roosting tree was present, some trees were totally occupied by male bats with a few juveniles in the lower branches, whereas the adult female bats and subadults roosted in the nearby trees along with a few male and juvenile bats. Juvenile packs of 25 to 50 individuals of both sexes were mostly observed to roost in the lower branches of trees and they roosted mostly in trees, which had good foliage with high shade at the lower crown regions. During the mating season, in breeding camps the female bats moved towards the adult male bats and formed groups. Several female bats (2 to 12 females) roosted with an adult male bat. Bat groups were formed in a manner of bunchy cluster and the bats hung one above the other. Usually the adult male bats were not observed to change their roosting sites and the female bats were observed to change their roosting sites often. The group formation in the breeding camps could be observed throughout the mating periods and a variation in the size of the groups could be observed, when the females moved to nearby groups.

3.4.2 Behaviour of male bats

Male bats in the diurnal roosts mostly roosted in the top and outer regions of the trees and they maintained an inter-individual distance of 1.5 to 2 ft. Adult male bats in the non-breeding camps did not tolerate any close physical contact with other individuals (both male and female individuals) and also did not accept intrusion of other bats into their territory and expressed agonistic or amicable behaviours. The male bats actively repelled against their conspecifics whenever other bats moved into their territory. Behaviour during such conditions included shaking of the wings, harsh audible vocalizations, chasing, biting robustly and fighting. 'Boxing' was also noted, where the sequence involved wing flapping, harsh vocalization, chasing from
the tree and fighting. It occurred for a slight duration (≤ 2 minutes) and could be observed at regular intervals whenever intrusion occurred. The adult male bat was observed to have definite roost site fidelity. During the breeding season, when it formed a group with females it did not allow the intrusion and movement of another bachelor male nearby and was found to be always alert. A bachelor male in the colony was found to roost mostly in the territories of the trees and was found to be less aggressive in its behaviour than other adult male bats. These bats were found to change their roosting places at regular intervals and were found to shift their roosting sites, by flying from one branch to another at regular intervals.

3.4.3 Behaviour of female bats

Female bats probably roosted in the core regions of the trees both in the breeding and non-breeding camps. Like the adult males, the female bats were also found to have inter-individual roosting space (1ft to 1.5ft). Female bats were observed to be more sensitive and alert, and changed roosting sites at a greater rate than the males. Female bats were found to involve in ‘fight’ with the other individuals during the intrusion and avoided body contact with males but they lacked aggression, when compared to male bats in similar conditions. Female bats which were reared in the captive chambers were found to roost with less inter-individual distance (0.5 to 0.75ft) and were found to avoid fighting and they allowed others to roost nearby but did not allow any body contact. Even though these female bats did not accept the intrusion of other bats to roost nearby and showed their conflict during the non-breeding periods, in the breeding roost during the mating season these bats were observed to roost in groups of two to twelve individuals with a male bat without any fighting.
3.4.4 Behaviour of juvenile and subadult bats

Juveniles and subadults of both sexes were found to usually roost in the lower branches of trees. Juveniles were found to be more active than the adults. They were found to roost in a dense manner, unlike adult bats. They were observed to move and crawl through the branches of trees and were found to make audible noises often. Subadult bats were found to roost along with the adult bats and they were also found to roost with inter-individual distances as the adult bats did.

3.4.5 Male - male interaction

During the month of mid August to early September (Pre-breeding season), when the colony size was around 1500 individuals at Srivaikundam roost site, 95.5% of them were males. Adult male bats were found to involve in a unique characteristic male-male interaction, which was not observed during other periods. Male bats were observed to have physical contacts with other male bats roosting nearby. Male bats engaged in such activity were of varying morphological sizes; one male bat was smaller in size than the other. The smaller male bat was found to be either a subadult or a bat which was nearing its adult stage. During this behaviour, the adult bat which was larger in size moved towards the ventral side of the smaller sized bat and snuffled at the lower abdominal region and then towards the reproductive organ and then it moved towards its dorsal side by holding the bat with its claws. Licking of the reproductive organ was also observed. While moving towards the dorsal side of the smaller sized bat, the larger sized adult male forcefully held the smaller sized bat with the wings and clawed fingers. Bats which were involved in such behaviour griped the other bat by biting robustly at the neck region and in some other cases the smaller bat escaped and was found to change its roosting branch. The complete
process of homosexual behaviour existed for a period of 30 seconds to 3 minutes, and it was observed commonly among individuals of the nearby roosts in the study area during the pre-breeding months. An adult male bat, which was reared in captivity, also showed such a type of behaviour during the month of September with a subadult male bat.

