Use of alternate founding strategies in a primitively eusocial wasp *Polistes wattii*

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April 2019

Certificate of Examination

This is to certify that the dissertation titled "Use of alternate founding strategies in a primitively eusocial wasp *Polistes wattii*" submitted by Ms. Kunika (Reg. No. MS14172) for the partial fulfilment of BS-MS dual degree programme of the Institute, has been examined by the thesis committee duly appointed by the Institute. The committee finds the work done by the candidate satisfactory and recommends that the report be accepted.

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Dated: April 24, 2019

Declaration

The work in this dissertation has been carried out by me under the guidance of Dr. Rhitoban Raychodhury at the Indian Institute of Science Education and Research Mohali.

This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgement of collaborative research and discussions. This thesis is a bonafide record of original work done by me and all sources listed within have been detailed in the bibliography.

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In my capacity as the supervisor of the candidate's project work, I certify that the above statements by the candidate are true to the best of my knowledge.

Dr. Rhitoban Raychodhury

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Abstract

The paper wasp genus *Polistes* (Hymenoptera:Vespidae), makes a salient model group for behavioural studies. This genus is abundantly found in both temperate and tropical climates. The nesting cycle varies according to the environment they live in. The tropical wasps remain active throughout the year while the temperate species use hibernation as a survival strategy during harsh winter. We studied the nesting cycle of one of the most commonly found species in north India: *Polistes wattii*. Although *P. wattii* is a tropical wasp, it follows a colony cycle similar to the temperate wasps, i.e. they go into hibernation during winter. In temperate environment, after hibernation new nests are initiated (founded) either by single female (single founding) or by multiple females (multiple founding) and the nests grow till date summer. *Polistes wattii* shows a very different founding strategy compared to the usual temperate wasps. In spring the nests are always initiated by a single wasp, while in summer both single and multiple foundreses initiate nests. Here we present a comparitive analysis of different founding strategies of *P. wattii* and show how they help the wasps maximize reproductive fitness.

Chapter 1

Introduction

When many insects live together in a group and if some of them are capable of reproducing than they are called social insects. Eusociality is characterized by three features- 1) Overlap of generations 2) Cooperative brood care 3) Reproductive division of labor (Michner, 1969; Wilson, 1971). The important feature of eusociality is the presence of caste that is non reproductive but is committed to a helper role.

- Overlap of generations:- The older generations of spring are able to help the younger generations because there is overlapping of generations.
- Cooperative brood care:- Some individuals which are directly or indirectly related along with the mother helps in co-operative care of offsprings.
- Reproductive division of labor:- It has evolved from sterile caste (not all individuals get to reproduce) which have certain characteristics associated with helping behavior.

All the eusocial wasps are from family Vespidae which is further divided into three subfamilies: i) Stenogastrinal ii) Polistinae iii) Vespinae. Eusociality has the advantage that it provides extended care of young ones. In insects, time for a single adult is really short for providing extended care of the young. Overlapping care is successfully provided if the insects are present in group even if the adult lifetime is short. The ecological success of insects living together is may be due the resulting high offspring survivorship. Wasps, bees, ants, and termites form an integrated group of social insects, in which some workers who are not reproducing will help to rear the offsprings

of fertile individuals.

Phylum	Class	Orders		Details
Arthropoda				
	Insecta			
		Isoptera		All eusocial, many advanced
		Hemiptera		~50 species eusocial
		Thysanoptera		~6 species eusocial
		Cleoptera		1 species "Ambrosia beetle"
		Hymenoptera		
			Ants	All species (except a few highly derived species) ~14000
			Bees	Only 300-400 of ~ 4000 species are eusocial
			Wasps	Most are not social, ~900 species are eusocial

Source: quora.com

There are two types of eusocial insects:

1. Highly eusocial insects
2. Primitively eusocial insects

1.1 Highly eusocial insects

In a group of eusocial insects if females develop into morphological distinct queens and workers, which means if there is any difference in the morphology of reproductive and non-reproductive castes, then they are known as highly eusocial insects e.g., ants bees and some wasps. Here caste determination takes place in pre-imaginal stages.

There is no flexibility in the roles played by social insects. And caste determination is quite an irreversible process (Gadagkar, 1990).

Figure 1.1: Ants
Credits: David Nash

Figure 1.2: Termites
Source: quantumagazine.com

Figure 1.3: Honey Bees
Source: thought.com

1.2 Primitively Eusocial insects

A caste system in which there is no morphological difference in the reproductive and non-reproductive castes such group of insects are known as primitively eusocial insects e.g. *Polistes wattii*. These insects have an opportunity for direct reproduction, also single and multiple queens can co-exist. According to some studies here caste determination takes in imaginal stages so they have flexibility in the social role of insects. That is why they can be considered as good model system for the study of origin of Eusociality (Gadagkar, 1990). In these insects, if dominant queen dies than other female reproductive can take the role of the queen (Jeanne 1970; Litte 1979; Gadagkar 1987).

Figure 1.4: Primitively Eusocial insects(*Polistes watti*)

1.3 *Polistes*

The genus *Polistes* (Hymenoptera: Vespidae) makes a salient model group for behavioral studies. *Polistes* is found in both temperate and tropical regions. They are commonly known as paper wasps because their nest is usually made up of papery material along with saliva. They usually build their nests on human habitation. According to some reports species of *Polistes* can now learn and remember the chemical cues (hydrocarbons) which are picked up from the nest to differntiate nestmates from non-relatives. This cuticular hydrocarbon is obtained from plant matter and the substance applied by foundress which is formed when nest is made and, the foundress applied substance which if formed when the nest is made. All the species are predatory, they feed on a large number of caterpillars and thus can be considered as beneficial. The most extensively studied species in the temperate regions is *Polistes dominulus*.

1.3.1 *Polistes dominulus*

It is a temperate species of paper wasp which is native to Europe. It is introduced and invasive in North America (Weiner et al., 2012). *P. dominula* is a model species in animal communication studies (Cini et al., 2009), and so there is plenty of literature on this subject using this social wasp. Males and non-reproductive females of this species survives during autumn, spring and summer but not in winter and reproductive

females persist for a longer duration but hibernates in winter. Female reproductives in many temperate species of *Polistes* at the end of nesting cycle leave their nest, mate and goes into hibernation (Dapportoet al. 2004). Nests are initiated by single or multiple foundresses in the spring. It was first discovered in Boston, during late 1970s. This wasp has been reported from places like Maine, Vermont, Connecticut, New Jersey, Maryland, Virginia, Pennsylvania, Ohio, Michigan, and Wisconsin, New York. It has recently been discovered in other places like California, Colorado and Washington. It is also found in Middle East, eastward into China, Africa and Southern Europe.Its number has rapidly increased from last twenty years.

Figure 1.5: *Polistes dominulus*
Source: ozanamals.com

1.4 General Life cycle of *Polistes*

- Founding phase: This is a pre-emergence phase when reproductive females starts the nest in the spring. Firstly, it starts making the petiole and forms a single brood at the end of it. Then further adds the cells to it which are in hexagonal shape. First brood is of workers which helps queen in nest construction and other things.
- Worker phase: In early summers, new workers are emerged which assist foundress in foraging, protection from predators and taking care of young ones.
- Reproductive phase: This phase begins when the first set of female reproductive are produced. These females now go into hibernation. Males that are produced

during this phase will mate with females and die.

- Intermediate phase: This is the phase when no more new individual are produced, workers will start dying and female reproductives will overwinter by hibernating to protect themselves from cold temperature.

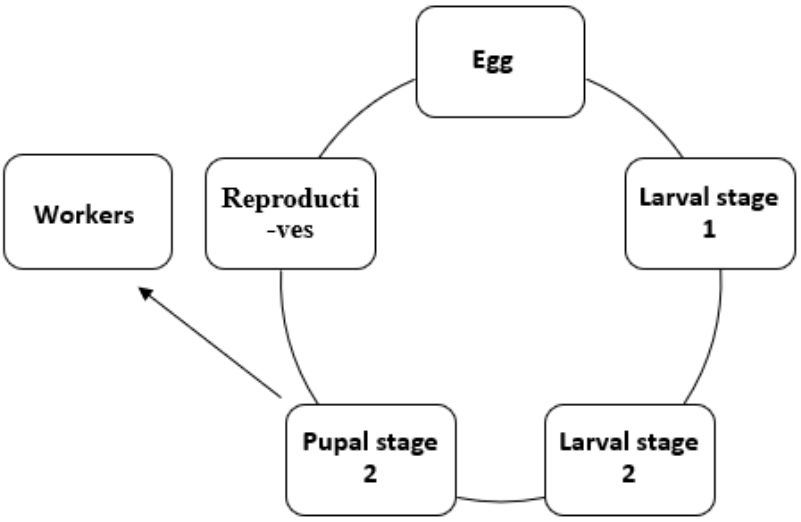


Figure 1.6: Lifecycle of *Polistes*

1.5 *Polistes wattii*

Common Name: Paper wasp

1.5.1 Taxonomic Classification

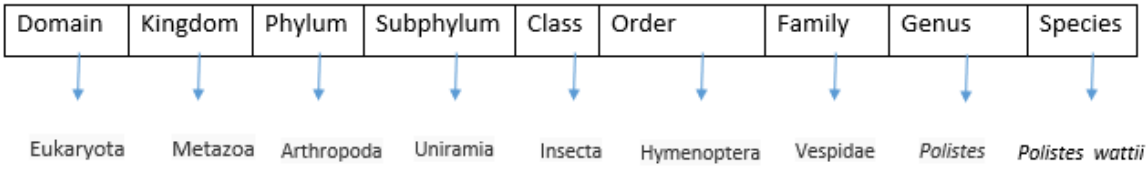


Figure 1.7: *Polistes wattii*

1.5.2 History of introduction

Polistes wattii is a temperate species of *Polistes* which has recently moved to tropical regions. It follows almost similar colony cycle to that of temperate species of *Polistes*. It is the most commonly found species of north India.

