TEMPORAL FLIGHT PATTERNS IN DIURNAL AND NOCTURNAL INDIAN CARPENTER BEES

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by

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to

SCHOOL OF BIOLOGY

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Certificate

This is to certify that the work contained in this project report entitled "**Temporal flight patterns in diurnal and nocturnal Indian carpenter bees**" submitted by Preeti**, IMS09014** to Indian Institute of Science Education and Research Thiruvananthapuram towards partial requirement of **Master of Science** in Biology has been carried out by her under my supervision and that it has not been submitted elsewhere for the award of any degree.

Thiruvananthapuram

Dr. Hema Somanathan

April 2014

Supervisor

Declaration

I declare that the matter embodied in this report: "**Temporal flight patterns in diurnal and nocturnal Indian carpenter bees**" is the result of investigations carried out by me in the School of Biology, Indian Institute of Science Education and Research, Thiruvananthapuram, India under the supervision of Dr. Hema Somanathan**.**

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made whenever the work described is based on the findings of other investigations. Any omission which might have occurred by oversight or error in judgment is regretted.

Signed

Preeti

Acknowledgements

Dedicated to

My family, Frisky and Peehu

Abstract

Closely related species can partition resources in space and in time. While spatial partitioning is a well addressed ecological phenomenon, temporal partitioning is less commonly seen in nature. Temporal partitioning, into the day or night among closely related species would closely reflect the physiology and morphology of the species. Physiological constraints are in turn governed by the ambient conditions under which the animal is active. In this study I discuss the role of different environmental variables such as light intensity, ambient temperature, wind speed, sun rise, sun set, moon rise, moon set times, lunar phase and astronomical twilight on flight activity in the nocturnal carpenter bee, *Xylocopa tranquebarica* and two sister congeneric species *Xylocopa tenuiscapa* and *Xylocopa leucothorax*. I examine the extent of temporal partitioning in these three sympatric species of carpenter bees in the Western Ghats. I have also described the structure of orientation flights in the three species. I compare orientation flights in the nocturnal bee X. *tranquebarica* under moonlit and moonless conditions and also contrast these with orientation flights in the two diurnal carpenter bee species.

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Chapter 1

Introduction

Competing species are engaged in evolutionary arms race for shelter, food and survival. Species evolve various strategies to ensure their survival. Some of the best studied survival strategies are the avoidance of competition, predation and parasitism. Survival strategies also include those that maximize food acquisition, and consequently reproductive fitness. Competition can be at an interspecific level, where different species compete for resources, or at the intraspecific level, where individuals of same species compete for resources. Efficient navigation and foraging helps organisms to minimize competition. Organisms can decide to forage during the day or at night, in different weather conditions, solitarily or in social groups to minimize intraspecific and/or interspecific competition as well as to maximize resource procurement (Becon 2006; Morin 2011). Competition avoidance strategies can be best addressed in sympatric species where multiple species have to utilize same resources and confront heterospecific or conspecific competition every day. Resource partitioning is among one of the strategies to minimise competition wherein species either utilize resources in different regions in same geographical area, known as spatial partitioning or use the same resources in same region but at different times, known as temporal partitioning. The theory of competition and niche partitioning comes mostly from mathematical models (Roughgarden 1976, Stewart *et al.* 1973) and a few experimental studies (Felten *et al*. 2009). Niche partitioning has been studied in plants (Sharitz *et al.* 1973), lizards (Schoener 1974, Mattingly *et al*. 2004), parasites (Stadler *et al*. 2011) and insects (Schlyter *et al*. 1993, Agarwal *et al*. 2009).

1.1. Niche Partitioning

Studying sympatric species gives us an opportunity to investigate heterospecific competition and its effects on community structure and organisation. Studying closely related species living in the same ecological environment utilizing the same resources gives us an opportunity to understand how evolution might have shaped their niche and resource preferences. Sympatric species differentiate their niches temporally and spatially to reduce

competition for food and shelter. Spatial partitioning in *Anolis* lizards has been studied extensively, which utilize different parts of the same tree for shelter (Schoener 1974). Temporal partitioning is rather rare in nature in comparison to spatial partitioning. A well-studied example is two species of mice found in rocky desert, viz., *Acomys cahirinus* which is nocturnal and *A. russatus* which is diurnal. In the absence of nocturnal species, *A. russatus* forages in the day and the night (Gutman *et al.* 2005). Another example of niche differentiation in sympatric ant species demonstrating partitioning at both temporal and spatial levels where the former is seasonal while the latter is prominent throughout the year (Albrecht *et al.* 1999, Berstein 1979).

