Евразиатский энтомол. журнал 14(6): 532–542

Biological observations on a paper wasp *Polistes (Gyrostoma) olivaceus* De Geer (Hymenoptera: Vespidae) in Vietnam

Изучение биологии бумажной осы *Polistes (Gyrostoma) olivaceus* De Geer (Hymenoptera: Vespidae) во Вьетнаме

Phong Huy Pham
Фонг Фам

Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Hanoi Vietnam. E-mail: phong.wasp@gmail.com or phongpham82@iebr.ac.vn.

Институт экологии и биологических ресурсов, Вьетнамская Академия наук и технологии, Хоанг Куок Вьет-роуд 18, Ханой Вьетнам.

Key words: colony cycle, hibernaculum, immature stages, protection habits, survivorship rate.

Ключевые слова: жизненный цикл колонии, зимняя спячка, незрелые стадии, защитное поведение, выживаемость.

Abstract. Bionomics of a paper wasp, *Polistes (Gyrostoma) olivaceus* (De Geer, 1773), is described and discussed based on 34 nests collected in 14 provinces and cities in Vietnam in a period of four years (2010–2014) along with the dissection of some selected nests. Nest sites, nest architecture, colony size, size of development stages, and habits of *P. olivaceus* are also reported. The colony cycle of *P. olivaceus* can be divided into five stages as follows: 1) Post-hibernant stage, 2) Solitary stage, 3) Emergent stage, 4) Pre-hibernant stage, and 5) Hibernant stage. The duration of the colony cycle is about 270 days, the duration of the immature stages is eggs — 6.5 days, larvae — 27.1 days, and pupae — 13.8 days and total duration — 47.5 days. The survivorship rate of the immature stages is eggs — 84.7%, larvae — 81.9%, and pupae — 95.8%.

Резюме. Описана экология бумажной осы *Polistes (Gyrostoma) olivaceus* (De Geer, 1773) на основании изучения 34 гнёзд, собранных в 14 провинциях и городах Вьетнама в течение четырёх лет (2010–2014). Проведено препарирование отдельных гнёзд, отмечено их расположение, строение, размер колонии, размеры стадий развития и поведение ос. Жизненный цикл колонии *P. olivaceus* можно разделить на пять этапов: 1) постзимовочный этап, 2) одиночный этап, 3) этап становления колонии, 4) предзимовочный этап и 5) зимовка. Продолжительность жизненного цикла колонии составляет около 270 дней, продолжительность стадии яйца — 6,5 дней, личинки — 27,1 дней, и куколки — 13,8 дней; общая продолжительность — 47,5 дней. Выживаемость в стадиях яйца — 84,7 %, личинки — 81,9 % и куколки — 95,8 %.

Introduction

The social wasps belong to the family Vespidae, including three subfamilies (Stenogastrinae, Polistinae, and Vespinae) with 37 genera [Pickett, Carpenter, 2010]. Of these, *Belonogaster*, *Parapolybia*, *Mischocyttarus*, *Polistes* and *Ropalidia* are of particular interest. They form a separate behavioural category characterized by simple, open nests that can be easily studied, and a rather primitive level of sociality because one or a small group of queens (inseminated females) found new colonies and rear the first brood in this group [Gadagkar, Joshi, 1982].

Polistes is a cosmopolitan genus of 218 species [Pickett, Carpenter, 2010], most of which are tropical or subtropical in distribution. Adults are slender, elongated wasps with a pointed, spindle-shaped abdomen, and show little obvious morphological differentiation into the queen and worker casters. This genus has been widely studied and is considered as key genus for understanding evolution of the social insects and social behavior among wasps [Carpenter, 2003].

Polistes olivaceus (De Geer, 1773) is one of the more defensive *Polistes* species. While it will tolerate activity near the nest, the workers will be quick to spot, locate and attack all that moves and comes too close. However, the attack is frequently aimed solely at the intruder. The sting of this species can be quite painful [Barthelemy, 2008; Pham, 2014a]. For these reasons, it is really difficult for researchers to carry out studies on biology and behaviors of the one.

Whereas many other species in the genus *Polistes* have received considerable attention on biological and behavioral studies [Cervo et el., 2000; Gamboa et al., 2002; Giannotti, Mansur, 1993; Giannotti, Machado, 1994a, b; Giannotti, 1997a, b; Gobbi, Zucchi, 1980, 1985; Gobbi et al., 1993; Harris, 1979; Hermann, Dirks, 1975; Jeanne, Morgan, 1992; Jeanne, 1979; Joan et al., 1983; John, 1971; Karsai et al., 1996; Khalifa, 1953; Klalin, 1979; Liebert, 2004; London, Jeanne, 1997; Makino, 1989; Miyano, 1980; Pfenning et al., 1983; Pickett, Wenzel, 2000; Post, Leanne, 1982; Pratte, Jeanne, 1984; Rau, 1942; Reeve, 1991; Richards, Richards, 1951; Shellmann, Gamboa, 1982; Tibbetts, Reeve, 2000; Tibbetts, 2007; Turillazzi, 1980; Vinícius et al., 2009; West Eberhard, 1969; Yamane, 1969, Yamane, Okazawa, 1977; Yoshikawa, 1957], there is very little information on biology of