This species is of great biological interest from a number of viewpoints. Most of the study is done on temperate *Polistes* and not much is known about the Tropical *Polistes*. *P. wattii* is a tropical social species that follows the colony cycle of temperate wasps. It makes a salient model group for behavioral studies. It was first described by Cameron in 1900. It shows sexual dimorphism and is holometabolous

1.5.3 Distribution

Polistes wattii is widely distributed in India, Pakistan, Iraq, China, Iran, Saudi Arabia, Mauritius and Afganistan (Das and Gupta 1989, Carpenter 1996, Gusenleitner 2007, Mahmood et al. 2012). But specifically in India it is found in Himachal Pradesh, Punjab, Uttar Pradesh, West Bengal, Meghalaya, Gujarat, Orissa, Madhya Pradesh, Delhi, Rajasthan, Uttarakhand, Jharkhand, Jammu and Kashmir and Rajasthan (Kumar, et al.,2010)

Figure 1.8: Distribution of *Polistes* in India

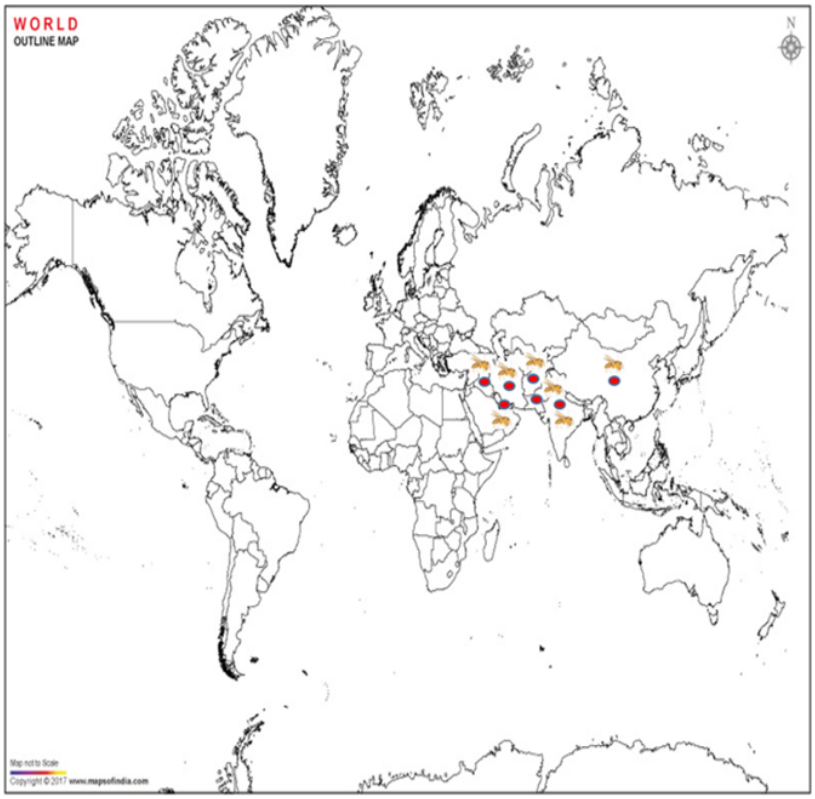


Figure 1.9: Distribution of *Polistes wattii* in World

1.5.4 Description

Polistes wattii is a yellow colored paper wasp. Like all other paper wasps its waist is also very thin. Nests are upside-down, and open cells are visible from below. It is around 13mm long, its legs are colored like thorax but only except the hinder tibiae which are black. And the base of petiole, which is the prominent part of second segment is infuscated. The third joint of the antennae is largest compared to the other three. This species of *Polistes* has unicolorous body, and its clypeus is wider than usual, an antennal keel is also thicker. Above it is a constricted furrow, also below the ocelli it has a small groove which is not very distinct (Cameron, 1900).

Females

Females have tapered ends at the abdomen. Clypeus is touching the eyes. Its forewing is around 16-20mm in length, and the body is usually brown in color (Khalid Khan et al., 2018).

Males

Males have a blunt end at the abdomen. Clypeus is not touching the eyes. And the apophysis of the subgenital plate is extended and tapered and also not compressed at the apex. It has heavy pubescent with head and thorax of almost uniform yellow color.

Figure 1.10: Head

Figure 1.11: Thorax

Figure 1.12: Abdomen

Figure 1.13: Lateral Thorax

Figure 1.14: Lateral abdomen

1.5.5 Habitat

They usually build nests in human inhabitant areas like buildings, balcony and parking areas e.t.c. They use paper and saliva to build their nests. According to some reports they are also found in vegetable fields.

1.5.6 Reproductive biology

Female reproductives or overwintering founding queens produce workers who are females, but they do not reproduce. Even if there are more than one foundresses, only one of them becomes queen. This dominant queen is the one which produces more number of wasps. Again in summer, it produces workers who are reproductive. Along with these female reproductives, males are also produced which then mate and mated females become foundresses in next season.

1.5.7 Behaviour and life history

Female reproductives which comes from hibernation begins new colonies each spring. These females goes into hibernation in some protected areas. In some species of *Polistes* they hide in the stump of dead trees, between walls , under siding and sometimes within the cells of its nests. New nests are constructed each year by the queens, but some of them also use previous year's nests.

The dominant queen deposits small eggs to a cell that hatch in several days. She feeds her larvae some insects or masticated caterpillars. When the first brood of larvae emerges as worker females, then they start limiting her activity from laying eggs to expand the number of workers. These workers then assist her I doing work like collecting food, helping in nest construction and defense of the colony. With suitable environmental conditions and availability of food materail, development of larvae is completed and they become adult wasps.

1.5.8 Longevity

Mated female reproductives may survive for a longer duration even after hibernation. Males and non-reproductive females cannot tolerate harsh winter but they can survive in summer, autumn and spring season. This also depends upon the factor that whether the nests are started by single foundresses or multiple foundresses. Sometimes they are separated from the other wasps which can also lead to reduction of proportion of wasps which survived for longer duration.

1.5.9 Seasonality

The most important factors that affect the number of wasps is temperature and humidity(Souza et al., 2010). During November, December, January, and February the weather is really cold in North India. Reproductive females goes into hibernation during this time, and other workers and males die.

But as the temperature increases in the mid of February, the hibernating females get active and starts building nests. With the start of spring in the months of March

and April the population of wasps starts increasing and the number of workers also increases. In summer, colony reaches to the maximum size. Number of multiple founded nests increases and set of male and female reproductive are produced.

In autumn, when the temperature and humidity conditions are optimal at that time female and male reproductives mate. The number of workers starts decreasing as no more brood is produced. After this they slowly start going into hibernation as the temperature starts decreasing.

1.5.10 Social impact

Species of *Polistes* can sting humans and as they usually built nests near human settlements, so chances of an attack are more. According to some studies, these have allergens so they can have allergic responses. They are not generally that aggressive but will attack if provoked in order to defend their nests.

1.5.11 Environmental Services

Environment plays an important factor in the fitness of nest founding females (Tibbetts et al., 2011). Most of the wasps of Vespidae family has important role to play in the terrestrial ecosystem, and they can also be used as biological control agents as they feed on caterpillars and other insects(Fateryga 2009, Rasnitsyn and Quicke, 2002). If new species are introduced, then there can be unpredictable consequences. Most important concern is of the sting. According to some entomologist species of *Polistes* adversely affect the species of other insects like butterflies.

1.5.12 Phylogenetic Position

Phylogenetic tree of *Polistes wattii* inferred using mitochondrial CO1 barcoding region showed that *P. wattii* is closest to *P. olivaceous*.

