



A Review of Our Meagre Knowledge of Asian *Polistes*, and a Call for More Studies

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Abstract | *Polistes* is considered as one of the most widely and abundantly distributed, speciose genera of primitively eusocial wasps. The biology and behaviour of *Polistes* have been crucial to understanding the cooperation and conflicts among the nest members and have contributed greatly to our understanding of the functionality and evolution of eusociality. However, despite the wide geographical distribution, our perception of the genus has been shaped largely by the studies on the temperate species of *Polistes*. The diversity of *Polistes* species in Asia has been reflected through taxonomic reports but their nesting biology and behaviour are mostly unknown. Empirical studies on their behaviour in response to alternate conditions, like experimental removal of the queens, availability of extra food, etc. are also rare. The geographical origin of *Polistes* is also disputed. The speculation that *Polistes* originated in oriental regions can neither be confirmed nor refuted due to the lack of knowledge on Asian *Polistes*. Such missing information creates a large lacuna in our understanding of the origin and routes of dispersal of the genus. Here, we review the scattered studies on Asian *Polistes* and attempt to summarise and analyse the available taxonomic, behavioural and phylogenetic information. To date, 76 *Polistes* species have been reported from 31 Asian countries, out of which Vietnam, India and Japan have the maximum numbers of species. We also review the available behavioural studies on *Polistes*, mostly qualitative and conducted in Japan to show how these can provide a different perspective on *Polistes* biology. We also try to point out the major questions that need to be answered to get a broader overview of Asian *Polistes*. We suggest that more behavioural and phylogenetic studies on various species of Asian *Polistes* could provide the answers to questions like the geographic origin of the species, the evolution of hibernation (reproductive diapause) in the species, the diversification of nest founding strategies, the queen control on worker reproduction, etc.

Keywords: *Polistes* taxonomy, *Polistes* behaviour, Faunal records, Review of *Polistes*

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Primitively Eusocial: Eusociality is characterized by overlap of generations, cooperative brood care and reproductive caste differentiation. When eusocial organisms show morphological caste differentiation along with reproductive caste differentiation, they are called highly eusocial. When reproductive caste differentiation takes place among morphologically alike individuals, such societies are called primitively eusocial. Eusociality is predominantly found in the class Insecta and it shows a fine gradation from solitary to highly eusocial.

Paper wasp: Polistine wasps scrape cellulose fibres from trees and masticate them into paper pulp to build open nests. For this reason, all Polistine wasps are called paper wasps. Nests can be of various shapes but usually the nests are circular and hangs from the substrate with one stalk. These nests are made of hexagonal cells and in each cell the queen lays an egg. The egg hatches in that cell and completes its development through larval and pupal stages. Before pupation the larva spins a convex silk cap at the opening of the cell. The pupa transforms into the imago in the closed cell and the imago comes out by opening the pupal cap.

1 Introduction

The primitively eusocial, paper wasp *Polistes* (Hymenoptera, Vespidae, Polistinae) is one of the most widely distributed genera of social insects. More than 200 species belonging to four subgenera^{1, 2} of *Polistes* have been reported from all continents except Antarctica. Understandably, *Polistes* has gained its due attention from the taxonomists but the genus has also been an attractive model for behavioural studies. The primitively eusocial status of the genus, i.e. reproductive caste differentiation in the absence of apparent morphological differences among the reproductives and the workers, has intrigued social insect biologists, ethologists and evolutionary biologists. Attempts to decode how the queens achieve their reproductive status have given rise to a plethora of behavioural, biochemical, physiological and theoretical studies. However, the most interesting interpretations about *Polistes* biology came from behavioural studies.

Polistes, as a typical member of Subfamily Polistinae, construct gymnodomous (uncovered) nests with less than a hundred individuals. Often these nests are made in man-made structures and are present in close proximity to human settlements. Due to such nesting habits and small colony size, the behaviour of individual wasps and that of the whole colony can be easily observed and recorded. Many interesting behavioural observations and empirical studies on various species of the genus have shaped our understanding of the biology of *Polistes*. However, most of these studies have been carried out on temperate species of Europe, North America and the neotropical species of South America.^{3–5} Although there are faunal records for at least 76 species from 31 Asian countries (Table 1) only a few species from Japan have been subjected to behavioural studies. There are at least two well-documented invasive species of *Polistes*, *P. dominula*, which invaded North America from Europe and *P. chinensis* which invaded Australia from Asia. Understandably, most studies have also been conducted on these two morphologically similar and phylogenetically close species.^{6, 7} Nevertheless, there is another widely distributed species in Asia – *P. wattii*, which has been reported from 12 Asian countries and appears to have a wide distribution like *P. dominula*. *P. olivaceous*, a phylogenetically close species to *P. wattii*,⁸ has been reported from 8 countries. Here, we attempt to review the available studies (Supplementary Tables 1 and 2) on various Asian species of *Polistes* and explore the need for more studies on Asian *Polistes*.