P. olivaceus. Barthelemy [2009] only briefly mentioned on its nest and habitat as follows: Nest is un-protected, one sided symmetrical and compact (disk-like) paper comb construction with eccentric pedicel. Cells unspecialized (i.e. no major difference in size for male, queens and workers). Nests of this species are similar in shape and size to those of *P. japonicus*. Cocoon caps generally white, densely woven forming a depressed dome but sometimes with a short tubular cell extension with hemispherical end. The pedicel, the apical part of comb and a portion of the substrate is smeared with a hard coating secretion. Colony size is small to medium colonies, rarely exceeding fifty individuals in Hong Kong, although bigger colonies can be found. This is an aggressive species and nests should be approach with great care. Pham [2014a] described and analyzed hibernation on the nest of this species. Therefore, the present paper is the first report on biological observations of *P. olivaceus*.

Materials and Methods

A total of 34 nests of *P. olivaceus* were collected in Vietnam with a period of 4 years from 2010 to 2014. 14 provinces and cities where the nests collected are Bac Giang (1 nest), Bac Ninh (2 nests), Dien Bien (1 nest), Dong Nai (2 nests), Hai Phong (1nest), Hanoi (9 nests), Hoa Binh (2 nests), Ho Chi Minh (2 nests), Lao Cai (1 nest), Nam Dinh (1 nest), Quang Binh (1 nest), Quang Ninh (1 nest), Son La (2 nests), Thai Binh (8 nests) (Fig. 1). These nests were collected taking precaution not to bias the sampling in favour of any particular size class of nests and to collect entire combs along with all the adults and immature stages. The number of petioles, cells, eggs, larvae, pupae and adults were determined, and all adults were also sexed. Nesting habits, nest sites, nest architecture, colony size, the duration of the immature stages, cycle and longevity of colony and related problems of *P. olivaceus* were analyzed and discussed.

Observation on the development stage of egg, larva, and pupa was carried out with six naturally occurring nests at 19 Group, Nghia Do Precinct, Cau Giay District, Hanoi Capital from the beginning of April to the end of June, 2012. The distance among these nests was only about 20m. To carry out this observation cells of the nests were numbered and the nests were positioned with 4 small red spots of dry paint around the nests with a distance of 20 cm from (Fig. 2). With cells that were next built they would be numbered next. The observation also assisted by a magnifier (with magnification of 15). For other observations, I carried mainly out them in 2012, 2013, and 2014. Measurement of eggs, larvae, pupae, and adults was made with the ocular micrometer attached to a stereoscopic microscope. Pictures were taken by a digital camera Canon SD3500 IS.

All statistical tests were performed using Analysis Tool (Descriptive Statistics) with a confidence level for mean of 95% in the Microsoft Excel 2007.

Fig. 1. Map showing provinces and cities studied.
Рис. 1. Карта изученных провинций и городов.

Results and Discussion

Nest sites. Throughout Vietnam, *P. olivaceus* was widely distributed from North to South region, from the lowland to the highland areas (from 0 m altitude at Xuan Thuy National Park, Nam Dinh Province to more 1000 m at Da Bac District, Hoa Binh Province; Moc Chau District, Son La Province; Sapa District, Lao Cai Province; Muong Nhe District, Dien Bien Procince). Its nests were found in various sites such as in abandoned houses, beneath the eaves, inside houses, under rocky cliffs or on trees (also see Table 1). These nest sites are similar to those of two *Polistes* species studied previously such as *P. snelleni*, *P. biglumis* [Yamane, 1969].

These nest sites were often built at airy and wide places. It was rarely to see nests at gloomy and damp places. This can be suggested that before the nest foundation the founder carefully choose the nest site as well as calculates for opportune to develop the nest.

On the trees, the nest site was fairly secret and was able to avoid effect of wind or rain. The nests were

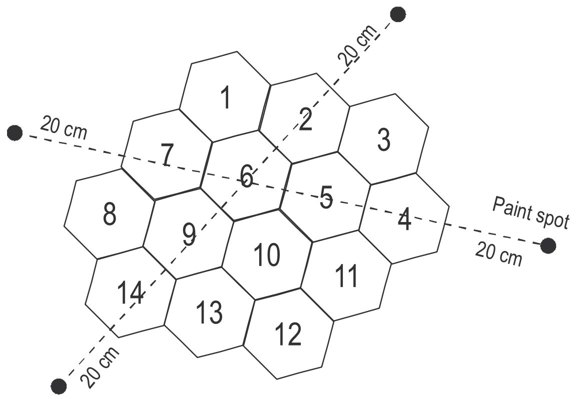

Fig. 2. Cells of the nest numbered.
Рис. 2. Нумерация ячеек гнезда.

usually hung on twigs of the tree, and the height of the nest depended on that of trees but about only 1–5 m from the ground. Trees frequently chosen for nesting were Bananas (*Musa sapientum*) (directly stuck on the veins of under surface of drying old leaves folding up tree trunk), Sea almond (*Terminalia catappa*), or Malayan banyan (*Ficus microcarpa*). The age of trees also has an important relation to complete life cycle on the nest (from founded to declined nest). This is one of the reasons that the nest of *P. olivaceus* is seldom built on short day cultivated plants.