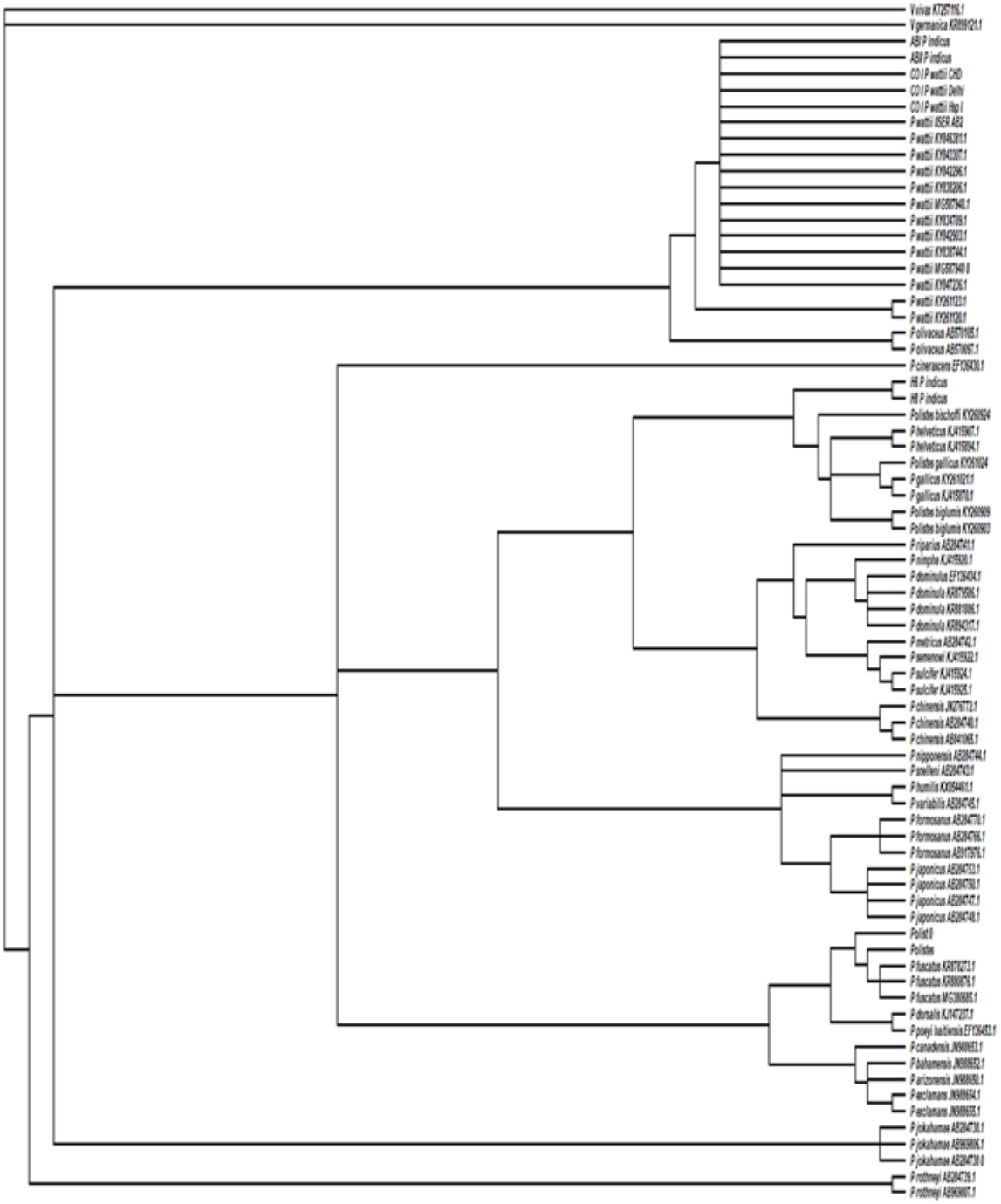


Figure 1.15: Phylogenetic tree of *Polistes wattii*

1.6 Nest Architecture

Tropical wasps usually make two kinds of nests. Genera like *Polistes* , *Ropalidia*, *Belanogaster*, and few others construct uncovered nests, and in the petiole of these nests, they secrete ant- repellent. On the other hand remaining genera of Vespidae build enclosed nests which are protected from ants. The paper wasp, *P. wattii* construct

its nest with plant fiber and saliva. After petiole, it forms a single cell at the end and further starts building more number of cells to it. These cells are hexagonal in shape. It can construct a single comb or multiple combs. If it forms multiple combs, then it uses a unique way of stacking combs to each other. Envelope of one comb is used to stack another comb on it. Nests which are smaller in size are usually built by single wasps or two or three wasps but nests which are larger in size are constructed by more than one wasps.: Nests of *P. wattii* consisted of single or multiple uncovered combs with thin petiole. Nests were found at different heights.

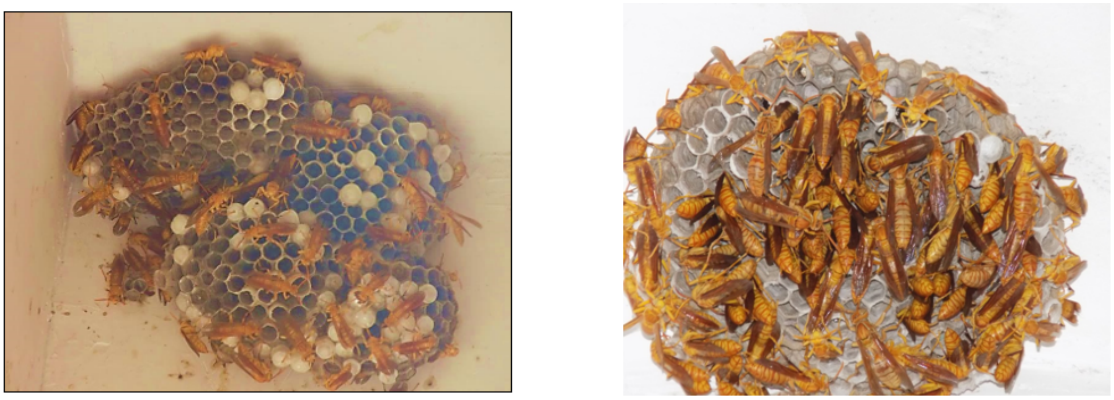


Figure 1.16: Nests of *P. wattii*

1.7 Founding strategies

Initiation of the nest is known as founding. Founding can be done by a single queen or multiple queens. And these mated female reproductives are called foundresses. Species of genus *Polistes* are capable of two types of colony foundation (Jeanne 1980):

- Independent founding - In this type of colony founding, nests are started either by single foundress or a group of foundresses, and it consists of primitively eusocial species. *Belanogaster, Parapolybia, Polistes, Mischocyttarus and Ropalidia* shows independent founding.

    1. Solitary founding

    2. Multiple founding

- Swarm founding - In this type of founding a large group of foundresses and workers forms the nest, and it is comprised of highly eusocial insects. This founding shows a high level of eusociality.

1.7.1 Multiple founding

It has mostly 2- 3 members but sometimes involves more than seven wasps. Here dominance hierarchy can be achieved very quickly, and one dominant queen will do the maximum reproduction. Even if one of the members dies, still larvae becomes adult wasp, and that is one of the advantages multiple founded nests have(Strassmann and Queller, 1989; Reeve, 1991; Reeve and Nonacs, 1997). According to some previous studies, cooperative nest foundation have advantages of productivity and survival with some exceptions. Most of the times foundresses are closely related to each other, which provides potential benefits to subordinates(Reeve, 1991). In this case dominant foundress lays potential egg layers, and other females engage mostly in foraging and rarely in reproduction(Jandt et al. 2014).

Figure 1.17: *P. olivaceous*

Figure 1.18: *P. wattii*

1.7.2 Solitary founding

Nests with single queen face high rates of usurpation because many times nest have no wasps while the foundresses forage (Gamboa 1978; Klahn 1988). According to many studies, solitary nests get abondaned due to loss of foundress (Metcalf and Whitt 1977; Gibo 1978; Tibbetts and Reeve 2003).Nests with single foundresses have to deal with usurpation. Workers emerge late than the multiple foundresses. But is some species solitary species of *Polistes* like *P. aurifer*, it has same reproductive success like that of multiple founded nests and till now it has not been found that its subordinates will have less success(Liebert et al., 2005)

Polistes species	**Foundress Range**
P. fuscatus	1–139
P. dominula	1–198
P. lanio	1–10
P. metricus	1–3
P. exclamans	1–117
P. apachus	1–24
P. carnifex	1–12
P. major	1–12
P. bellicosus	1–177
P. dorsalis	1–6
P. carolina	1–7
P. exclamans	1–117
P. annularis	1–397
P. riparius	1–2
P. snelleni	1–2
P. biglumis	1–2
P. chinensis antennalis	1–1
P. simillimus	1–198
P. ferreri	1–42
P. formosanus	1–2
P. gallicus	1–3