2 Diversity and Distribution of *Polistes* in Asia

In Asia, the focus of scientific work on *Polistes* has been mostly confined to taxonomic reporting. Using the available literature on such taxonomic records, we have prepared a database of species distribution of *Polistes* in Asia (Table 1, supplementary table 1). Carpenter¹ described four subgenera of *Polistes*, *Gyrostoma*, *Polistella* and *Polistes s.str* and *Aphanilopterus*. Species belonging to first three subgenera occur in Asia, while subgenus *Aphanilopterus* mainly includes the South American species. According to the literature, Vietnam has the maximum number of reported species (35). Other species-rich countries in Asia are India (30), Japan (17), South Korea (11), China (10) Iran (10), Pakistan (9), and Nepal (9) (Table 1, Fig. 1). Plotting the numbers of species reported from different countries on the map (Fig. 2) shows the wide distribution and species density of *Polistes* in Asia. Despite the small geographic area, the species richness (number of species) of Vietnam can be contributed to the favourable, coastal, warm and humid climate and strategic biogeographic position as many species in Vietnam overlap with India and Japan. The species richness in India is also not surprising, given the large geographic area and various climatic regions. However, the same does not seem to be true for China. The relatively low species richness of China is probably due to the reporting bias caused by a lack of interest in taxonomic work or due to the publication of such work in regional language, which were not accessible to us. Nepal has 9 reported species, but 8 of them are also available in India. These species seem to have a continuous distribution due to the absence of any biogeographic barrier between the two countries.

Some species have a wider distribution and have gained more attention from social insect biologists. The most common species (according to available literature) are *P. wattii*, *P. olivaceous*, *P. rothneyi*, *P. stigma*, *P. sagittarius*, *P. strigosus*, *P. tenebricosus*, *P. chinensis*, *P. nimpha*, *P. indicus*, *P. biglumis* and *P. gigas* (Fig. 3). *P. chinensis* has been studied in both Asia (mostly Japan) and New Zealand because of its invasive status.

It can be assumed that taxonomic documentation of *Polistes* has not yet been conducted in many countries of Asia, or many regions of each country. The taxonomic studies are often published in print-only journals or in regional languages and have limited accessibility. We may have missed some species due to

Table 1: Tentative distribution of *Polistes* (based on locations of taxonomic reports) in Asia (references in the main manuscript were selectively used to keep the manuscript short, for an exhaustive list of references please see Supplementary Table 1).

Species	Locations of reporting
<i>Polistes adustus</i>	India ⁵⁶ , Nepal ⁵⁷ , China ¹ , Bhutan ⁵⁸
<i>Polistes affinis</i>	Vietnam ¹⁰ , India ²
<i>Polistes angusticlypeus</i>	India ²
<i>Polistes assamensis</i>	India ¹
<i>Polistes associus</i>	India ² , Pakistan ¹
<i>Polistes atrimandibularis</i>	Iran ¹
<i>Polistes badius</i>	Yemen ⁵⁹
<i>Polistes biglumis</i>	Uzbekistan ⁶⁰ , Iran ⁶¹ , Japan ⁶²
<i>Polistes brunus</i>	Thailand Laos, Cambodia, Vietnam ¹⁰ ,
<i>Polistes buruensis</i>	Philippines, Sunda Island ⁶³
<i>Polistes caobangensis</i>	Vietnam ^{64, 65}
<i>Polistes capnodes</i>	Philippines ⁶⁶
<i>Polistes caspicus</i>	China, Hongkong, Taiwan, Japan ¹
<i>Polistes chinensis</i>	China, Japan, South Korea, Taiwan ¹ , Vietnam ¹⁰
<i>Polistes chuyangsin</i>	Vietnam ¹⁰
<i>Polistes clandestinus</i>	Vietnam ⁶⁷
<i>Polistes communalis</i>	Vietnam ¹⁰
<i>Polistes curcipunctum</i>	Vietnam ⁶⁷
<i>Polistes daehanicus</i>	South Korea ⁶⁴
<i>Polistes dawnae</i>	India ² , Myanmar ¹ , Vietnam ¹⁰
<i>Polistes delhiensis</i>	Vietnam ¹⁰ , India ²
<i>Polistes diabolicus</i>	Indonesia ⁶³
<i>Polistes diakonovi</i>	Japan ⁶⁸
<i>Polistes dominula</i>	India ² , Pakistan ⁶⁹
<i>Polistes dubius</i>	Philippines ¹
<i>Polistes ephippium</i>	Iran, India ² , China
<i>Polistes extraneus</i>	Indonesia ¹
<i>Polistes fastidiosus</i>	Saudi Arabia, Yemen ¹
<i>Polistes formosanus</i>	Japan, Vietnam ¹⁰ , Taiwan ⁷⁰
<i>Polistes gigas</i>	Vietnam ¹⁰ , Hongkong ⁷¹ , Taiwan ⁷² , India ²
<i>Polistes gilvus</i>	Vietnam ⁶⁷
<i>Polistes humilis</i>	Vietnam ¹⁰
<i>Polistes indicus</i>	India, Pakistan, Iran, Oman, UAE, Saudi Arabia, Nepal ¹
<i>Polistes iranus</i>	Iran ¹
<i>Polistes jadvigae</i>	Japan ¹² , South Korea ⁷³
<i>Polistes japonicus</i>	Japan, South Korea ¹ , Vietnam ¹⁰
<i>Polistes jokahamae</i>	China ⁷⁴ , Japan ⁷⁵ , India ² , Vietnam ¹⁰
<i>Polistes khasianus</i>	Vietnam ¹⁰ , India ²
<i>Polistes latinis</i>	India ²
<i>Polistes lepcha</i>	India ¹ , Vietnam ¹⁰
<i>Polistes maculipennis</i>	Nepal ⁵⁷
<i>Polistes mandarinus</i>	Japan, Taiwan ¹ , Vietnam ¹⁰