1.2. Factors affecting foraging in flying insects

Temporal niche differentiation is differentiation of niche on time axis over the scale of day, months or season. It is expected that foraging should start at a time when navigation is easiest. The morphology and physiology of an organism can reflect their lifestyles and conditions under which the species must navigate to find food, mates and shelter. For nocturnal and crepuscular species, light intensity plays a major role (Kelber 2005, Narendra *et al.* 2010, 2013). However ambient temperature, wind speed and precipitation can also affect the foraging activity (Jayatilaka 2011). Bees are among the most popular model species for studies of navigation and vision.

1.2.1. Eye design and ambient light intensity

A fundamental consideration for foraging animals is choosing conditions that maximise resource acquisition. Insects have compound eyes, with many facets to capture light. Compound eyes are of two types, superposition and apposition eyes. Nocturnal insects have superposition eyes, an eye design specially adapted for dim light conditions. In superposition eyes, light from many ommatidia, the photoreceptor unit, is superimposed on a light sensitive region, the rhabdom. In this type of eye, visibility is enhanced at the cost of resolution. On the other hand, diurnal insects generally have apposition eyes in which light from each lens falls on a separate rhabdom. In this case, insects have better resolution but lower visibility in dim light (Fernald *et al*. 1992). However, many species with apposition eye design are well adapted to low light levels, for instance, bees, ants, wasps (Kelber *et al*. 2006, Narendra *et al*. 2010, 2013). To increase the sensitivity, these species have larger lenses, more ommatidia and hence larger eye size as compared to strictly diurnal species. Additionally apposition eyes also function as neuronal superposition eyes under dim light. Nocturnal species with apposition eyes also have larger ocelli. (Somanathan *et al*. 2008, Kelber *et al*. 2006, Warrant

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et al. 2006). Light intensity can affect the navigation efficiency of foraging insects because of their eye design. In the nocturnal bee, *Megalopta genalis* which has been studied extensively, the onset of foraging time is completely governed by the levels of light intensity (Kelber 2005).

1.2.2. Effect of Temperature

Insects are either ectotherms or endotherms. In ectotherms, the common mode of temperature regulation is by convection. Convection is a mode of heat transfer in which movement of fluid transfers heat. In ectothermic flying insects the body temperature rapidly rises in thorax because of the high muscular activity as a result of rapid wing movement. When the temperature of the thorax exceeds 40^0 C during flight, the hot blood is transferred from thorax to abdomen, which increases the surface area for heat dissipation (Chappell 1982). It has been shown in ants, in deserts, that they regulate their foraging activity with reference to environmental temperature (Bernstein 1979, Jayatilaka 2011). Thus ambient temperature can affect insect activity as maintaining body temperature is an expensive process.

1.2.3. Effect of wind speed

Another environmental variable which can affect flight activity of flying insects is wind speed. It could be difficult for small insects to fly in high wind speeds while large insects can fly more easily even if the wind speed is high. It has been shown that under high temperatures, wind can reduce the temperature by 1 or 2 degrees (Chappell 1982). For flying insects, wind speed could be advantageous or disadvantageous depending upon their body size and ambient temperature.

1.3. Objectives

In this study, first I examine the roles of environmental factors such as light intensity, ambient temperature, wind speed, lunar phase and precipitation on the flight activity and structure of orientation flights of the nocturnal carpenter bee, *Xylocopa tranquebarica,* in comparison to two diurnal sympatric congeneric species, *Xylocopa leucothorax* and *Xylocopa tenuiscapa*. Nest I examine the extent of temporal overlap between the two diurnal species in terms of frequency of flight activity and compare them with the nocturnal *X. tranquiebarica*. Finally, I compare the manner in which foraging flight activity and the structure of orientation flights change over time (months) and with lunar cycle (full moon to new moon) in these three study species.

Chapter 2

Study species, Methods and Materials

2.1. Biology of carpenter bees
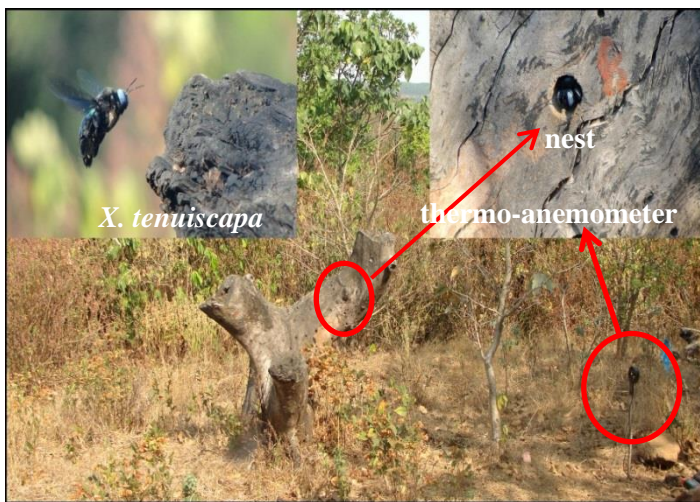
Figure 1. An open nest of X. tenuiscapa with nest entrance in right side