P. humilis	1–21
P. jokohamae	1–4
P. nimphus	1–5
P. nipponensis	1–1
P. tepidus	1–7
P. versicolor	1–504
P. tenebricosus	1–3
P. japonicus	1–1
P. stabilinus	1–16
P. carnifex	1–4
P. stigma	1–10
P. cinerascens	1–8
P. apachus	1–2
P. aurifer	1–8
P. bahamensis	2–3
P. flavus	1–6
P. humilis	1–3
P. crinitus multicolor	2–15
P. smithii	1–7
P. instabilis	1–69
P. carolina	1–87
P. sagittarius	1–4
P. gigas	1–5
P. variabilis	2–7
P. mandarinus	1–1
P. tenebricosus	1–3
P. dorsalis	1–10
P. tepidus malayanus	2–5
P. nimphus	1–3
P. canadensis	1–3275
P. olivaceous	1–6

P. pacifus	1–1
P. rubingousous	1–1
P. riparius	1–1
P. snelleni	1–2
P. satan	1–53
P. subcericeus	2–6
P. rubiginosus	1–17
P. chinensis	1–4
P. bahamensis	1–3
P. rothneyi	1–1
P. crinitus	1–5
P. marginalis	1–1
P. subcericeus	2–6
P. infuscatus	1–10

Table 1.1: Foundresses Range for *Polistes* species

1.8 Nesting cycle

The Colony is started by mated female reproductives in the beginning of spring. Many new nests are seen in March sprouting here, and there The nest is usually initiated by a single queen. It enlarges the colony by adding more number of the cell to it. She lays an egg and feeds the larvae, and the workers that emerge from these cells then assist with the further building and development of the colony. In summer both male and female reproductives emerge. These reproductives mate then males die and female reproductive after mating goes into hibernation in mid of November. In tropical wasps, nests can be initiated in any season(Giannotti 1997, Prezoto 2001) with few exceptions.

Nesting cycle usually has four phases(Jeanne, 1972):

- Foundation phase
- Post-emergence phase
- Aggregation
- Desertion or abandoned

1.8.1 Nesting cycle of Temperate *Polistes*

Polistes wasps in temperate regions have annual colony cycles. After coming from hibernation foundresses have three options 1) It can start the nest alone 2) It can start nest with few more foundresses 3) It can use some already existing nests. In temperate zones first-born daughters are workers. Colony cycle of temperate *Polistes* is short compared to tropical ones. Foundation and desertion of nests depend on climatic conditions, these two events occur at only specific season of the year in temperate wasps (Yamane 1996).

1.8.2 Nesting cycle of *Polistes wattii*

Female reproductives of *Polistes wattii* after coming from hibernation starts forming nests. In March we see lots of nests sprouting here and there in parking areas balcony

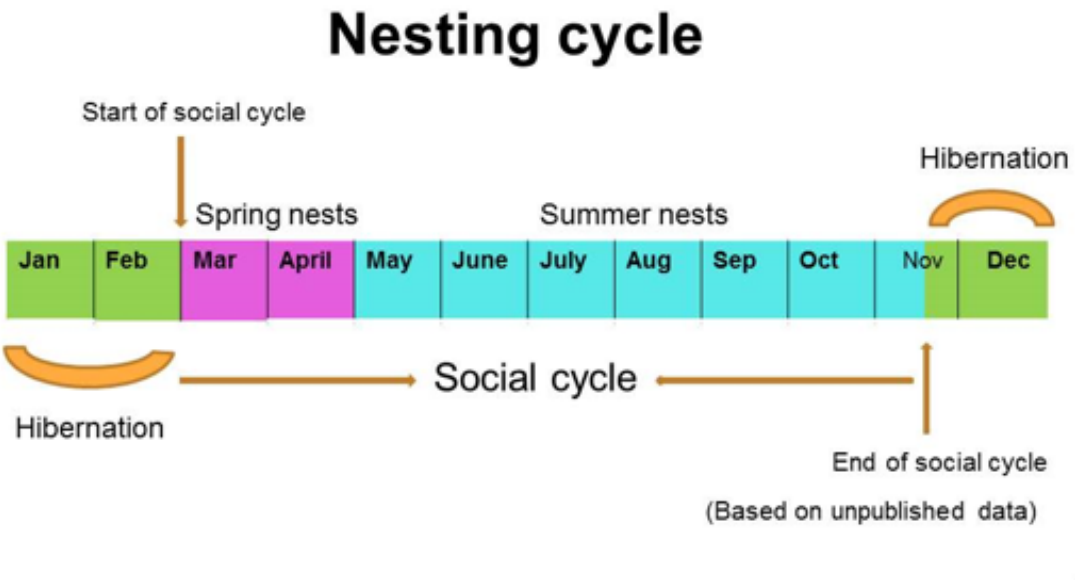


Figure 1.19: Nesting Cycle of *Polistes Wattii*

e.t.c. These are called spring nests which starts with single wasps or few wasps. In summers multiple founded nests are formed which are constructed by more than one wasps, they are known as summer nests. During this time male and female reproductives emerge. These males and females mate with each other after which males die. After mating female reproductives goes into hibernation in around mid of November. It is a temperate species of Paper wasps but has longer colony cycle.

Chapter 2

Solitary and multiple founding strategy: Is it seasonal?

2.1 Introduction

In a colony of wasps, insects stay together in a nest with an egg-laying queen and non- reproducing workers. Most of the wasps are solitary, where an adult reproductive female live and breed independently. Variation in season affects colony development of species of genus *Polistes* . Climatic changes can also affect productivity of insects. Seasonal changes constrict chance for nest founding and offspring growth because food resources are available abundantly only in a few seasons. These constraints in different seasons can result into species level differences in the evolution of species level differences in social behaviour (O'Donnell and J. Joyce, 2001). The effect of seasonality on colony development is different in temperate and tropical regions. Species richness, phylogenetic analysis and pattern of distribution of species shows that solitary founding strategy evolved in tropical regions(Vecht 1965, Reeve 1991). So tropical species of *Polistes* are good model to study evolutionary origins of eusocial behaviour of wasps. According to some previous studies climatic factors determine variation among populations of paper wasps in solitary founded nests. In this study, we quantified seasonal patterns of solitary and multiple founded nests. My first objective was to see when do they opt for which founding. Now in most *Polistes* wasps, the nests

are only initiated by hibernated females and they may opt for either strategy. In *Polistes wattii* hibernated as well as fresh females initiate the nests and both solitary and multiple founded nests are observed.

2.2 Method and Material

For data collection I chose two academic institutions, where nests are abundantly found and usually remain undisturbed. All data were collected from IISER Mohali campus and Panjab University campus. Field observations were conducted from May to November (Summer- Autumn) 2018 and December- January (Winter) 2018-2019. In summer average temperature was around 36°C and in winter average temperature was 17.5°C. All observations were made on nests, in the evening for every alternate day. During this period I recorded the initiation of every new nest in the area and collected data till the nest was either abandoned by the wasps or was destroyed by humans. I recorded the number of wasps and pupa from each nest. Due to the height the status of brood could not be recorded correctly. Photographs were taken with digital camera for identification and recording.

New nests were discovered within 2-3 days, so whenever new nests were sighted I recorded number of foundresses. In subsequent observations, wherever possible, following information was recorded every alternate day: cell initiation, number of workers emerged, total number of wasps in each nest. We remained at nesting site for few minutes so that we can record presence of any foragers.

2.2.1 Spring nests

For nests initiated in spring data was collected from nesting sites in Indian Institute of Science education and research, Mohali. These nests were surveyed for two months i.e March and April. Every nest was given a unique code and information of number of wasps and number of pupae was recorded.

Figure 2.1: Spring Nest

2.2.2 Summer nests

Observations were conducted from May 2019 to the first week of December 2019. Whenever a new nest was found it was given a unique name and number of wasps and number of pupae were recorded from it. In May, June, July, August and September data was recorded in the evening around 6:00 pm. But in October, November and December data was collected a little early that is around 5:00 pm.

Figure 2.2: Summer Nest

Months	Solitary Foundresses	Multiple Foundresses
March	63	0
April	62	0
May	3	12
June	8	8
July	7	9
August	1	3
September	0	2

Table 2.1: The total number of nests initiated by the solitary and multiple foundresses.

2.2.3 Statistical analysis

To see when solitary founded nests are initiated and when multiple founded nests are formed statistical analysis were done. This analyses follow the method of Fisher (1932) and these analyses were performed using Microsoft Excel and Statistica. For Fisher's exact test level of significance 0.05 was applied throughout.

Null hypothesis

Both the strategies should be seen throughout the year. Graph showing different letters are significantly different from each other (Fisher's exact test, , P¡0.05).

2.3 Result

- Null hypothesis: Both the strategies should be seen throughout the year is rejected.