Table 1: (continued)

Species	Locations of reporting
<i>Polistes marginalis arabicus</i>	Saudi Arabia ¹
<i>Polistes metricus</i>	Vietnam ¹⁰
<i>Polistes nigrifrons</i>	Indonesia ¹
<i>Polistes nigritarsis</i>	India, Vietnam ¹⁰
<i>Polistes nimpha</i>	Iran, Pakistan, Japan, Mongolia, India ¹
<i>Polistes nipponensis</i>	Japan, Vietnam ¹⁰ , South Korea
<i>Polistes olivaceus</i>	Bangladesh, Vietnam ¹⁰ , Iraq, India, Pakistan, Nepal, Afghanistan, Saudi Arabia ¹
<i>Polistes opacus</i>	India ²
<i>Polistes paco</i>	Vietnam ¹⁰
<i>Polistes philippinensis</i>	Philippines ¹
<i>Polistes quadricingulatus</i>	Pakistan ⁷⁶ , India ²
<i>Polistes relicinicypeus</i>	Vietnam ¹⁰
<i>Polistes riparius</i>	Japan, Vietnam ¹⁰
<i>Polistes rothneyi</i>	Japan, Iran, South Korea, China, Pakistan, India, Nepal, Vietnam ¹⁰
<i>Polistes rubellus</i>	India ²
<i>Polistes rugifrons</i>	India, Taiwan, China ¹
<i>Polistes sagittarius</i>	China ⁷⁷ , Vietnam ¹⁰ , Philippines, Nepal, India, Indonesia ¹
<i>Polistes santoshae</i>	Vietnam ¹⁰ , Bhutan ⁵⁸ , India ²
<i>Polistes semenowi</i>	Iran, Turkmenistan ¹
<i>Polistes shirakii</i>	Taiwan ¹
<i>Polistes similis</i>	India ²
<i>Polistes simulates</i>	Indonesia ¹
<i>Polistes smithii</i>	Oman, Yemen ¹
<i>Polistes snelleni</i>	Japan, South Korea Vietnam ¹⁰
<i>Polistes stigma</i>	Vietnam ¹⁰ , India ¹ , Pakistan ⁷⁸ , Nepal ⁵⁷ , Indonesia ⁷⁹ , Japan ⁸⁰ , Taiwan ⁸¹
<i>Polistes strigosus</i>	India ² , Vietnam ¹⁰ , Hongkong ¹ , Japan, Nepal, Taiwan
<i>Polistes sulcifer</i>	Iran ¹
<i>Polistes takasagonus</i>	Taiwan ¹
<i>Polistes tenebricosus</i>	India ² , Indonesia ⁶³ , Philippine ¹ , Nepal ⁵⁷ , Bhutan ⁸² , Vietnam ¹⁰
<i>Polistes tenellus</i>	Yemen ¹
<i>Polistes tenuispunctia</i>	South Korea ⁸³
<i>Polistes variabilis</i>	Vietnam ¹⁰
<i>Polistes wattii</i>	India, Pakistan, Afghanistan, Iraq, Uzbekistan, Turkmenistan, Iran, Tajikistan, China, UAE, Saudi Arabia, Oman ¹
<i>Polistes yamanakai</i>	China, South Korea, Japan ¹

the non-accessibility of literature. Therefore, the species richness of each country and the distribution of each species must be an under-estimation. Many species have been reported from multiple countries (Fig. 3) but we do not have an accurate distribution map for most of these species due to a lack of proper phylogeographic studies. Furthermore, we plotted

the distribution and species richness according to political boundaries (Fig. 3) but political boundaries are not representative of physical landscapes.

There are many papers on the occurrences and morphological descriptions of many *Polistes* and other Vespidae wasps from India. However, data from India (30 species) could