3.4.6 Male - female interaction

While the female bats were observed to avoid roosting nearer the male bats during the non-breeding periods, during the mating seasons (late September to mid October) they were observed to move towards the dominant males and were roosting closer to them in groups. Several females (up to 12) were observed to roost in groups with a dominant adult male. Dominant males with enlarged testes were found to exhibit various behavioural components like being incredibly alert, chasing away the males roosting nearer to it, and snuffling at the females nearer to them. The females, which were attracted by such adult male bat moved towards it and hung in hordes by touching one another. A bunchy cluster of around 2 to 12 females could be seen roosting along with an adult male, but the change in the number of females in a cluster occurred regularly. The males which roosted singly also mated with the adult females which were roosting singly and not in groups. As this was observed during mid September to early October months of the year, the trees were mostly naked with withering of leaves and the bats hung as groups in direct sunlight. Fanning and grooming was observed to be very common during such times and with less calling and fighting compared to the other seasons.
At the time of mating the male bats moved to the nearby females and showed allo-grooming behaviour. The male and the female bats faced one another and the male bat held the female bat by its wings and was observed to bite some times and involved in intercourse. During such activity the male and female bats were facing themselves ventrally. A male bat was engaged in such behaviour for around 4 to 5 times at an interval of 3 to 7 minutes with the females in the group. Male bats were engaged in such behaviour more than once with the same female individual. This behaviour occurred between 10:30 and 11:30 hrs at a greater rate (42.3% of the total mating observed).

3.4.7 Parturition

Parturition in *P. giganteus* occurred in the month of late February and in early March. A total of 11 parturitions were closely observed in the wild during this period. Before the time of parturition pregnant bats moved towards the high shadowed regions in the tree with thick foliage and were continued to be restless, alert and stretching both the wings. Grooming was observed to be common in parturient females, and they normally groomed at the abdominal region, and licked the vagina. Before delivery bats were observed to have a violent to moderate contraction of the abdomen accompanied by the abdominal wall getting tensed up. The contractions were arhythmic with an interval of rest and continuous spams of 5 to 12. The bats moved into head-up posture at the time of delivery.

Head of the young one always came out at the time of delivery and after a delay of 15 to 18 minutes slowly the trunk came out. With a pause of 3 to 4 minutes, finally, the legs came out. The newborn remained quiescent until the head and trunk
emerged. The amnion is ruptured before the presentation of head and trunk. Later the neonate slowly became active as the mother repeatedly licked the infant and guided the young one towards its nipple with its wings. Umbilical cord was observed to be attached with the young ones, and placenta came out only after 1 hour and 10 minutes after the parturition. The placenta was deciduate and following the parturition the mother bat ate the placenta. Placentophagia was observed to be common in all the parturient females. The bats grown in captive-rearing-chamber also showed a similar kind of behaviour, where detached placenta was not observed in the floor of the observation chamber. But in the case of an aborted pup the placenta was found to be attached to it and the mother bat did not eat the placenta. The umbilical cord was not severed and it remained attached to the newborn and later the cord gradually dried up and fell down after a period of around 3 hours and 10 minutes after parturition.