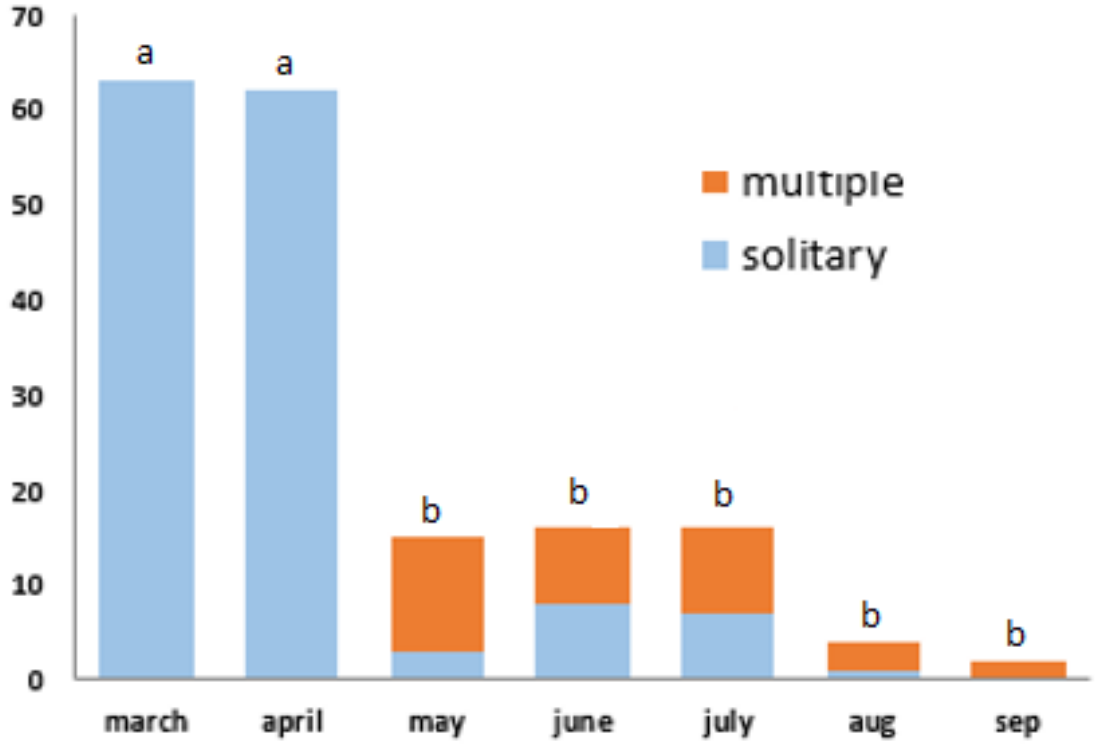


Figure 2.3: Number of solitary and multiple foundress nests

- Hibernated wasps initiate nests alone while fresh wasps can opt for either strategy.

2.3.1 Spring nests are only initiated by Solitary foundresses

There were distinct time periods in which nests were initiated. The first batch of nest was initiated in Spring. It was seen that around first week of March new nests were formed. All these nests which were initiated during this time were started by solitary foundresses. None of them was initiated by multiple foundresses. Proportion of nests initiated in March and April by single foundresses were much more than nests started in May, June, July and August by solitary foundresses.

2.3.2 Summer nests are only initiated by Multiple foundresses

Second batch of nest was initiated in Summer. It was seen that in Summer they started and by the end of November they all were deserted. Most of the nests which

were initiated in May, June, July and August were started by multiple foundresses. Number of nests initiated by single foundresses were less in these months than the nests formed by multiple foundresses.

Chapter 3

Which strategy results in longer survival of nests?

3.1 Introduction

During the founding period of nests *Polistes wattii* displays different kind of nests forming behavior. In temperate species of *Polistes*, foundresses in spring after coming out of hibernation may initiate nest alone, forms association with other females or usurp already established colonies. Females that adopt these abandoned nests may have lost there multiple founded associations.(Nonacs & Reeve 1993).

3.1.1 Solitary founded nests

Solitary founded nests are flimsy and weak but because they are mostly initiated in spring, so they get more time. And in solitary founded nests, queen has to maintain the nests bring the food, build the nests and do everything on her own.

3.1.2 Multiple founded nests

On other hand multiple founded nests are bigger and stronger but they get less time, and also in multiple founded nests queen has to only lay eggs an workers perform other duties.

Figure 3.1: Solitary founded Nest

Figure 3.2: Multiple founded Nest

3.2 Method and Material

Field observations were conducted in IISER Mohali and Panjab University campus. Photographs were taken, videos were recorded and binoculars were used to observe the nest clearly. This field study was done from May (2018)- January (2019). All observations were made on nests during the time from initiation to dessertion. The following observations were recorded during each observation period- cell initiation, survivorship and productivity and then were compared. To find the possible foundations, study area was monitored every alternate day.

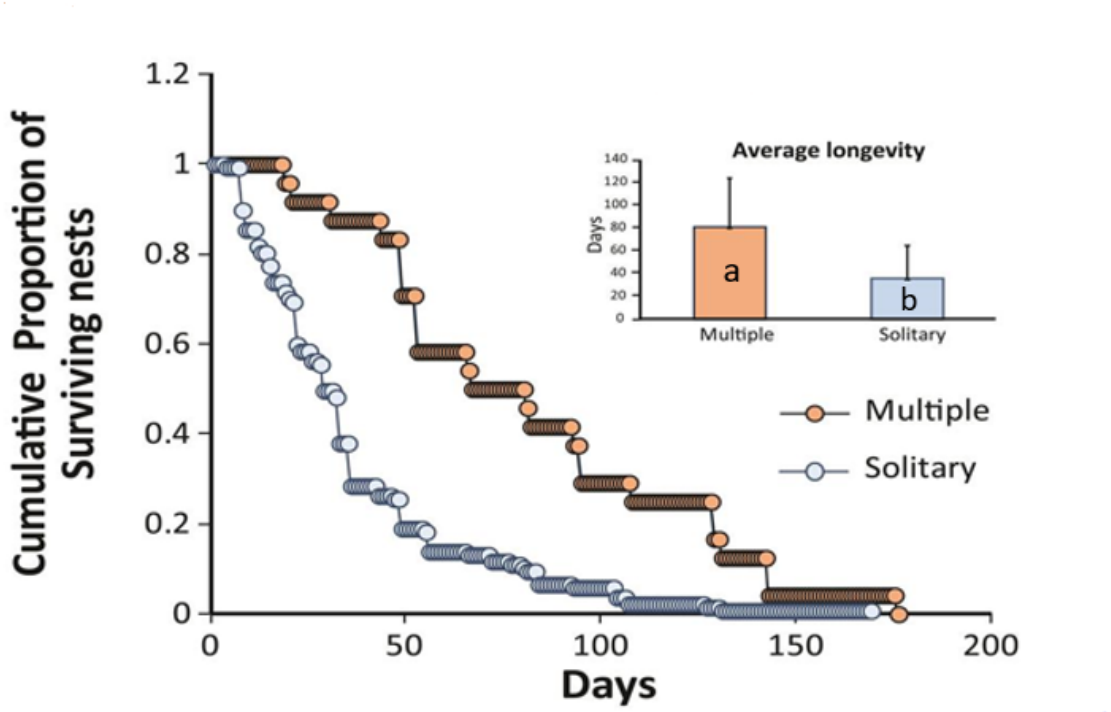
3.2.1 Statistical analysis

In order to see which of the two strategies (Multiple or solitary founding) survive for the longer duration, Survivorship curve for average longevity was made. For this analyses Statistica and Microsoft Excel were used. The Mann – Whitney U- test was used to check the differences in duration for which nests survived. And the level of significance was 0.001 applied throughout.

Null hypothesis

There should not be any difference between the survival duration.

	Solitary	Multiple
Sample size	137	24
Mean ± S.D	76.5 ± 42.8	35.5 ± 28.9
Range(days)	4 – 167	18 – 175



Bars carrying different letters are significantly different from each other (Mann-Whitney U test, U = 2721.5, P¡0.001)

3.3 Result

Null hypothesis

There should not be any difference between the survival duration is rejected.

3.3.1 Multiple founded nests

Multiple founded nests survive longer because it has more wasps to help and assist reproductives. Number of egg layers are also more. If we analyze data through survivorship curve then we can see that cumulative proportion of surviving nests in multiple is one and number of nests are surviving for longer time. 50% of multiple founded nests survived till 76 days therefore chance of survival is more.

3.3.2 Solitary founded nests

Solitary founded nests on an average survive for less number of days than the multiple founded nests. From survivorship curve it is clear that solitary founding nests are declining very fast. 98 out of 137 died before average, and the average is pulled by those who survived for more days. 70% of solitary founded nests died before surviving 35 days. The chance of survival is less for the nests started by single foundresses.

Chapter 4

Which strategy produces more wasps?

4.1 Introduction

In solitary founded nests there is a single egg layer and no worker to help in colony maintenance. But in multiple founded nests there are multiple egg layers and workers to help.