Figure 2. A nest under the closed canopy

The genus *Xylocopa* (commonly called carpenter bees) includes diurnal and nocturnal species. They nest in dead and dry tree logs. Carpenter bees are found mostly in tropical and sub-tropical forests and rarely extend into temperate habitats. These bees are considered to be subsocial where some species are seen to reside with their daughters (Mordechai 1978) or are solitary. A nest can have one to ten individuals. Like many other hymnopterans, *Xylocopa*, also have apposition eyes. The study species included three sympatric species, *Xylocopa tranquebarica* (nocturnal species), *Xylocopa tenuiscapa* and *Xylocopa leucothorax* (both diurnal species). *Xylocopa tranquebarica* can forage under minimal light levels on moonless nights (Somanathan *et al.* 2008). The diurnal bee, *Xylocopa tenuiscapa,* however*,* was also observed to occasionally extend foraging into the night as well, without any correlation with lunar cycle, probably to visit flowers that open at night or to avoid competition with other diurnal species. The nocturnal *X. tranquebarica* forages under low temperatures probably helped by its furry

body to maintain high body temperatures, although *Xylocopa tenuiscapa* lacks such insulation (Somanathan 1999). Nests can be made in dry wooden logs in open grasslands (referred to as open nests here after; Figure 1) or inside canopy (referred to as closed nests; Figure 2).

2.2. Study site

The study was conducted in Bhimashankar Wildlife Sanctuary (19° 21'-19° 11' N, 73° 31'-73° 37' E, 900m elevation) Maharashtra state, in the Western Ghats of India from 1st October 2013 to 1st April 2014. The study sites were spread over hilly areas with vegetation consisting of seasonal cloud forest, open grassy patches with rocky outcrops, paddy fields and abandoned agricultural land.

2.2.1. Astronomical Data

The astronomical data that includes information about moon rise, moon set, sun rise, sun set and astronomical twilight time at the field site was obtained from United States Naval Observatory website (http://aa.usno.navy.mil/data/).

2.3. Onset and offset of flight activity

Since the nocturnal bee and one of the diurnal bee can forage in very dim light condition, to test the effect of light intensity, I observed open and close nests where light intensities are different at a given time. Sites in open areas are mainly grasslands with patchy distribution of trees and where light directly falls on the nest. Closed sites were located under the canopy and light barely reached the nest entrance. On each observation date, the time, light intensity, temperature and wind speed was recorded when a bee left or entered the nest in both closed and open habitat. For *X. tranquebarica*, the nocturnal bee, three nests in open and four in closed canopy were observed. Although some nests were abandoned over the period of observation, the data from those nests are included in some of the analysis. For *X. tenuiscapa*, 5 nest trees with 30 nests in total were observed. All the nests were in the open. In *X. leucothorax*, 6 nests in open and 4 nests in the closed canopy were observed.

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Species	Onset of flight activity		Offset of flight activity	
	Period	Total hours	Period	Total hours
X. tenuiscapa	0530-1030 hours	135 hours 33 minutes	1600-1930 hours	26 hours 32 minutes
X. leucothorax	0600-1100 hours	318 hours 30 minutes	1600- till sunset	36 hours 18 minutes
X. tranquebarica	1700-2000hours	107 hours 31 minutes	0430-0700 hours	39 hours 56 minutes

Table 1 Summary of field observations from October 2013 to March 2014

2.4. Measurement of ambient conditions at open and closed nest sites

Light intensity was measured using an EXTECH Data logging Light Meter (HD450) with a highly sensitive silicon detector. This light meter can detect light only after sunrise and before sunset. Hence light intensities were recorded as zero once the sun was 18^{0} below the horizon (called astronomical twilight) and at night. Temperature and wind speeds were measured with EXTECH Vane Thermo-Anemometer/ data logger (SDL310). Data was collected over 4 moon phases i.e. new moon, first quarter, full moon and third quarter. Onset data for all the three species was collected within 2 days before and after each moon phase. In the month of October 2013 there was intermittent rain during which observations were discontinued. To compensate for this, data was collected on other days when the weather was clear.