3.4.8 Mother - young relationship

*P. giganteus* exhibited interesting social interactions during breeding namely mother-infant relationship. The adult mother bat showed meticulous care towards its young ones from the day of parturition to the weaning stage. The mother bats typically interacted with their young ones. During the neonate stage of the young ones, i.e. upto 27 days after parturition, mother bats were observed to take their young ones to the foraging areas and nurse them throughout this period. Mean forearm length of the young ones at this stage was $81.17 \pm 1.22$ mm ($n = 3$). Juveniles were often found to change from the mothers’ nipples from one side to another at regular intervals in diurnal roost. Observations in the captivity also revealed such behaviour during day and night (foraging) time.
When the juveniles became volant, at an age of 27 to 30 days after parturition, the mother bats were observed to leave their young ones in diurnal roosts as groups in a tree branch having dense leaves. Mean forearm length of the volant young ones was 89.8 ± 1.47 mm (n = 3). Volant groups of around 20 to 25 individuals could be observed in a group. A total of 18 groups of such kind was observed in a single camp during our study period. During this condition, an adult female bat was observed to roost nearer to one of these groups for a period of 1 hour to 3 hours even after the emergence of the last bat and it was not found to involve in nursing the pups. Such a behaviour in the camp of female bats was observed only during the volant stage of pup, until the young one reached the stage of weaning. Returning of the mother bats to the roost during the volant stage of pups was very earlier (at around 1 hour to 2 hours and 30 minutes) and they roosted nearer to the pups at a distance of 2.0 to 3.0 ft in the nearby branches and they did not involve in nursing. Mother bats carried their young ones by around 05:30 hrs and moved to their roosting sites, only after a delay of 2 hours to 2 hours and 45 minutes from its time of returning to the roost. Young ones gave more audible vocalizations when the mother bats were nearby, than during other times. Mother bats were observed to adopt their own young ones only and not the young ones of the other.

After returning from foraging, the adult mother bats suckled their own young ones and spent the remaining time in the diurnal roosting periods totally with their volant young ones and they never let them free. Volant bats started their wing flapping by as they are attached to the mother bat itself. Observations in the captive chamber revealed that pups in the later volant stage moved by crawling towards the
fruits hanging and started eating. The age of the young ones at this stage was around 100 days and the mean forearm length reached 112.2 ± 0.12 mm (n = 3).

When the young ones reached their later volant stage, at an age of around 120 days, mother bats showed another pattern of emergence with a delay of 1 hour to 1 hour and 15 minutes in their emergence and they left behind their young ones in groups as observed in the volant stage. At this stage young ones that were left in the roost were observed to fly to the nearby fruiting trees (50-70 mts from the roost) and to aggregate into groups (weaned groups) and to return to the roost before dawn. The weaned young ones were observed to feed on the leaves of Ficus religiosa and on the fruits of Azadirachta indica trees nearer to the day roost in groups. Weaned pack of young ones of around 75 to 80 individuals was observed to forage in a tree nearer to diurnal roost. The mean length of the forearm reached 119.57 ± 0.55 mm (n = 3).

During the diurnal roosting periods the mother bats left their young ones freely and cared for their young ones by being nearer to them. Weaned pups were involved in grooming and also in wing flapping and they moved from one roosting site to another in the same tree, and the mother bats managed to keep them in their own site. Mother bats chased away the kites and crows that fly nearer to the roost and cared for their young ones. When the mother bats emerged for foraging, young ones in the weaned stage flew to the nearby trees and returned to the diurnal roost at regular intervals. When the young ones were completely weaned, they avoided to roost nearer to their mothers and moved to separate roosting sites and usually avoided contact with their mother. Weaning occurred at an age of 127 to 130 days of age.
3.4.9 Diurnal activity budgets

*P. giganteus* showed several behavioural attributes during different climatic conditions in its day roost. In a normal sunny day, the colony was found to be more active at two periods compared to others; one was before dawn and the other was before dusk. The bats were observed to engage in calling, fighting, grooming and flying and were alert during that time, which was counted as post-return and pre-emergence behaviour (Graph 3.1).