- Solitary
    1. The queen has to maintain the nests.
    2. Initiated mostly in spring so has longer time to survive.
- Multiple
    1. The queen has to only lay eggs and workers perform other duties.
    2. Initiated in summers so shorter time available to them.

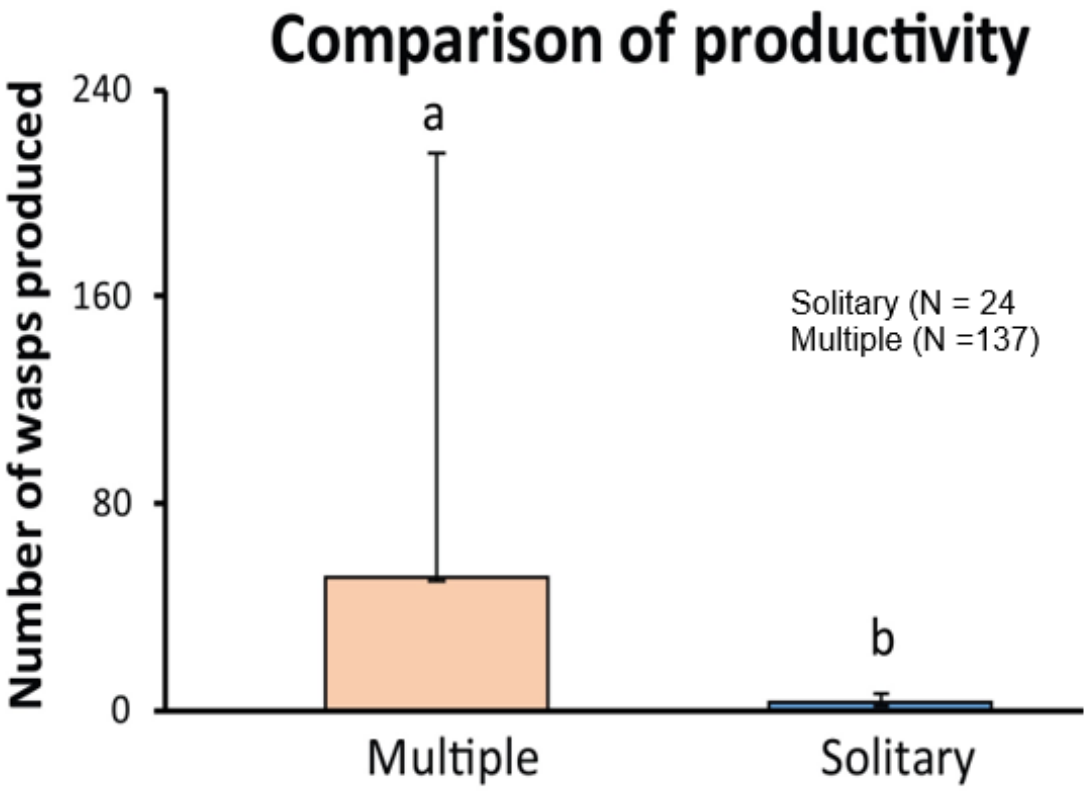
4.2 Method and Statistical analysis

Nesting colony of *P. wattii* was studied soon after founding the nest. When a multiple foundresses initiate the nests then linear dominance hierarchy is formed. Among these

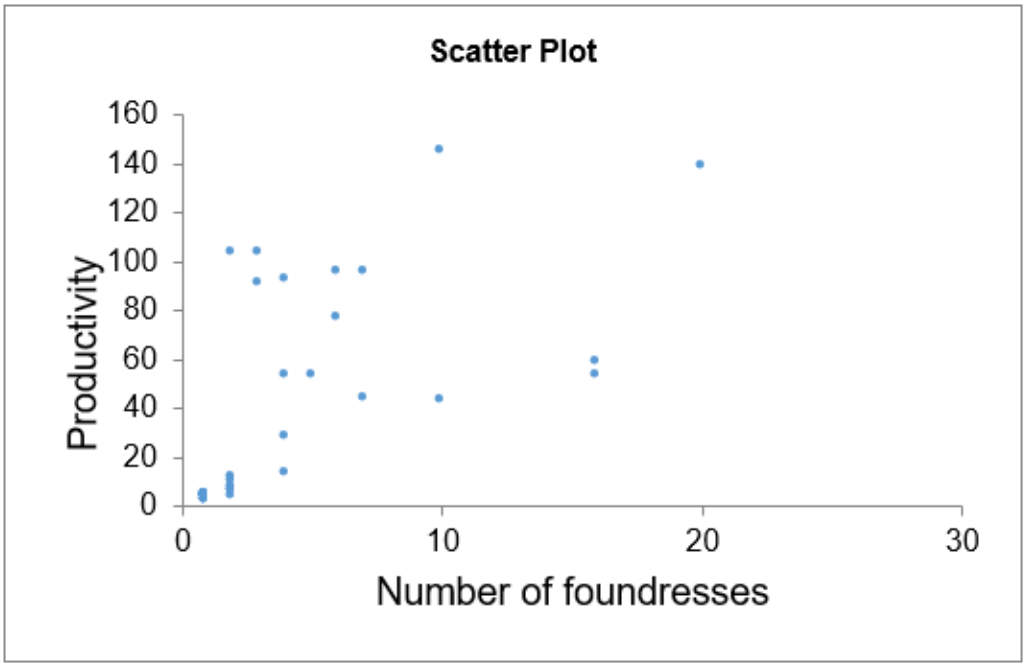
foundresses the one which is dominant, is the one which is going to lay maximum number of eggs by physically dominating other cooperating foundresses (Tibbetts and Reeve, 2000). Productivity was estimated by number of wasps. I counted the number of wasps in each comb over the entire season. Reported productivities are of nests which survived longer until the colony was abandoned or deserted. For statistical analysis Mann- Whitney U- test was used where the level of significance was 0.05.

Null hypothesis

No difference in productivity



Bars carrying different letters are significantly different from each other (Mann-Whitney U test, P<0.05)



Pearson Correlation Results for:
Variable Range = Sheet1!$A$2:$B$39

Descriptive Statistics

Variable	Mean	Std Dev.	Std Err	N
Column A	4.053	4.673	0.758	38
Column B	35.632	43.136	6.998	38

Correlation Matrix (R)

	Column A	Column B
Column A	1.000	0.639
Column B	0.639	1.000

t Statistic

	Column A	Column B
Column A	-	4.985
Column B	4.985	-

Correlation Significance (P)

	Column A	Column B
Column A	-	0.000
Column B	0.000	-

Figure 4.1: Pearson correlation and regression results
Column A: Number of Foundresses, Column B: Productivity

4.3 Result

Null hypothesis

No difference in productivity is rejected.

4.3.1 Multiple founded nests

They produce more wasps and this is a way of maximizing fitness. It has both direct and inclusive fitness because not only the queen can reproduce but also other female reproductives help in reproducing. It makes sure that before the onset of winter maximum number of reproductives are produced for the next year. So it can be stated that it is a way of maximizing fitness.

4.3.2 Single founded nests

They produce less number of wasps than multiple founded nests but they are essential of assuring fitness. It only have direct fitness but first set of brood is very important so this strategy is a way of assuring fitness.

Correlation and regression analysis showed that this result is highly significant.

Chapter 5

Can we predict the production of reproductives?

5.1 Introduction

Nests are found by mated female reproductives. We have seen two types of pupae – White colored pupae (bulged) and grey colored pupae (flat). Now in May solitary founded nests are only in need of workers than we only see pupae. When females and males who will enter hibernation are produced there we see majority of white pupae and so in October only white pupae are there. Most of the colonies were observed from their time of initiation or foundation until the nests were deserted.

Figure 5.1: Grey pupae

Figure 5.2: White pupae

5.2 Method and Material

Data was collected from May (2018) to January (2019) where nests were in the buildings , parking areas, windows of balcony in campus of IISER Mohali and Panjab University campus. Nests were censused every alternate day and this censuses was done until the end of nesting cycle. Number of pupae was estimated or recorded by counting the cells in each comb which had pupae inside them. Photographs were taken and videos were recorded to compare different kinds of pupae. Monthly proportion of white and grey pupae were compared.