2.5. Structure of orientation flights
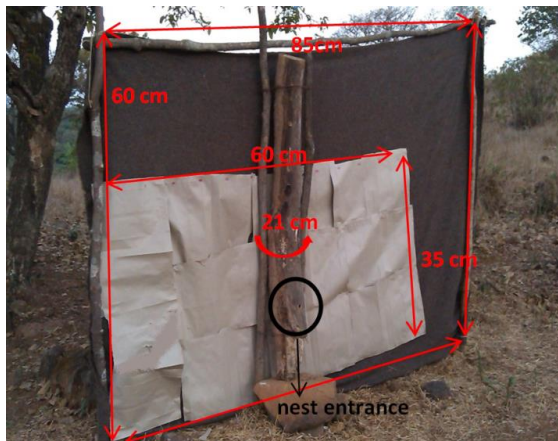
Figure 3. Nest set up for recording orientation flights

To examine the structure of orientation flights, orientation flights were recorded each night with and without a moon using a web camera in IR light for a lunar cycle from full moon till new moon. These recordings were made from 16th March to 31st March 2014. For comparison, the structure of the orientation flights of the two diurnal sister species was recorded. The recordings were made for one nest for the nocturnal *X. tranquebarica* and for one nest of the diurnal *X. tenuiscapa*. The dimensions of the setup are given in Figure 3.

2.6.Data Analysis

2.6.1. Factors determining onset and offset of flight activity

For all the three species, environmental variables like light intensity, ambient temperature, wind speed were recorded for each flight. To examine which of these factors determine onset of flight activity, I used Principle Component Analysis (PCA). The biplot shows the relationship between original variables and subspace dimensions. Each arrow represents the projection of data onto a subspace. Angles between the projections show the correlation between the variables while the length of the projection shows the strength of that variable to explain the maximum variation.

2.6.2. Flight durations

To check if the flight durations varied significantly across months, non-parametric Kruskal-Wallis tests were performed for each of the three bee species.

2.6.3. Flight activity and temporal partitioning between three sympatric species

I used the 'spaa' package in R (Zhang 2013) which has an in-built function to calculate niche overlap using the Czechanowski similarity index (Albrecht *et al.* 2001). The data matrix was randomized 1000 times to generate random data. The significance of observed similarity index was tested by comparing randomized similarity indices with observed index. Since the flight frequencies of both the diurnal bees were very different because of differences in the numbers of nests aggregated in *X. leucothorax* as compared to *X. tenuiscapa*, the raw abundance values were normalized to fall between 0 and 1.

2.6.4. Change in the structure of orientation flights with moon cycle

This analysis is based on video recordings. Flight videos were converted into frames to track the path of the leaving or returning bee using ImageJ (MTrackJ plugin). Orientation flight paths near the nests of *X. tranquebarica* were compared during moonless and moon-lit nights.