At early in the morning during sunrise the bats were observed to face their body towards the sun light and hold their wings half folded exposing the ventral side of the body to sun light. And after that the bats were involved in grooming for longer periods. As the temperature increased and the sunlight penetrated through the branches at a greater rate, the bats started flapping their wing (flapping behaviour), thereby fanning one side of the body and folding the other wing to cover its body and as the time progressed it folded one side and then flapped the other. All the individuals in the colony were very active until 10:00 hrs in the morning. After this the colony was seen usually with less noise during 11:00 to 02:00 hrs and the bats were involved in fanning, depending on the temperature and sunlight penetration. Flying and fighting was mostly absent and the bats were observed to be less alert during this time. After 02:00 hrs the bats started calling, grooming and were engaged in wing fanning behaviour. This behaviour was low after this time and again increased gradually at 03:00 hrs. After 04:30 hrs the wing flapping behaviour was lower and the bats faced the sunlight, thereby exposing the ventral side of the body to sunlight and were involved in grooming behaviour. Calling, flying, grooming and fighting were observed to be common at this time (Plate 5 – Fig 5). When the
GRAPH 3.1 DIURNAL ACTIVITY BUDGETS OF *PTEROPUS GIGANTEUS*

- ROOST TEMPERATURE (°C)
- AUTOGROOMING
- CALLING
- RESTING
- WING FLAPPING
- WING STRETCHING
- FIGHTING

TIME INTERVAL IN HOURS

BEHAVIOURAL ACTIVITY (%)
temperature and sunlight penetration increased bats flapped their wings to a maximum of 115 beats/min (Graph 3.2). Even though the bats avoided sunlight, during morning and evening the bats opened their wings to expose their body to sunlight and thus kept themselves in the normal level (up to 29°C) of sunlight necessary for their living.

In winter season when the sun light was mild in the cloudy weather, wing flapping was observed to be very much minimized and it occurred only depending on the sunlight penetration and the bats were very normal in other behaviour as observed in normal sunny days, but the period of exposing the body towards the sunlight was observed to be more. In autumn months and cloudy days also the wing flapping behaviour was found to be very low.

In rainy days the bats were observed to wrap their body with the wings and were very calm with no other behavioural aspects. As the rain stopped the bat stretched its wing and groomed its body and flying was observed to be very common. During drizzling flying of bats from one tree to another or around the roosting site was observed to be higher with calling at a greater rate. When sunlight occasionally shone on such days, the bats were observed to open their wings totally and expose their body towards sunlight.

3.4.10 Pre-emergence behaviour

During the pre-emergence period, the bats were involved in various behavioural activities. The rate of time spent in each activity was: fighting (13.67%), flying (30.48%), calling (25.72%), wing flapping (<2%) and auto grooming (27.11%). Wing flapping was absent at emergence time and other behaviours such
GRAPH 3.2 WING FLAPPING ACTIVITY OF *P. GIGANTEUS* WITH REFERENCE TO CHANGE IN TEMPERATURE

- **RATE OF WING FLAPPING / MIN**
- **% OF BATS INVOLVED**

**TEMPERATURE IN °C**

**PERCENTAGE**
as calling (70 to 90%) and auto grooming was at a greater rate (80 to 90%) (Graph 3.3). The movement of bats from tree to tree and from branches to branches was found to be high. The bats flew to nearby trees (distance of 1Km) and then returned to their roosting tree often before emergence.

3.4.11 Emergence activity

The study on the emergence behaviour of P. giganteus colony reveals that mean emergence time of first bat was 18: 25 hrs (n = 52) (Graph 3.4). A positive correlation exists between the emergence of the first bat and the light intensity period (r = 0.99; df = 49; P < 0.01). The emergence of the first bat occurred mostly after a light intensity (lux), less than one was recorded. A positive correlation was also observed between the emergence of the first bat and sun set time (Graph 3.5). The emergence of first bat mostly occurred after 10 to 20 minutes after sun set ($R^2 = 0.90; P <0.01$).

The bats emerged in various directions during various seasons and months (Graph 3.6). Even though bats were found to move in all directions, the rate of dispersion was high towards one or two directions and not in the same proportion towards the other direction.