5.3 Observations and Result

Two types of pupal caps

- Grey colored (flat)
- White colored (bulged)

5.3.1 Proportion of grey and white pupae in different months

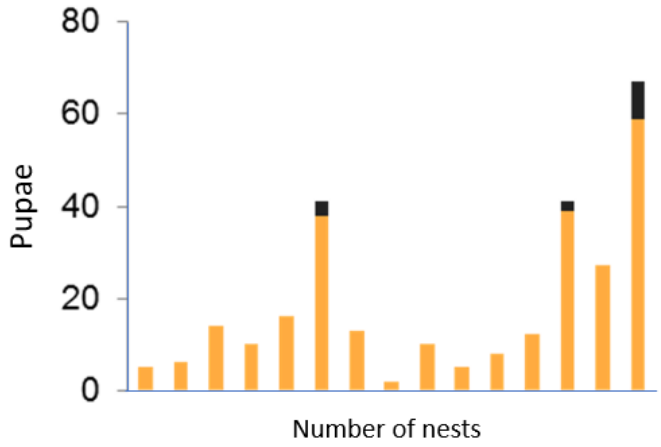


Figure 5.3: May

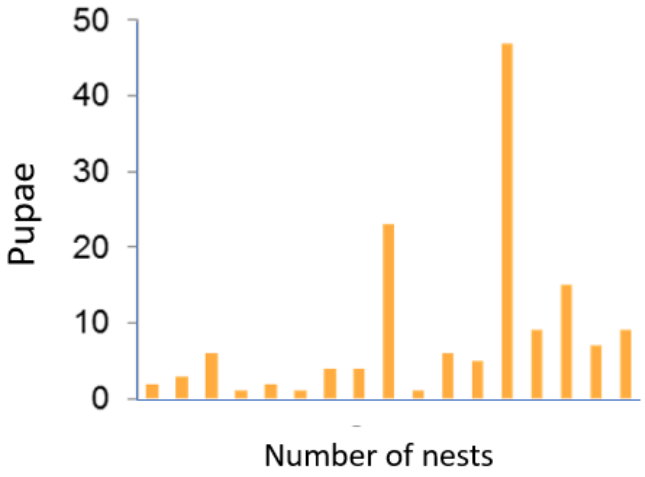


Figure 5.4: June

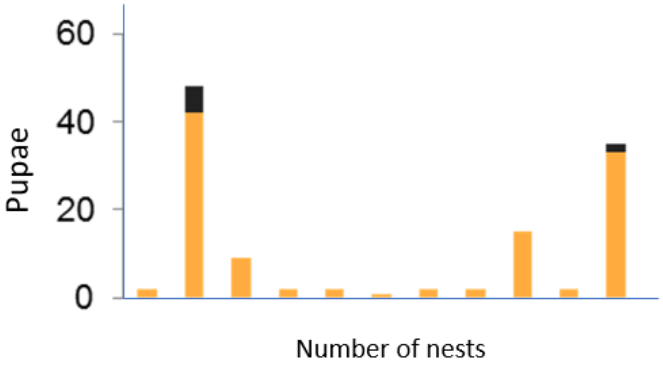


Figure 5.5: July

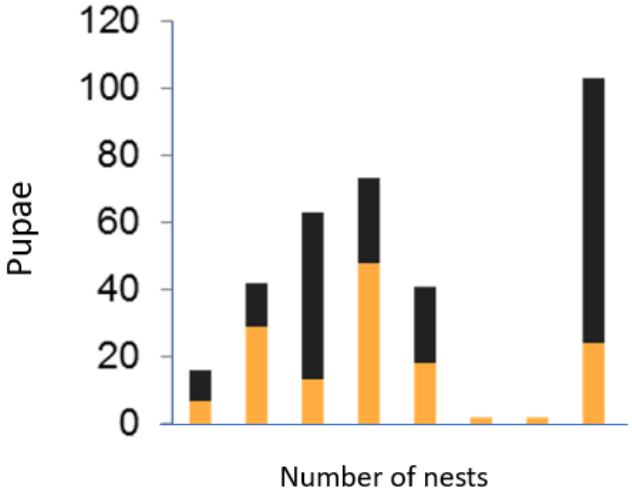


Figure 5.6: August

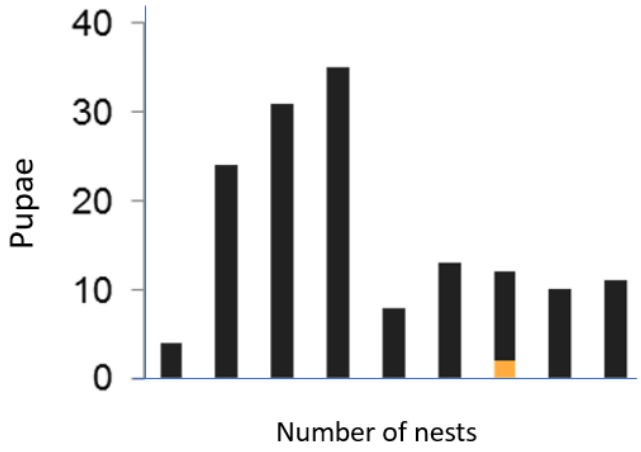


Figure 5.7: September

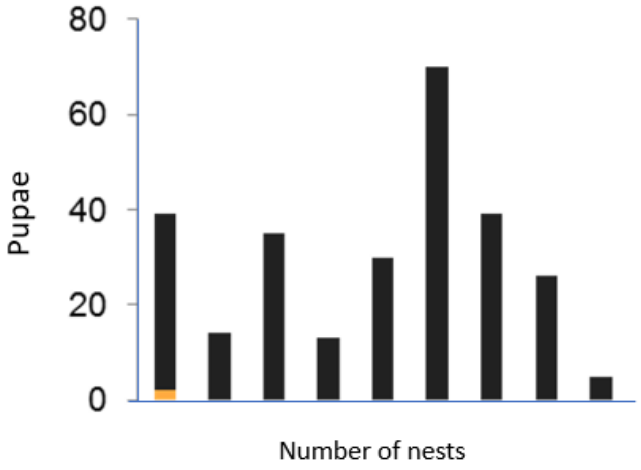


Figure 5.8: October

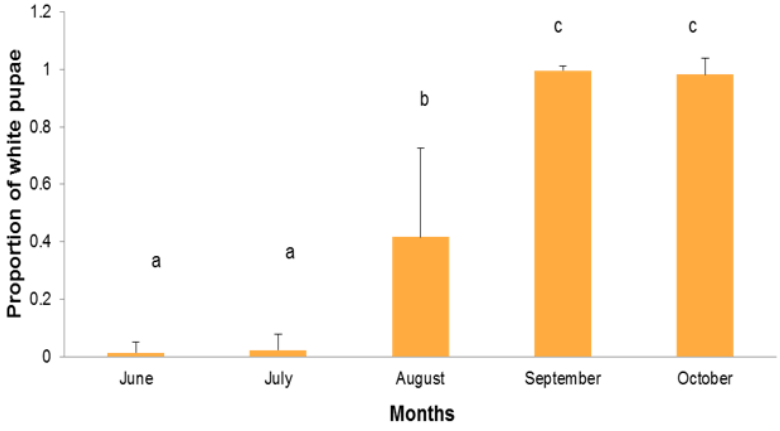


Figure 5.9: Monthly change in proportion of white pupae

5.4 Discussion

Solitary founded wasps are only in need of worker than we only see grey colored pupae. In June and July we see few white pupae and mostly grey pupae, but in August when males and females who will enter hibernation are produced there we see majority of white pupae and in October only white pupae are found in nests. And in September and October we do not expect workers to come because no more brood is required . This was the biggest base of our prediction that grey colored pupae are of workers and white colored are of reproductives.

5.5 Future outlook

Proportion of white colored pupae are more in summer and late summer. We observed initiation of nests throughout the summer. Therefore, reproductives are probably produced throughout the summer as well. So with these observations we wanted know if it is possible to identify the gyne destined brood. We need molecular data to see if this is even possible or not. Our lab will be working on molecular ways of finding out that grey colored pupae are of workers and white colored are of reproductive.

Chapter 6

Comb architecture of *Polistes wattii*

6.1 Introduction

Nests of Polistes species from around the world.

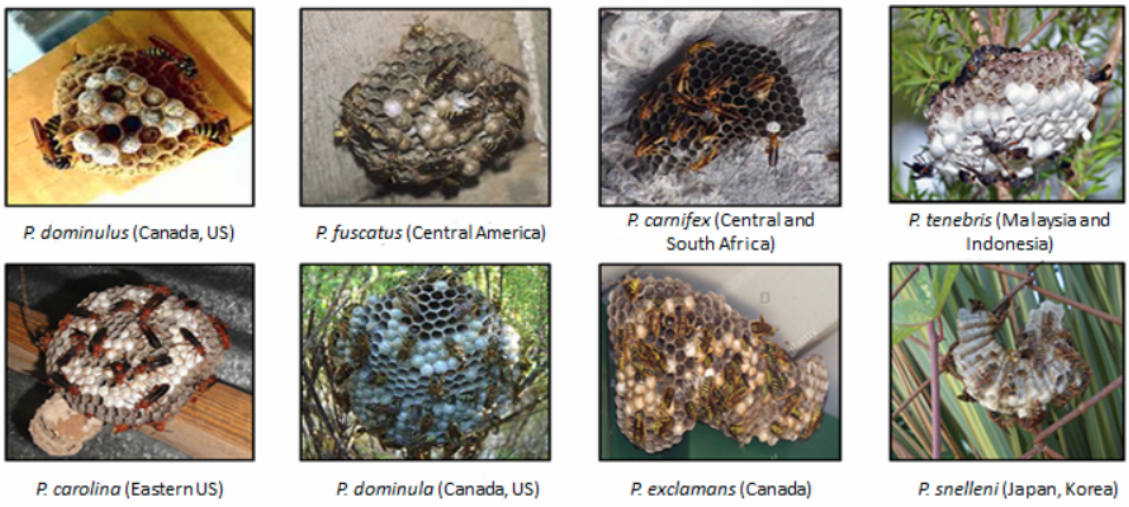


Figure 6.1: Nests of *Polistes* species from around the world.