Chapter 3

Results and Discussion

3.1. Factors determining the onset of flight activity

The result of the PCA suggests that most of the variables that are related to light intensity
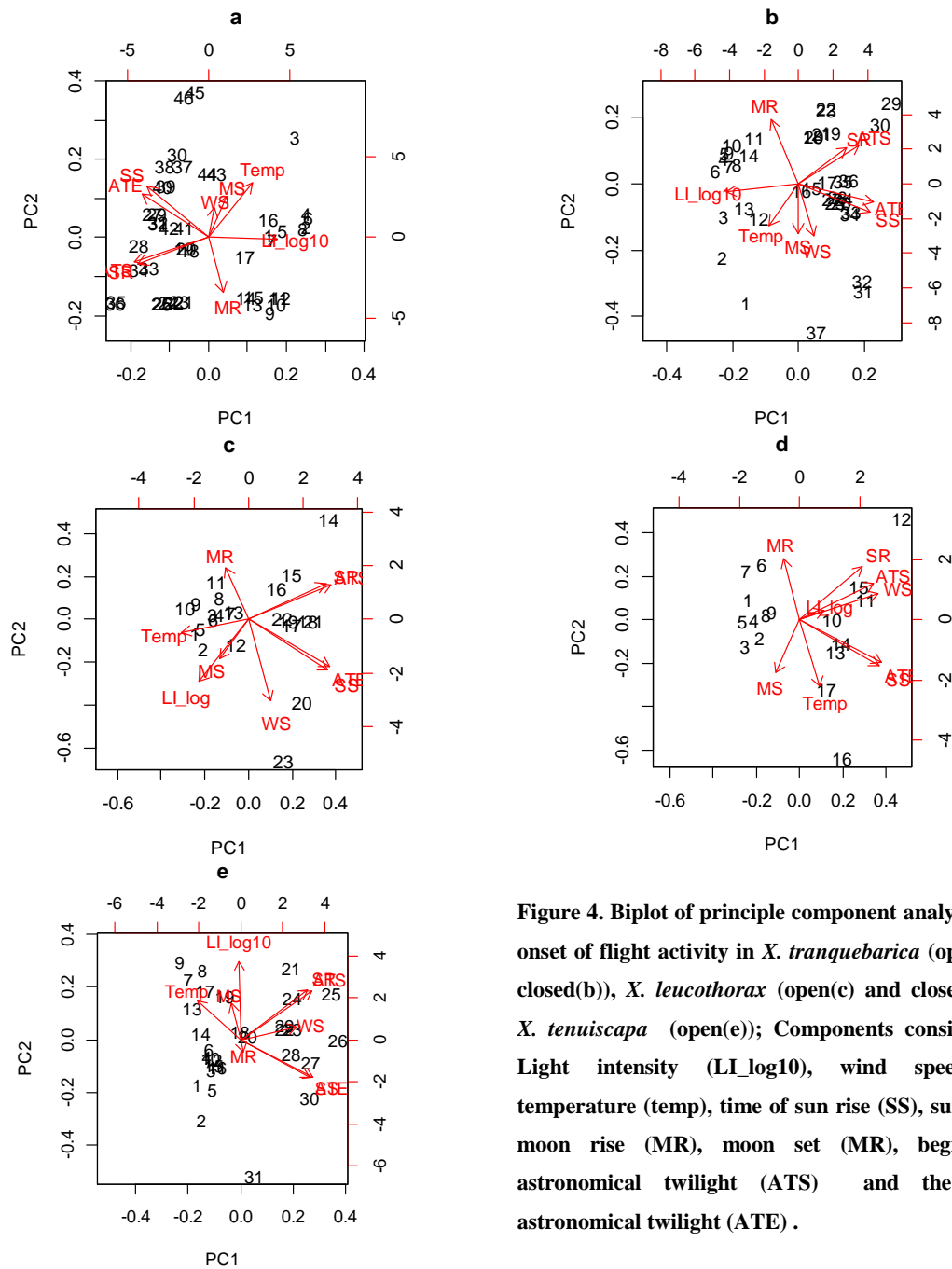
Figure 4. Biplot of principle component analysis for the onset of flight activity in *X. tranquebarica* (open(a) and closed(b)), *X. leucothorax* (open(c) and closed(d)) and *X. tenuiscapa* (open(e)); Components considered are Light intensity (LI_log10), wind speed (WS), temperature (temp), time of sun rise (SS), sun set (SS), moon rise (MR), moon set (MR), beginning of astronomical twilight (ATS) and the end of astronomical twilight (ATE) .

have stronger effect in all the three species, except for the moon rise time in *X. tenuiscapa*. This high light intensity dependence on the onset decision could be because of their apposition eyes. Light intensity, at the time of onset, has least effect in closed nests of *X. leucothorax*. Light intensity after sun rise increases exponentially, reaching a relatively stable range and then again enters exponentially decreasing phase at the time of sun set. In closed nests of *X. leucothorax,* onset time is delayed as compared to open nests. The perceived change in light intensity is very less in closed nests as compared to open nests. This could be the reason for less light dependence in closed nests of *X. leucothorax*. None of the components alone could explain more than 40% of the variation in the time of onset of flight activity. Time of moon rise affects onset in closed and open nest sites in *X. leucothorax* and *X. tranquebarica*. Effect of other variables (SR, SS, ATS and ATE) is similar for all the five cases (Figure 4).

The length of the projection in biplot suggests that temperature has a stronger effect in open and closed nests of *X. leucothorax*. In other two species, length of the projection of temperature is comparable to that of *X. leucothorax* but amongst variables within species, temperature doesn't have enough effect. This could be because, *X. tranquebarica* forages at night and has furry body which can act as an insulator as during nights temperature ranges from 4-22^{0}C. *X. tenuiscapa* lack fur and also has relatively larger body size, which can help in heat dissipation at higher temperatures, as larger the surface area, larger is the heat dissipation through convection (Chapell 1982). *X. leucothorax* forages only after sunrise when temperature goes till 30-33^{0}C, and because of its furry thorax, heat dissipation could be difficult. This could be the reason why temperature has more effect on onset decision of *X. leucothorax* as compared to other two species (Figure 4).