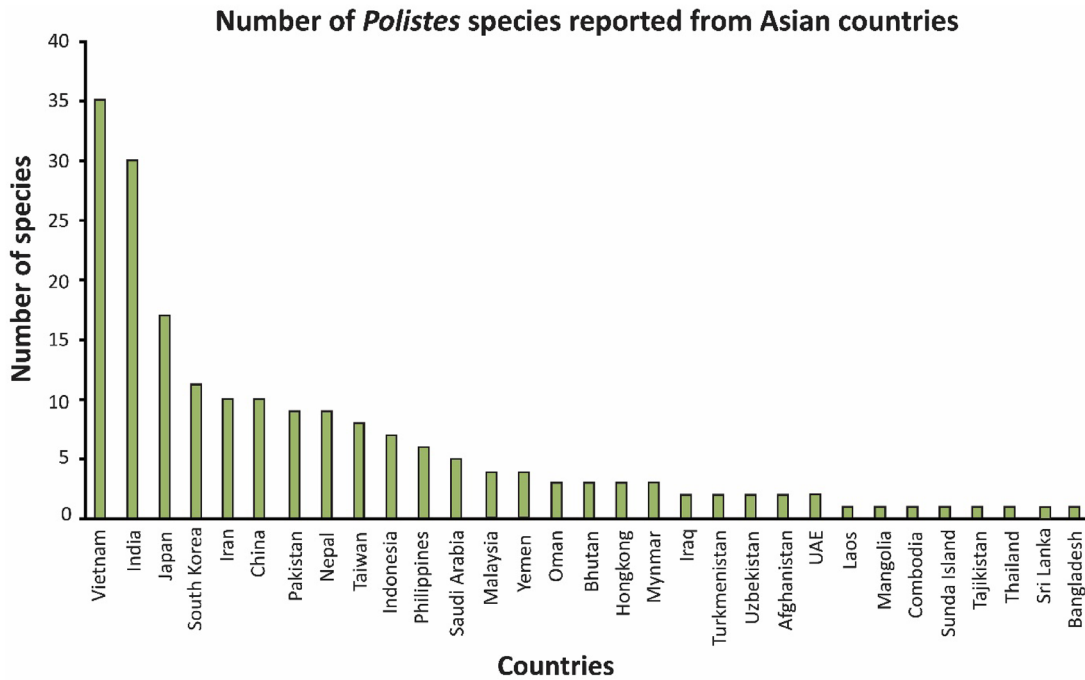


Figure 1: *Polistes* species richness of different Asian countries. Only the countries with at least two reported species are shown here.

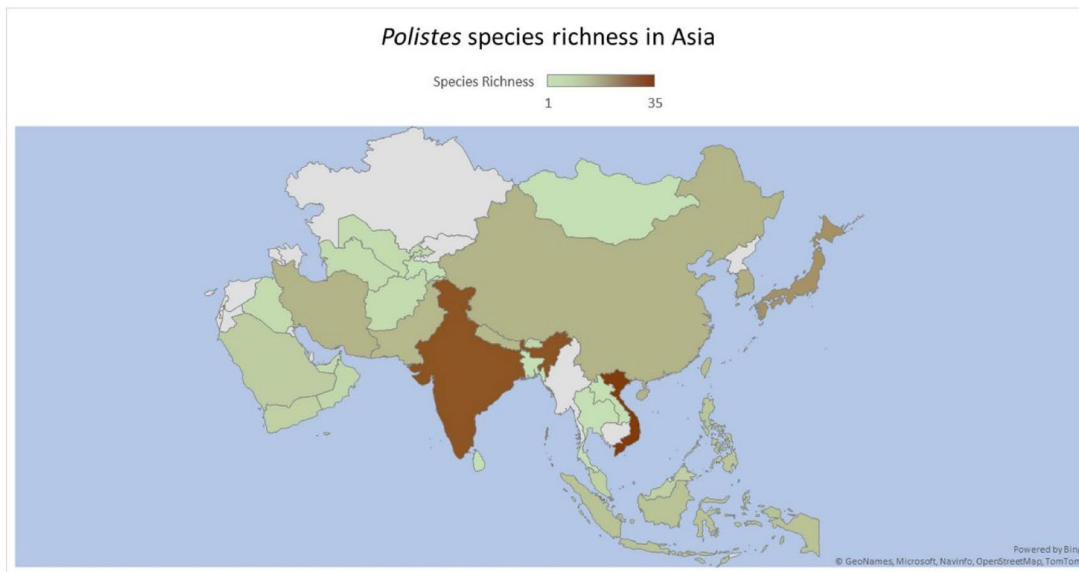


Figure 2: Distribution and density of *Polistes* species in Asia. The gradient is representative of numbers of species reported from different countries.

also be underestimated, given that different climate specific zones and landscapes are present in India and a thorough sampling from all the states is awaited. The species diversity of India

has been assessed by morphological identification and awaits molecular confirmation and phylogenetic interpretation. Despite the limitations and flaws, the database presented here is