Most social wasps form round combs. The structure of comb is formed by different material, volume and dry weight of nests is different in every *Polistes* species because some species invest more and some invests less in the building of comb. Some species build nests in linear fashion and some in non linear fashion but few species like *Polistes*

fuscatus can construct it in both linear and nonlineral way. There are many factors like gravity and height which can influence cell shape. In *fuscatus* species there were either round comb or oval shape comb (Jeanne et al,. 1986). There are very few species which form multiple comb nests like *P. excalaman* (STRASSMAN, 1981) P. fuscatus (D. Post, pers.comm,.) and *P. metricus* (GAMBOA, 1981).

6.2 Material and Method

The study area was searched and censored every alternate day during the summer, autumn and winter. Nests were found in between ceiling beside walls, in the balconies and mostly outside of the building. Number of the wasps were counted and nest enlargement was recorded. Multiple combs and single combs were compared with help of video recording and photographs. Clusters of *P. wattii* were found in May 2018 at that time the temperature was really high. They were followed for one month, data was collected from May 2018 – June 2018

Figure 6.2: IISER Mohali Campus Map

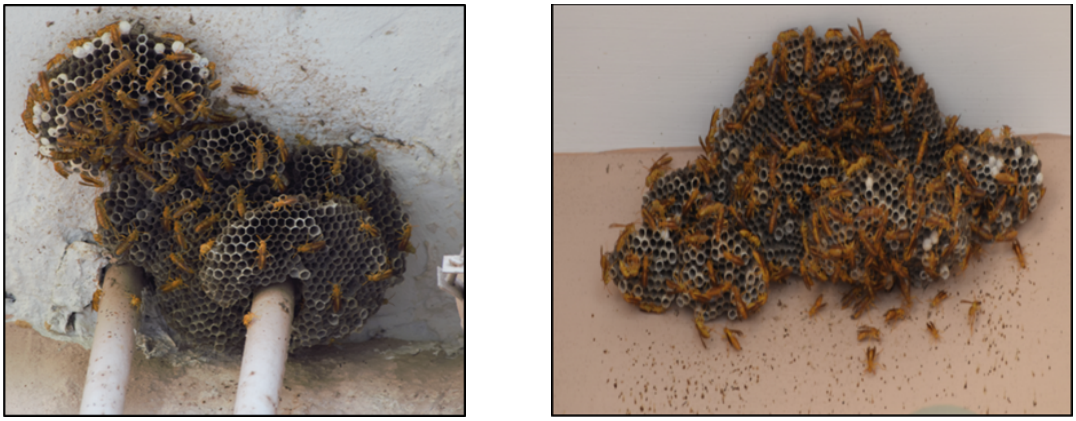


Figure 6.3: Multiple comb nests

Figure 6.4: Single comb nest

6.3 Observations and Discussion(Use of more complicated nest structure)

In this study nests of solitary and multiple foundresses were compared of species *Polistes wattii*. Nests which are produced by single foundresses grow at a slow rate, produces few wasps. These nests are really weak and flimsy so they do not survive for long summer. Most of the nests formed by solitary are constructed in spring which are abandoned in summer. Nest are open and very small in size. Nest initiated by multiple foundresses are mostly found in summer. Nest are much more stronger and big. In late summers multiple comb of nests are formed by *P. wattii* which are really big in size with multiple stacks.

Types of combs formed by *Polistes wattii* are Single and Multiple combs. Combs are made up of plant fiber and oral secretions. It consists of particular unit called cell

which is hexagonal in case of *Polistes wattii*. Multiple combs are formed in the nests which are initiated by many wasps and not by the solitary foundresses. These nests grow very rapidly and among all the species of *Polistes*, very few species including *P.wattii* makes multiple comb structure where as other species makes only one kind of comb which is mostly circular in shape.

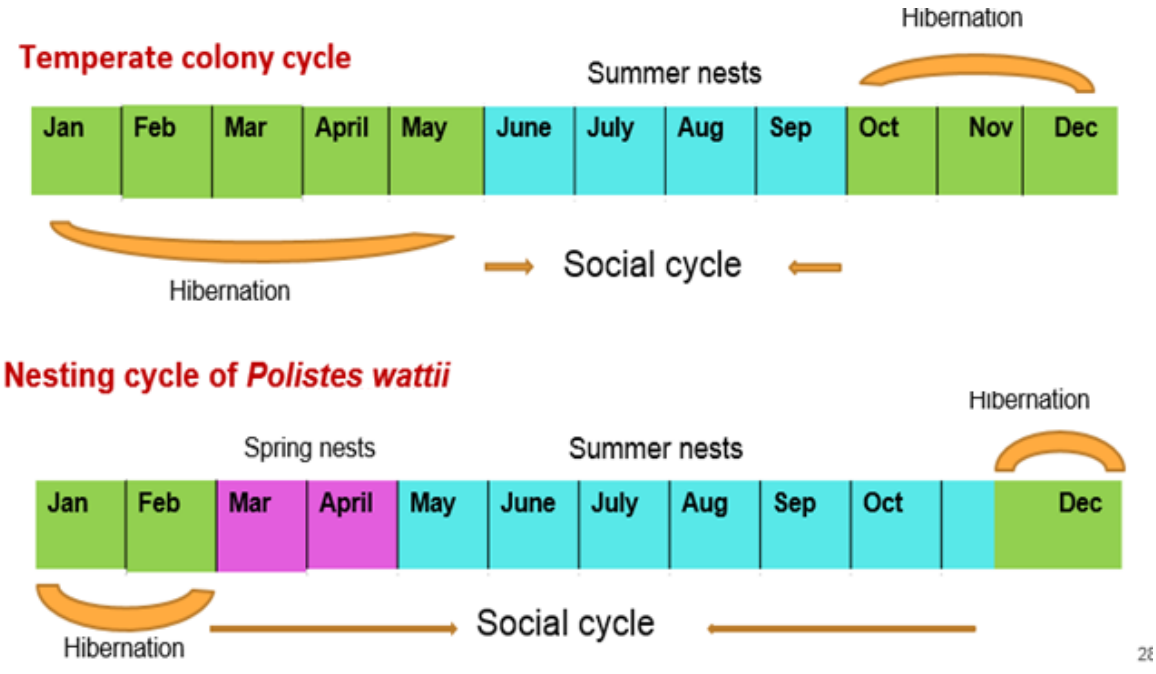
Discussion

Polistes is an ideal model for behavioral studies. It is found in both tropical and temperate regions . The sole purpose of this project was to see how the founding strategies of tropical wasp is different from temperate wasps. Most of the field study was conducted in IISER Mohali And Punjab University campus. The following information was recorded: nest initiation, number of wasps, number of pupae, survivorship and nest productivity. There are two types of *Polistes* wasps first one is tropical *Polistes* wasp which is commonly found in countries like Northern South America where climate is very warm throughout the year and wasps can initiate nests any time of year and continue there colony cycle as long as they want. In most temperate species of *Polistes* where weather is really cold in winter, the nests are initiated by a few overwintered wasps who are usually related and nests survive till the end of summer. The warmer temperature facilitates the colony cycle only for 3-4 months. Indian wasps on other hand start making the nests in March and they can be seen on nests till November. The overwintered wasps probably cannot survive and reproduce for such such a long time. The base of nests made by solitary overwintered wasps are also very weak to survive the long summer. These are likely the reasons why *P. wattii* have adopted the unique strategy of nest initiation in spring and reinitiating in summer. By compairing the solitary foundress nests (mostly spring nests) and multiple foundress nests (always summer nests), it is shown that the later nests survive longer and produce more wasps. It is postulated through this study that spring initiation is an effort to assure fitness in *P. wattii*. Both founding strategies are essential to survive the long summer.

Conclusion

This study has provided observational data on a tropical *Polistes*. It is expected that this work will help in Comparative analysis of tropical and temperate wasps. *P. wattii* follows a colony cycle of temperate *Polistes* but it has longer colony cycle than temperate zone species of genus *Polistes*. It has unique adaptations in response to the long summer.

- It has two founding strategies a) single founding b) multiple founding
- Use of complicated nest architecture
- Shortened hibernation period and extended colony cycle
- Initiation of nest in summer and spring
- Different kinds of pupae of reproductive and workers.



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