The effect of wind speed on the onset decision of *X. tranquebarica* (in both closed and open nests) is negligible. Magnitude of wind speed in *X. tenuiscapa* is comparable to that of *X. leucothorax*, however, relative effect with respect of other variables is less in former. Wind speed plays a strong role in both open and closed nest sites of *X. leucothorax* and (Figure 4). This could be because of the relatively smaller size of *X. leucothorax.*

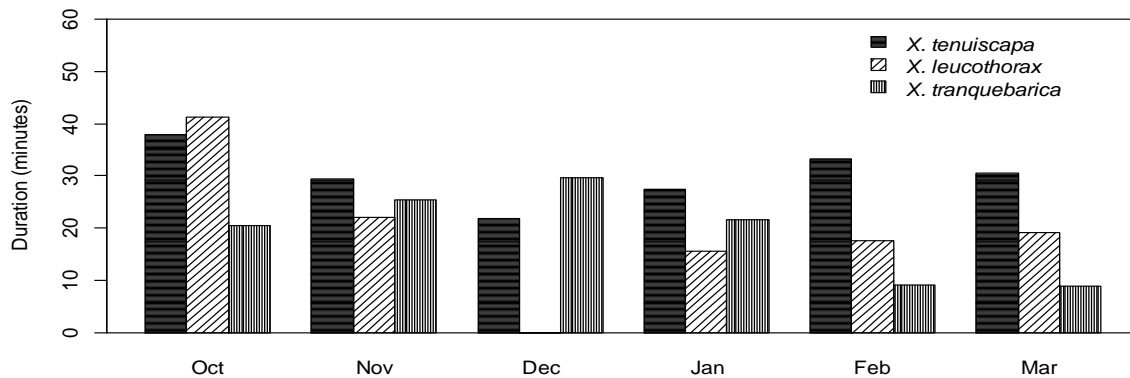### 3.2.Change in flight duration among different months

Figure 5. Month wise flight durations from October 2013 to March 2014 in the three carpenter bee species.

X. leucothorax had maximum flight duration in the month of October amongst the three species, which decreased over time with least activity in December and then stabilized. The variation in flight duration among months was tested using Kruskal-Wallis non-parametric ANOVA for all the three species. In *X. tranquebarica* and *X. leucothorax* change in duration among months is significantly different (df=5, P<0.001) while it is not significant in *X. tenuiscapa* (df=5, P= 0.65). In *X. tranquebarica* the flight duration changed in accordance with frequency of flights (Figure 6(a)) i.e as the duration decreases frequency increases. High flight activity of *X. tranquebarica* in the month of October could be to search for new nest sites after the rainy season while that in January onwards could be related to mating and provisioning of nests. For the diurnal bees, every time a bee returned, presence or absence of pollen load was noted. In case of *X. tenuiscapa* and *X. leucothorax,* although flight frequency was highest in October and November, percentage of bees returning with pollen was highest from January to March again suggesting brood provisioning (Figure 6 b,c). Flowering in this community extends from October till April with peak flowering between January and March. Since the high pollen collection, which is in turn the indicative of brood provisioning, starts from January, it could be hypothesized that these species synchronize their breeding time with peak flowering. However, this needs to be verified experimentally.
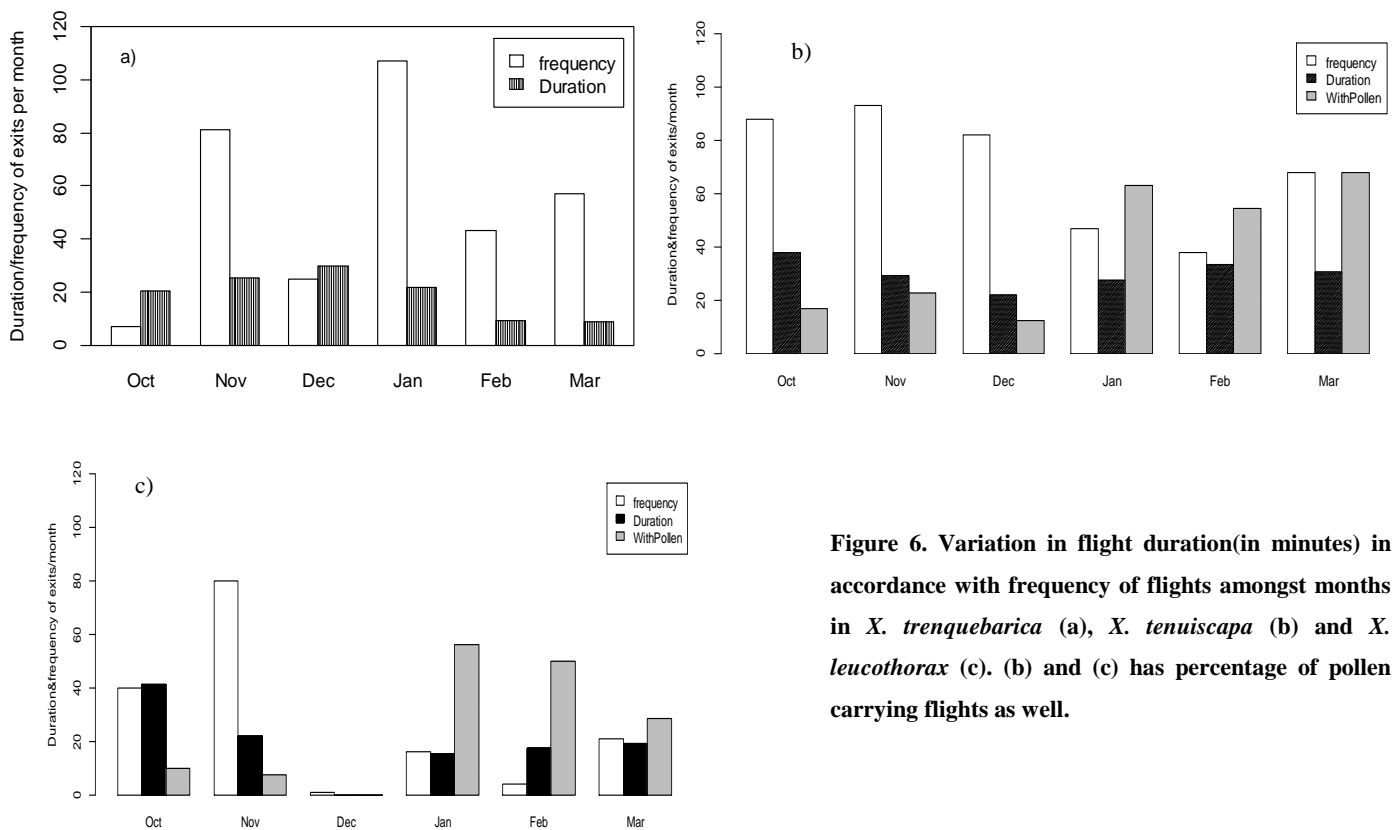
Figure 6. Variation in flight duration(in minutes) in accordance with frequency of flights amongst months in *X. trenquebarica* (a), *X. tenuiscapa* (b) and *X. leucothorax* (c). (b) and (c) has percentage of pollen carrying flights as well.