The study on emergence pattern of Pteropus giganteus in relation to different moon phases reveals that, the emergence gate in the colony during the new moon was $22.3 \pm 5.44$ minutes (mean ± SD, n = 10), in the second quarter phase it was $26.1 \pm 6.42$ minutes (n = 10), in the full moon phase it was $28.89 \pm 7.37$ (n = 9) and in the last quarter of the moon phase, the emergence gate was $22.44 \pm 4.83$ minutes.
GRAPH 3.3 PRE-EMERGENCE ACTIVITY OF *PTEROPUS GIGANTEUS*

- **FLYING**
- **AUTOGROOMING**
- **CALLING**
- **FIGHTING**
- **WING FLAPPING**

**PERCENTAGE**

**TIME (IN MINS) (ONE HOUR BEFORE EMERGENCE)**

0 10 20 30 40 50 60 10

70 60 50 40 30 20 10 0
GRAPH 3.4 EMERGENCE OF *P. GIGANTEUS* WITH REFERENCE TO THE TIME OF SUN SET

- TIME OF SUN SET
- FIRST BAT
- LAST BAT

LACTATION PERIOD
EMERGENCE GATE

MONTHS OF THE YEAR

OCTOBER
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
GRAPH 3.5 REGRESSION LINE SHOWING THE EMERGENCE OF FIRST BAT VS SUN SET TIME

\[ y = -25.25x^2 + 39.671x - 14.793 \]

\[ R^2 = 0.9035 \]
FIGURE 3.6 MONTH WISE EMERGENCE DIRECTION OF P. GIGANTEUS IN SRIVAIKUNDAM ROOSTING SITE DURING THE STUDY PERIOD

PERCENTAGE

MONTHS

- First fort night of the month
- Second fort night of the month

EAST | WEST | NORTH | SOUTH
(n = 9). The mean emergence gate of these post-partum adult female bats was 55.3 ± 30.26 minutes (mean ± SD, n = 12).

3.4.12 Phase angle difference

Figure shows that Ψ₀ varied from 0 to -0.38 hrs and Ψₑ varied from 0 to + 01.56 hrs. The bats had their largest (most +ve or less -ve) Ψ₀ and smallest (less +ve or more -ve) Ψₑ in longer photoperiods and also when the colony size was more; smallest Ψ₀ and largest Ψₑ in shorter photoperiods. As a result, the seasonal variations in Ψ₀ and Ψₑ roughly mirror image. The midpoint (Ψₘ) of activity i.e. the time interval between the midpoint of activity and midpoint of dark time was - 6 to + 51 minutes. The seasonal course of Ψₘ showed relative variations compared to Ψ₀ and Ψₑ (Graph 3.7). The activity period of P. giganteus between the emergence of first bat and returning of last bat is shown in the figure 8. Change in activity period could be observed in several months of the year and the period of activity ranged from 9 hours 30 minutes to 11 hours in normal seasons and it varied during lactating periods to around 5 hours to 5 hours 30 minutes (Graph 3.8).

3.4.13 Returning activity

The mean returning time of first bat to its roost was at around 04:30 hrs and the returning time stretched to a period of 01:30 hrs after the returning of first bat. The timing of returning of the home flier varied between 04:30 hrs and 06:00 hrs paralleling the sunrise time, which varied between 05:59 hrs and 06:40 hrs (Graph 3.9). Regressions were calculated for the returning activity in relation to sunrise (Graph 3.10) and there exists a positive linear correlation with the coefficient nearer to 1.
GRAPH 3.7 PHASE ANGLE DIFFERENCE OF EMERGENCE AND RETURNING ACTIVITY OF *PTEROPUS GIGANTEUS*
GRAPH 3.8 ACTIVE PERIOD OF *PTEROPUS GIGANTEUS* IN VARIOUS MONTHS OF THE YEAR

MONTHS OF THE YEAR

OCTOBER '02

NOVEMBER

DECEMBER

JANUARY '03

FEBRUARY

MARCH

APRIL

MAY

JUNE

JULY

AUGUST

SEPTEMBER

OCTOBER

TIME

16:30 18:30 20:30 22:30 0:30 2:30 4:30 6:30

SUN SET

SUN RISE

ACTIVITY PERIOD

(I bat emergence - last bat return)
GRAPH 3.9 RETURNING OF *P. GIGANTEUS* WITH REFERENCE TO TIME OF SUN RISE