Geographic distribution of a few frequently reported *Polistes* from Asia

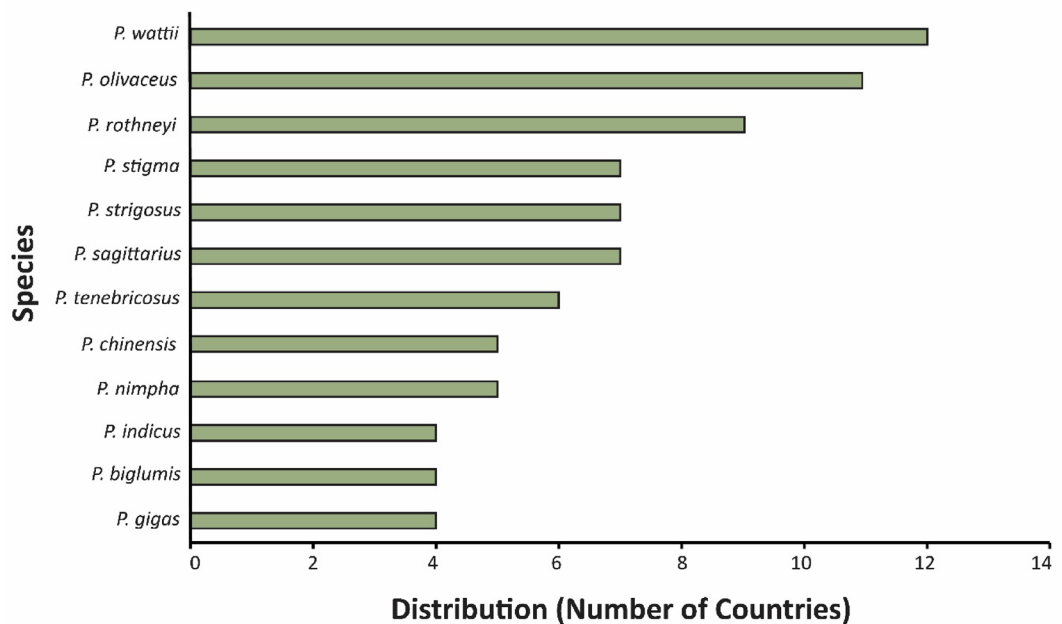


Figure 3: Distribution of the most frequently reported species in Asia.

an attempt to understand and analyse the distribution of *Polistes* in Asia.

3 Origin of *Polistes*

Polistes is undoubtedly the most abundant and widely distributed genus of Polistine wasps. The other well-studied and diverse genera of Polistine wasps, the neotropical *Mischocyttarus*, afro-tropical *Belanogaster* and *Ropalidia* and palearctic and oriental *Parapolybia*, are restricted to narrower geographic distribution. Ecological success of *Polistes* over a wide range of geographical areas has given rise to many hypotheses including its geographic origin. The rich species diversity of *Polistes* in Asia has led to the hypothesis that *Polistes* may have originated in the oriental tropics or South East Asia and invaded the new world through Beringia and other parts of the world; the subsequent species diversity of the American continents is the result of such secondary radiation.^{6,9} Molecular phylogenetic analysis failed to unambiguously confirm or reject this hypothesis but proposed that *Polistes* colonised the new world through South America and not Beringia.⁶ From such trees made with sequences that were available for *Polistes* from different parts of the world, it appears that the old world and new world taxa form sister clades and the former originated in Southeast Asia. Phylogenetic trees

made with morphology or behavioural traits show that Asian species usually group together.⁶ Recent molecular phylogenetic analysis conducted with almost all species found in Vietnam shows the presence of subgroups even within the subgenus *Polystella*.¹⁰ Interestingly, *P. wattii* was never included in any phylogenetic tree until now despite its wide distribution in Asia. The recent inclusion of *P. wattii* in a phylogenetic tree shows that it forms a separate clade with *P. olivaceus*. *P. wattii* and *P. olivaceus* are two of the most reported species with overlapping geographical distribution in Asia (Fig. 3, Table 1) and their separate clade formation in the phylogenetic tree suggests the possibility of their unique ecological and behavioural traits.⁸ In this context, ecological comparison of old world and new world species and phylogenetic analysis with more Asian species may help resolve the questions regarding the origin of *Polistes*.

4 *Polistes* of Asia: Behavioural Data (Supplementary Table 2)

There are some behavioural studies available on following Asian *Polistes* – *P. chinensis antennalis*, *P. rothneyi*, *P. japonicus*, *P. jokahamae*, *P. snelleni*, *P. riparius*, *P. nimpha*, *P. olivaceus*, *P. biglumis*, *P. stigma* and *P. wattii*. Most species reported from Japan have been subjected to observation-based

Table 2: Foundress strategy (initiation of nest by a solitary female or multiple females in Asian *Polistes*.

Species	Foundress strategy	References
<i>Polistes chinensis</i>	Solitary/ rarely multiple	21, 48, 84
<i>P. riparius</i>	Solitary/ occasionally multiple	85
<i>P. snelleni</i>	Solitary/ occasionally multiple	21, 85
<i>P. jadvigae/ P. jokahamae</i>	Solitary/occasionally multiple	21, 24
<i>P. japonicus</i>	Multiple	25
<i>P. stigma</i>	Solitary/occasionally multiple	22
<i>P. biglumis</i>	Solitary	86
<i>P. dominula</i>	Both solitary and multiple	20
<i>P. wattii</i>	Solitary in Spring, multiple in summer	8
<i>P. olivaceous</i>	Solitary founding	54

natural historical studies or behavioural experiments. Such studies reveal interesting but scattered facts like *P. chinensis* and *P. rothneyi* have short nesting cycles (approximately four months) in Okushiri Islands, Japan¹¹; the smaller females were more successful in founding nests in *P. jadvigae*¹² etc.

There are at least 3 species (*P. nipponensis*, *P. riparius* and *P. stigma*) that are reported and studied in both Japan and Vietnam. It would not be surprising if these species are present in eastern China or Taiwan. Observation-based studies have also been conducted on other *Polistes* species in Vietnam. Although these species have not been extensively studied, yet the available information still alludes to the diversity in nesting biology, nest architecture, queen–worker dynamics, male production and mating behaviour (see below).