3.3. Flight patterns and temporal partitioning in the three sympatric carpenter bee species
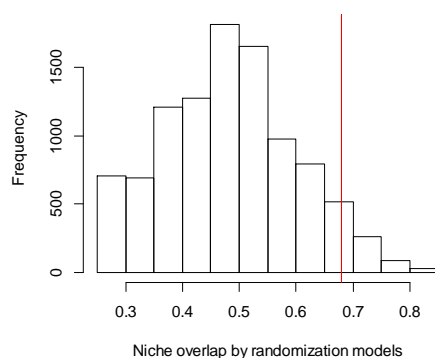
Figure 7. Distribution of all the randomized similarity values. Red line shows the confidence interval (0.95).

The role of environmental variables in niche partitioning, in bee species, has not been elicited before. Figure 8 shows the clear-cut partitioning in flight activity on a diel scale for the nocturnal and the two diurnal species. Overlap in foraging time is more between diurnal species as compared to diurnal and nocturnal species. To check the amount of niche-overlap, Czechanowski similarity index was calculated by a randomization model. Result from this analysis suggest a moderate level of temporal niche overlap between the diurnal species (niche overlap= 0.675, *P*=0.05) (Figure 7).

In ants, temperature plays an important role in annual temporal partitioning (Albrecht 1999). In my study, the attributing factors for temporal partitioning are yet to be determined. Apart from environmental factors, flight activity patterns of less dominating species can also be affected by the activity patterns of dominating species (Lynch et al 1980, Anderson 1992), and that's something we can work in future .
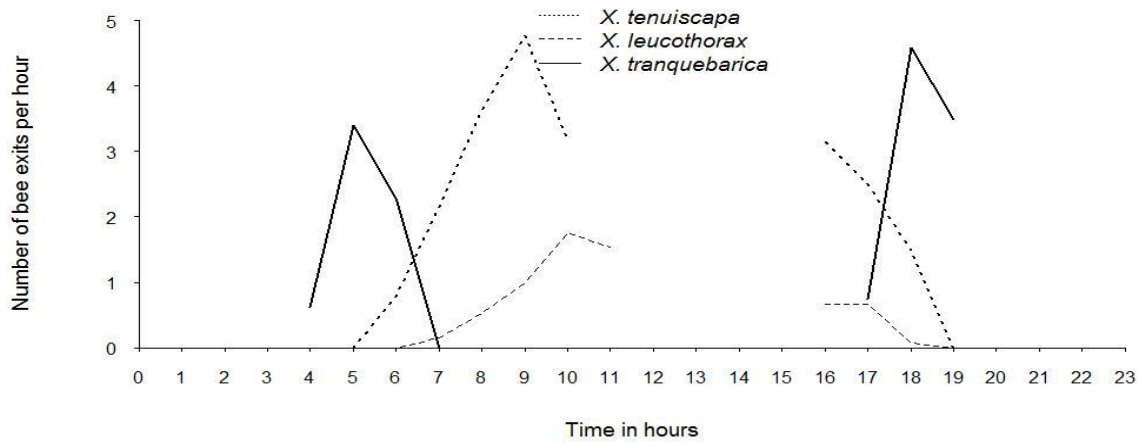
Figure 8. Frequency of bees exiting per hour in three *Xylocopa* species.