- **TIME OF SUN RISE**
- **FIRST BAT**
- **LAST BAT**

LACTATION PERIOD

MONTHS OF THE YEAR:
- OCTOBER
- NOVEMBER
- DECEMBER
- JANUARY
- FEBRUARY
- MARCH
- APRIL
- MAY
- JUNE
- JULY
- AUGUST
- SEPTEMBER
GRAPH 3.10 REGRESSION LINE SHOWING THE RETURNING OF LAST BAT VS SUNRISE TIME

\[ y = 2.1198x - 0.3256 \]

\[ R^2 = 0.9201 \]
During the post-partum period, the adult post-partum female bat returned to its roost at around 02:30 hrs in the morning (Graph 3.9). Returning of bats to their roost mostly occurred before the sunrise time and in some days a delay in returning was noticed mainly during the short day periods and also when the population size of the colony was maximum. In the month of September, when the population of the bats was high, the bats returned to their roost until 06:10 hrs in the morning, where a lux of 023 x 10¹ was recorded.

3.4.14 Post-return behaviour

In the post-return activity, the bats which returned to the roost, were found to involve in various behavioural activities. The post-return activity mostly comprised of calling (43.07%), autogrooming (42.19%), flying (3.86%), crawling (6.67%), and fighting (4.19%) (Graph 3.11). This period was found to be a period with varieties of behavioural activity in the roost compared with other periods. The bat returned to the roost and occupied a roosting place and it was found to roost in the same place till the time of emergence. In the morning fighting was found to be more between individuals, which roosted closer to each other. An aggressive calling and fighting was noticed among themselves. The bats were found to defend their territories from the intrusion of other bats and maintained an inter-roosting distance among them.

3.5 DISCUSSION

On studying the behavioural activities in the diurnal roosting sites of *P. giganteus*, various behavioural activities were noted throughout the study period.
GRAPH 3.11 POST-RETURN ACTIVITY OF *PTEROPUS GIGANTEUS*

![Graph showing activity percentages of Pteropus giganteus after return.](image_url)
The roosting hierarchy of *P. giganteus* showed that the males mostly roost in the peripheral regions in mid-crown regions of trees, the females roost in the core crown regions and the juveniles in the lower branches of the trees while the subadults roosted along with the adults, and sparsely roosting almost in all the regions. Species like *P. scapulatus*, *P. alecto* and *P. poliocephalus* were also reported to have a similar type of roosting hierarchy (Nelson, 1965a) as observed by us during our study. Neuweiler (1969) studied a similar roosting hierarchy in *P. giganteus*. This type of roosting hierarchy may be considered as a protection strategy. Adult males roosting in the peripheral regions protect the colony from the predators. They were observed to give audible noises when human beings moved nearer to the roosting sites, but dispersal flight in the colony occurred only when they were disturbed and until then they produced only noises. Juveniles roosting in the lower branches of trees get the opportunity to prevail from the direct sunlight and escape from the risk of predation. Such factors were also observed to be true in species like *P. poliocephalus* and *P. samoensis* (Nelson, 1965a; Brooke, 2001). The clustering of female bats in the colony during the breeding season was reported in species like *P. poliocephalus*, *P. alecto* and *P. scapulatus* (Nelson, 1965a; Vardon et al., 2001). This clustering and group formation during such periods helps the bats to escape from the temperature and also help them to save energy (Nelson, 1965a).