4.1 Nest Architecture

For some Asian species, the description of nests is available. Most species reported from Japan make small- to medium-sized, horizontally or vertically aligned single comb nests.¹³ Nest architecture of *P. riparius* and *P. biglumis* includes construction of long empty cells in the lower periphery of the nest which probably work as air chambers like the envelopes of vespine nests^{13–15} *P. olivaceous*¹⁶ and *P. wattii*⁸ nests may become very large with more than 1000 cells. Such large nests are not commonly seen in temperate *Polistes* with the only exception of *P. annularis*.⁵ *P. wattii* nests can be made of multiple combs (see later) which is extremely rare among *Polistes* species. *P. riparius* has also been reported to make large nests.¹⁴ This is in contrast to western temperate *Polistes*, which usually makes small- to medium-sized, circular

nests with a single stalk.³ The extended period of warmer days in South Asia could be a reason for such flexible shapes and sizes.⁸ *P. gigas*, *P. mandarinus* and *P. snelleni* construct cells eccentrically while *P. chinensis* and *P. jadvigae* (= *fadvigae*) make concentric nests.¹⁷ *P. mandarinus* makes nests within vegetation, particularly among cedar trees. The pupal caps of *P. mandarinus* have a characteristic bright yellow colour, which is probably an adaptation for camouflage among leaves.¹⁸ Nest reconstruction after a hornet attack has been observed in *P. jadvigae*.¹⁹

4.2 Nesting Biology

Globally, both solitary and multiple founding are seen in *Polistes*. Some species strictly follow one of the strategies and some can employ both. When a species can use both solitary and multiple founding, multiple founding appears to be a more successful strategy (Reviewed in²⁰). Some authors have suggested that Japanese *Polistes* follow only a solitary founding strategy. But multiple founding strategy has also been seen in some Japanese species (Table 2).²¹ Other Asian species like *P. olivaceous* and *P. stigma* occasionally use multiple founding strategy. In tropical areas, multiple founding should be more adaptive for various reasons²² and the same should be expected for *P. stigma*, *P. olivaceous* or *P. wattii* (in spring), which are more common in warmer countries. However, solitary founding is more prevalent even in these species. It should be noted that given the wide distribution of these species, and the low sample size in the available literature, variability within these phenotypes should be expected.

4.3 Hibernation and Nesting Cycle

One of the most prominent features of most *Polistes* species is reproductive diapause or hibernation of adult wasps. The females produced in the late colony phase prior to winter mate with males and pause the social life for a few months. During this time, the females find shelters (hibernacula) or gather at the back of the nest and spend the winter in total inactivity. These wasps emerge from diapause in spring or the beginning of summer and initiate nests alone or with other foundresses.³ All Asian (including Indian) *Polistes* for whom behavioural data is available, also follow the annual cycle. This widespread trait of overwintering or hibernation or diapause can be interpreted as an adaptation to survive harsh winter and also suggests a possible temperate origin of the genus.⁶ The absence of hibernation and ability to initiate nests anytime of the year in neotropical *Polistes* species of South America⁴ can be an adaptive variation.

4.4 Queen–Worker Dynamics

In primitively eusocial insects, the queen usually leads the dominance hierarchy and controls the workers through physical aggression. In western temperate *Polistes* species, the queen is the most dominant individual and she controls worker reproduction and centralised functioning of the colony through aggression.²³ There are at least three reported instances, where the *Polistes* queens maintain reproductive dominance without being physically aggressive. Incidentally, all three species with the non-aggressive queen, *P. jokahamae*,²⁴ *P. japonicus*^{25, 26} and *P. snelleni*²⁷ are from Asia. The absence of physical aggression by the queen is typically found in highly eusocial species and only a few primitively eusocial species are known to control worker reproduction without physical aggression. Often, the lack of a dominant queen leads to worker reproduction (reviewed in²⁸). Indeed, studies on worker reproduction using microsatellites reveal that worker reproduction, particularly male production by workers takes place in many Asian *Polistes*.²⁹ Workers of *P. snelleni* and *P. chinensis antennalis* are capable of mating and producing female offspring in the presence of the queen or in orphaned colonies^{27, 30, 31} although production of female offspring only by a singly mated foundress has also been reported in *P. snelleni*.³² In *Ropalidia marginata*, the behaviour of the docile queen and the succession of the next queen through aggression has

given rise to many interesting empirical studies.^{28, 33} Such empirical and observational studies of more Asian *Polistes* may change our view about how we perceive physical aggression in primitively eusocial organisms.