3.4. Structure of orientation flights with lunar cycle

X. tranquebarica performs longer elaborated orientation flights on moonless nights when the light intensity is very less as compared to the moonlit nights. Typical examples of orientation flight is during moonless and moonlit conditions are given in Figure 9.

Figure 1 Orientation flight path lengths in moonlit (a) and moonless (b) conditions.

Chapter 4
Conclusion

As expected there exists temporal partitioning in the three sympatric species. Flight durations are very variable in *X. tranquebarica* and *X. leucothorax* across months, while there is no specific significant pattern observed in *X. tenuiscapa*. Durations of foraging trips in the noctu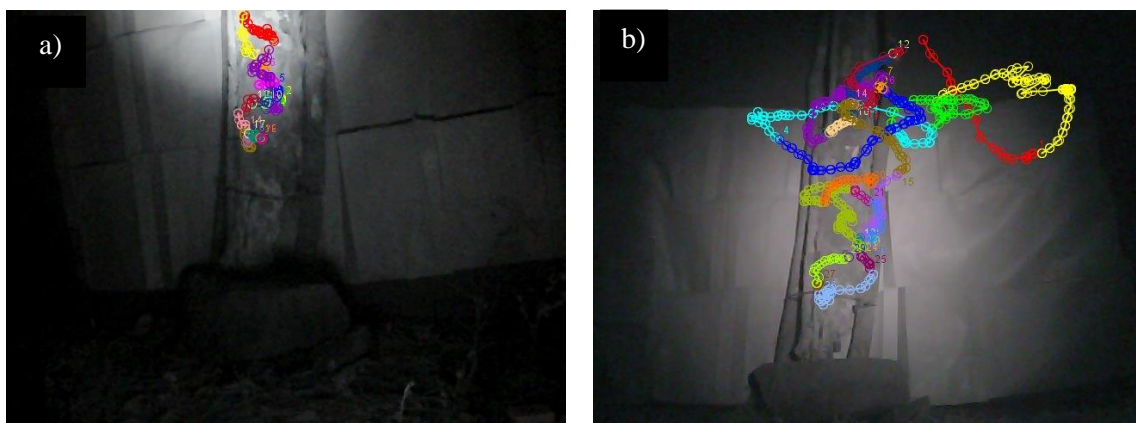rnal X. tranquebarica are more sensitive to light conditions at night, with flight trips being longer during bright nights as compared to dark nights. This suggests that despite the visual adaptations that this species possesses for nocturnal life, there are constraints to efficient foraging and returning to the nest under dark conditions.

In this study I have examined the effect of environmental variables on the onset of flight activity. In the nocturnal as well as in the diurnal diurnal species, light intensity related variables (sun rise, sun set, moon rise, moon set, and astronomical twilight) affected the onset of flights predominantly, while the effect of other variables vary between the two different nesting habitats (closed and open sites). Further analyses are required to determine the contribution of each variable on the onset of flight activity. In *X. tranquebarica* orientation flights are very sensitive to light intensity levels. During moonlit nights, bees find their nest entrance much faster than on moonless nights, which again points to visual constraints experienced by the nocturnal bee under dim light conditions and that vision is a primary cue for finding the way back to the nest in the dark.

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Appendix

A. Code to calculate Czechanowski similarity index

```
w<-read.delim('C:/Users/shivani/Documents/Rfiles/nicheoverlap.txt');w

m=as.matrix(w);m

iteration=10000

mv=as.numeric(m);mv

stra=c(rep(1,7),0,0,rep(2,5));stra

CTRL<-how(blocks=stra,within=Within(type='free',mirror=TRUE))

shuff<- shuffleSet(length(mv),iteration,control=CTRL);

niche= matrix(data=0,ncol=iteration);

for(i in 1:iteration)

{

k= matrix(data=mv[shuff[i,]],ncol=2)

niche[i]=niche.overlap(k, method= c("czech"))

}

x=niche.overlap(w, method= c("czech"));x # Czechanowski similarity index for original data set

hist(niche, main="",xlab="Niche overlap by randomization models")

abline(v=x)

abline(v=quantile(niche,0.95),col='red')
```