Diurnal roosting behaviour in males was extensively studied in various species like phyllostomids (Fleming, 1988) and *C. sphinx* (Balasingh et al, 1995). Males of *P. giganteus* were observed to involve in various behaviour and with contrast attitudes during breeding and non-breeding seasons. Seasonal variations in the behaviour of males were a common phenomenon in *Pteropus* species (Nelson,
In our study it was observed that during non-breeding season *P. giganteus* does not allow other bats to roost nearby and maintains an inter-individual roosting distance. Whereas, during mating periods by involving in various activities it attracts females thereby showing its dominancy. Behavioural sequences that male bats initiated was observed and reported in various species like *Phyllostomus hastatus* (Fleming, 1988), *Pteropus poliocephalus* (Nelson, 1965b) and *Cynopterus sphinx* (Balasingh et al., 1995; Nathan, 2001). The sequence of various characteristic behaviours adopted by male bats to attract females were well reported by Porter (1978) in *Carollia perspicillata*. *P. giganteus* guarded its females from the interference of other bachelor males roosting around during the mating seasons, but the female bats were observed to change their roosting site often. The guarding of the females by the dominant male bats is a phenomenon that may facilitate the dominant males to make a good gene flow to the offsprings as reported in *C. sphinx* (Storz, 2000a, b). The influence of bachelor males in reproduction other than dominant males contributes mainly towards an ecological balance.

Male-male interaction was observed to be a common phenomenon in gregarious roosting bats (Kunz, 1982). The social contact between adult males observed in *P. giganteus* is similar to that of the reports made with reference to various other species (Fleming, 1988; Nelson, 1965a). This type of interaction between males was observed only during the pre-breeding season and may be due to the proliferation of testicular activity, when males become sexually active for breeding. Copulation in *P. giganteus* occurs in the months of September and October. Copulation was observed only during diurnal roosting periods in the roost itself, whereas in species like *C. sphinx* copulation occurred during the night in their
diurnal roosting sites (Dr. Sripathi pers. comm.). During copulation the adult male bat held the female bat by its wings. Both the male and the female bats that engaged in copulation faced one another towards their ventral side. The behavioural process occurred during copulation was as akin to the observations made by Koilraj et al., (2001).

During parturition *P. giganteus* was observed to exhibit various behavioural expressions as reported in other *Pteropus* species (Martin et al., 1987). Placentophagy among mother bats and head first presentation of young ones are all similar to the reports made in other *Pteropus* species (Martin et al., 1987) and in megachiropterans like *Rousettus leschenaulti* (King Immanuel, 2002) and *Cynopterus sphinx* (Nathan, 2001). Parturition has been observed to occur in the day roost, which feature resembles that of most of the other species of bats like *Cynopterus sphinx* (Ramakrishna, 1950), *Rousettus leschenaulti* (King Immanuel, 2002), *Megaderma lyra* (Balasingh, 1990) and *Rhinopoma kinneari* (Anand Kumar, 1965); hence, it can be assumed that parturition in general occurs some time during the periods of rest (Wimsatt, 1979).

Mother bats of *P. giganteus* show greater care towards their young ones from neonate stage until they were weaned. Mother bats take the neonate young one to the foraging ground till they become volant. When the young ones become volant, the mother bats leave the young ones in the diurnal roost while they emerge for foraging. Mother-young relationship observed in *P. giganteus* was analogous to the observations made in various species like *Rousettus leschenaulti* (King Immanuel, 2002) and *Carollia perspicillata* (Sterbing, 2002), *Pteropus poliocephalus* (Nelson,
and also in a few microchiropterans like *Hipposideros speoris* and *Megaderma lyra*. Folsch (1967) reported that the mother bats of *P. giganteus* eat the after birth young ones. However, any such cannibalistic behaviour did not occur during our observation. Transport of young bats by mothers while foraging has been reported for several frugivorous and nectarivorous species (eg, *Carollia perspicillata*, Pine 1972; *Pteropus poliocephalus*, Bartholomew et al., 1964). Bradbury (1977b) reported that in nearly all species, female bats exhibited meticulous care of the young, and during the first few days of life the young never left the nipple of the mother and the young were even carried on foraging flights. Both mother and young showed allogrooming and it may be probably to establish the mother-infant relationship bond, which may be essential for proper weaning. Specific identifications of young by mother bats were reported for several species of bats (Nelson, 1965a; King Immanuel, 2002). *P. giganteus* also exhibit similar kind of relationship with their young ones.