4.5 Worker Reproduction and Behaviour

Ovarian development in workers is known in *Polistes*.^{8, 34} In queenless (orphan) colonies, egg-laying by multiple workers has been reported in *P. chinensis antennalis*³⁵ and *P. jadwigae*.³⁶ However, physical aggression among the workers was seen in the former but not in the latter species. *P. jadwigae* workers produced a few female offspring while *P. chinensis antennalis* workers produced only male offspring.³⁶ In orphaned colonies of *P. nipponensis*, workers could continue the nest and produce reproductives implying the mated status of workers. *P. stigma* workers also lay eggs in the presence of the queen.³⁷ In case of *P. wattii* in late colony phase, the nests attain large colony sizes and development of worker ovaries is a common phenomenon. Worker behaviour with respect to division of labour, dominance or nest construction has been reported in some studies^{26, 37–39} by the Japanese social insect biologists but many such behavioural studies lack quantification of behaviour and statistical comparison of data.

4.6 Male Production

Males are usually produced late in the colony cycle in western temperate *Polistes*. The gynes mate with the males prior to hibernation. However, male production during early colony cycle (spring) has been reported in *P. exclamans*, *P. gallicus* and *P. f. variatus*.^{40, 41} In *P. exclamans*, *P. metricus* and *P. annularis* the early male production has been associated with frequent queen death and subsequent takeover by mated workers.⁴⁰

We do not have much information on the male production of Asian species but early male production is also reported here. In case of *P. chinensis*, *P. rothneyi* and *P. jadwigae*,⁴² the males can be produced early in the colony cycle and the gynes can mate with them post hibernation in Spring (reviewed in³). In *P. chinensis* diploid males have been reported in early colony cycle.^{29, 43} In *P. wattii*, large number of males are produced in late colony cycle but occasionally males are also seen in spring.⁸

In social insects, males usually do not participate in any nest maintenance behaviour. Nevertheless, in some Polistine wasps, males were occasionally seen to feed larvae with food received from female workers.⁴⁴ In Asian *Polistes*,

this rare behaviour has been observed in *P. jadvigae* and *P. snelleni*.^{13, 45}

4.7 Mating Behaviour

In comparison to social behaviour, mating behaviour has received very little attention in *Polistes*. *Polistes* males usually aggregate in leks to mate with foraging workers and gynes. Such territorial behaviour of males and their mating behaviour or mating associated behaviours have been observed in *P. jadvigae*,⁴⁶ *P. snelleni*, *P. chinensis* and *P. mandarinus*.^{47–49} The timing of mating in *Polistes* may vary with respect to colony phase³ and the same is true for the Asian species. In *P. chinensis*, although the gynes destined for hibernation, emerge from August to September, mating occurs in November.⁴⁹ A similar late mating has also been observed in *P. jadvigae* (reviewed in⁴⁹). However, the unavailability of information on mating behaviour for most Asian species restricts us from making any comprehensive comparison of Asian *Polistes* with their western temperate or neotropical counterparts regarding mating or mating associated behaviours.

5 Asian *Polistes*: The Reasons to Study Them

Despite the wide diversity of *Polistes*, our perception of their behaviour is largely formed by the studies of temperate species of Europe, North America and Japan and the neotropical species of South America.^{3, 4} The research on Asian *Polistes* biology has been dominated by the work on *P. chinensis* in their native and invaded locations.^{21, 50–53} Behaviourally, *P. chinensis* is similar to its look-alike (particularly to novice eyes) and phylogenetically close species *P. dominula* (based on mitochondrial genes⁶). Studies on various Japanese and Vietnamese species show different features but it is difficult to infer a pattern on the behaviour of Asian *Polistes* from these unrelated studies.

All kinds of geographic and climatic conditions are available in Asia, which might be a reason for the rich species diversity of *Polistes* in this continent. It can be assumed that the environmental diversity and species diversity are also reflected in the behavioural diversity of different species. Exploration of their behaviour in a systematic manner, therefore, may result in the discovery of unique phenotypic traits and thus may open newer directions of social insect biology. A comparative behavioural study of the three subgenera of *Polistes*, that occur in Asia and a phylogenetic study including various species belonging

to these three subgenera from different locations will also be helpful in getting a comprehensive view of the genus in Asia. However, currently, we lack systematic behavioural work and molecular data on different Asian species to conduct such a study.

Most behavioural work on Asian *Polistes* has been conducted on Japanese temperate species. We did not find any extreme difference between the western temperate *Polistes* and Japanese (temperate-zone) *Polistes* in literature. The Vietnamese and Indian species are representative of the tropical weather but in both countries, *Polistes* research has been dominated by taxonomy and faunal records (but see^{8, 54}). Although we can expect behavioural or geographic and climatic adaptations in *Polistes* from warmer Asian countries, till now, there are very few studies to support that. From India, we have found a unique nesting cycle in *P. wattii*, which is very different from either the temperate or the neotropical nesting cycles.

6 *Polistes wattii*: A Lesser-Known Species with Interesting Features

Indian scientists have contributed an enormous amount of knowledge in the field of wasp biology. *Ropalidia marginata*, the Indian Polistine (Tribe: Ropalidini) wasp is one of the most extensively studied social insect species in the world.²⁸ However, we lag in our studies on Indian *Polistes*. In the last seven years, we have studied the nesting biology of *P. wattii* (Figs. 4, 5), which is abundantly found in North India and other Asian countries.⁸ Observational data indicate that this species is unique in many ways and it differs from all other known tropical and temperate *Polistes*. All temperate and most tropical *Polistes* species make almost circular small nests with a single stalk at the back and the nest usually hangs from a substrate.³ *P. wattii* makes nests of variable sizes and shapes and they can make nests in open spaces or in cavities (Figs. 4b, e, 5a). The nest architecture is extremely flexible and depends on the available space. Multiple combs are rarely found in *Polistes* with the exception of a few tropical species, as reviewed in.⁵ But in late summer, large nests of *P. wattii* with multiple combs stacked one below the other is a very common sight in North India (Fig. 5). Small combs are either connected to the substrate or to a previously built comb through one or more pedicels of varied widths.

Polistes wattii is also different than other known *Polistes* species in their nest founding



Figure 4: A collage of *Polistes wattii*: **a** A forager collecting water **b** a solitary foundress nest (nest initiated by a single female) in an open space. **c** Two wasps sitting as guards at the nest entrance. **d** Workers sitting outside the entrance of a nest built inside a cavity. **e** A multiple foundress nest (nest initiated by multiple females) in an artificial cavity.



Figure 5: **a** A nest in October with multiple combs (circular/oval nest parts that contain many hexagonal cells, where eggs are laid). **b** Deepak Nain collecting wasps from the nest. **c** Ruchira Sen collecting wasps from the nest entrance.

strategies. Temperate *Polistes* wasps initiate nests in spring, produce workers in the first batch and then males and gynes in the second or the last batch. These nests can be started by either a single female (solitary foundress) or by multiple females. In winter, the mated gynes survive the unfavourable conditions by hibernation/diapause. Neotropical wasps in South

America do not hibernate and can initiate nests any time of the year.^{4,5} Although *P. wattii* is an annual species that hibernates in winter, the nest founding strategy of *P. wattii* is different from any other known temperate and tropical *Polistes*. This species follows a strictly solitary founding strategy in spring but these nests do not survive beyond May–June and in summer,

they use multiple founding strategy and initiate nests again. Such a biannual, alternative nesting strategy has not been reported in any other *Polistes* species. In the middle of summer nest-free clusters of healthy and styloped wasps are seen, which may be linked with the initiation of summer nests by multiple foundresses.

7 Reasons Behind Lack of Behavioural Studies on *Polistes* in Asia

It can be assumed that the wide range of environmental and geographical conditions may have induced many behavioural specialisations in the Asian *Polistes* species but there are not many studies to support this assumption. Apart from the danger of painful sting imparted by female *Polistes*, there are some other challenges that restrict behavioural studies. First, quantitative behavioural experiments require standardisation of ethogram and long, meticulous observations. Those who are ready to do that often focus on the economically important organisms. Second, the convenience of collecting wasps and studying their morphological features in the lab has led to an abundance of taxonomic studies on wasps in Asian countries. Behavioural studies on *Polistes* have been mostly monopolised by western scientists on western species. It is, however, possible that there are some behavioural studies published in regional languages or in print-only journals in different countries of Asia but they remain hidden to current researchers. We may not have a proper explanation for the lack of studies on Asian *Polistes* till now but for a better understanding of the evolution and diversification of genus we need more behavioural and phylogenetic studies. One major exception is the biology of another polistine wasp, *Ropalidia marginata*, which has been extensively studied by Professor Raghavendra Gadagkar and his group.²⁸ However, it is not enough to make a comprehensive estimation of the social wasps of the continent and more such studies are required to follow particularly on *Polistes*.

8 Conclusion

Evans (1958) suggested, *Polistes* is the key genus to understand the evolution of eusociality.⁵⁵ Currently, our knowledge about this genus is biased with the available information on the new world species. We need to explore (but not limit ourselves to) the following questions to get a comprehensive view of the biology and behaviour of *Polistes*. (1)

Systematic behavioural ecology on representative species from different phylogenetic clades. (2) Population ecology of the more abundant species to understand the nature of their dispersal. (3) Behavioural experiments to document the mating behaviour and studying behavioural isolation among the sympatric species with similar colouration and markings. (4) The adaptive values of the intersexual and intrasexual body markings. (5) Identification of possible strepsipteran parasites from different species of Asian *Polistes* (reported from only *P. gigas*, *P. rothneyi*⁸⁷ and *P. wattii*⁸ and the effect of *Polistes*–Strepsiptera association on the behaviour and biology of *Polistes*. (6) The reason for the abundance of solitary founding in Asian *Polistes*.

Although there are some behavioural studies on Japanese *Polistes* and taxonomic studies from different countries of Asia, we know very little about the species that occur in the warmer countries of West and South Asia (Supplementary Table 1). For a better understanding of evolution of eusociality it is crucial that we ask questions regarding the geographic origin of the genus, the evolution of hibernation in the genus, the diversification of nest founding strategies, the queen–worker and foundresses dynamics, occurrence of worker reproduction etc. Such questions have been explored in temperate and neotropical species but our understanding will remain incomplete without studying the Asian species. We need to explore the behavioural, chemical and molecular ecological aspects of *Polistes* from different Asian countries to get a comprehensive perspective of the genus.

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Supplementary Information

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Data availability

This is a review article and therefore does not contain any raw data.

Declarations

Conflict of Interest

The authors declare no competing interest.

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