Transport of a pup during the lactation period is expected to increase a female's wing loading, decrease maneuverability and foraging efficiency (Norberg and Rayner, 1987) and increase energy expenditure (Hughes and Rayner, 1993). *P. giganteus* were observed to take their young ones to foraging areas till they attain volant stage and thereafter they left their young ones in diurnal roosting sites while they emerged for foraging. But in species like *C. sphinx*, mothers take their volant young ones to the foraging areas and leave their young ones in the night roosting sites (Gopukumar et al., 2003). Like other *Pteropus* species (Nelson, 1965a), *P. giganteus* was also observed to leave its young ones as a group in trees, which had high clusters of leaves. The trees with leaf clusters provide protection for bats
from predators. Mathai (2002) reported an instance of adoption behaviour in *P. giganteus*. However, any behaviour of such kind was not observed during our study both in captivity and in nature.

*Pteropus giganteus* was found to involve in various activities on its pre-emergence period and an increase and decrease in some behavioural activities were found towards its emergence time. Winchell and Kunz (1996) noticed a similar pattern on the behaviour of *Pipistrellus subflavus*. Even though *P. giganteus* was found to roost in an open foliage roost it had a peculiar light sampling behaviour thereby it was flying to a tree at a distance of 1 Km and returning to the roost prior to emergence. Calling was found to be more at the time of pre-emergence and post-return time and it might be a process of communication and territory defending behaviour. Bat communication has attracted considerable attention whether in roost, or in flight. Bats produce a wide variety of sonic signals within a range of their vocal repertoire (Hill and Smith, 1986). These vocalizations generally facilitate social interaction such as territorial spacing among individuals, mother infant communication and recognition and warning. Some bats are known to exhibit rapid vocal communication prior to emergence (O’shea and Vaughan, 1977). This observation has been reported in *Megaderma lyra* by Marimuthu and Neuweiler (1987).

The emergence of the first bat of *P. giganteus* in a colony occurs mostly after sunset time and a light intensity, less than one lux has been recorded. This may be mainly to avoid dehydration, as flight in the sunlight facilitates faster dehydration. The emergence of first bat mostly occurs after 10 to 20 minutes after sun set.
Jacobsen and DuPlessis (1976) reported that in Africa the time of emergence of the pteropodid, *Rousettus aegyptiacus* followed the sunset throughout the year and usually 20 to 40 minutes after sunset. The time of onset of activity of bats usually falls in certain ranges of luminance at dusk and keeps pace with seasonal progressions of sunset time. This is a general emergence pattern of behaviour observed in nocturnal animals (O’Shea and Vaughan, 1977) and the same was found in *P. giganteus*. Eisentraut (1952) and Gaisler (1963b) said that the subtropical bats leave the roost relatively at the same time in relation to sunset throughout the year. Gopukumar et al., (1998) reported the influence of moon phase in the emergence period of *C. sphinx*, and a similar pattern of delay in mean emergence in *P. giganteus* during the full moon than in the new moon phase was observed.

Kunz (1973b) and Gould (1971) suggested that difference in emergence behaviour was related to reproductive condition, and emergence among recently parturient females may be delayed from early emergence by maternal-infant relationship that is mostly encountered after parturition phase. A greater difference in the evening-gate of the parturient and post-partum females was also observed in *P. giganteus*. A fluctuation in time of emergence in *P. giganteus* was observed during the breeding periods. As in other chiropterans the returning of the bats to the roost mostly occurred before sunrise with a slight delay in return on some days. Erkert (1982) gives a conclusion for other bats, that sunset time is the major factor determining the time of emergence and only occasionally when unusual conditions like heavy rain or wind and high temperature the pattern was greatly modified.
According to Thomas and Fenton (1978), pteropodids that live in large colonies forage in groups. *P. giganteus* was found to emerge in various directions in various seasons and months, and the rate of dispersion was high in one direction or in two directions and this led to forage in groups in trees with high fruiting. Australian *Pteropus* species are probably known to forage in groups on *Eucalyptus* flowers (Nelson, 1965b). Studies by several authors lead to the conclusion, that in microchiropterans the factors like weather and quantity of insects may regularly influence flight time and flight duration but convincing evidence is lacking (Lunde and Harestad, 1986).