In case of rocky cliffs, the nest was built along road sides and was not almost defended. Most nests in this site were not directly exposed to insolations during the daytime. Hence the temperature at the nest was considerably raised when rocks absorbed the heat from the sun.

Into houses, the nest was built beneath the ceiling, about 3– 4 m from the floor (depending on height of the ceiling). Only two of 34 collected nests were found at the third floor, with an altitude of about 12 m. At this site the nest is clearly exposed, and avoids almost effects of rain or wind. However, people are sometime target of offensive of this wasp when any activity moves and comes too close its nest.

Fig. 3. Auxiliary petiole of the nest.
Рис. 3. Вспомогательный стебелёк гнезда.

In abandoned houses and beneath the eaves of houses, most nests of *P. olivaceus* were found (17/34 nests). At these two sites, the nest of *P. olivaceus* is not influenced by most activities of people.

From data of Table 1, it clearly showed that sites where minimum effects such as activities of humans, sunshine, rain, or wind to the nest were often chosen to build the nest by the queens of *P. olivaceus*. Or in other words, sites where nests are attached to are no moves (28/34 sites). In case of the nests on trees, when the wind is high eggs, larvae, or pupae are maybe thrown the nest out or the nest is maybe broken by the impact of adjacent branches.

Both nest petiole and nest axis were vertically made. Correspondingly, the founding queens always trended to make nests under horizontal surfaces (under ceiling, on twigs, beneath the eaves, or under cliffs).

Nest architecture. *Materials and colour*. Nest materials of *P. olivaceus* probably collected from weathered surfaces of herbs and woods. Slivers were mixed saliva into its mouth before for cell construction. The nest was principally grayish. Particularly, to petiole, it was made by special materials instead of using slivers. These special materials maybe were mixture of vegetable saps (not yet known) with its saliva. So this petiole was very hard and was black colour like tar.

Petiole. Column-like, 7–13 mm long (an average 10.82 ± 2.21 mm) and 3–5 mm thick (an average 3.76 ± 0.78 mm) (table 1), attached to the center of upper surface. Time to complete the petiole was about 1–2 days before emergence of the first cell. It seems to have the forecast to nest development that most nests that founding queens leave early have a short petiole (7–9 mm (11 nests)). To *Polistes* wasps in general, the nests vary in architecture from single serial arrangement of cells suspended from a single petiole (*P. goeldii*) to large horizontal combs supported by multiple petioles *P. fuscatus* (Downing et Jeanne 1983). Jeanne (1975) suggested that the function of the narrow petiole is to restrict entry by ants and that is thus represents a good site for efficient deposition of a glandular ant repellent. To *P. olivaceus*, however, depending on the nest size and nest site that it could make one or two auxiliary petiole(s). This auxiliary petiole was to help the firmed nest and was always smaller than the main petiole (Fig. 3).

Comb. Always concentric, horizontal and as a rule, directed downward. The width of the comb was variable from 24–152 mm, an average 76.23 ± 42.11 mm (table 1). The height of the comb depended also on the development of nest, ranged from 30–90 mm, an average 58.4 ± 24.11 mm. The thickness of the petiole has close relation with the width of the comb as well as cell number of the comb. The bigger the comb, the thicker the petiole and vice versa. In other words, since the comb is bigger it needs a thicker petiole to prop up weight of the nest.

Cell. Taken 3–5 days to complete in solitary stage (only one the queen), and 0.5–0.8 days in emergent stage (many workers). Wall of the cell was of 0.09–

Table 1. Characteristics of the nest of *P. olivaceus*
Таблица 1. Параметры гнёзд *P. olivaceus*

Nest No.	Life stage	Size of petiole (mm)		Size of comb (mm)		Size of cell (mm)			The number of petiole	Nest site
		L	T	H	W	H	W	T		
1	SS	9	4	31	25	26.61	5.43	0.10	1	Beneath the eave
2	SS	7	3	30	32	27.02	5.38	0.10	1	Beneath the eave
3	SS	8	3	31	26	26.62	5.44	0.10	1	Beneath the eave
4	SS	13	5	31	33	27.12	5.44	0.09	1	Beneath the eave
5	SS	7	3	31	27	26.74	5.38	0.10	1	Beneath the eave
6	SS	12	4	31	42	27.03	5.40	0.10	1	Beneath the eave
7	ES	9	3	31	39	26.67	5.37	0.10	1	Beneath the eave
8	ES	9	3	31	42	26.68	5.40	0.10	1	Beneath the eave
9	ON	7	3	32	28	26.88	5.41	0.10	1	In abandoned house
10	ES	13	5	87	124	26.87	5.43	0.10	1	Inside of house
11	ON	13	4	86	114	27.04	5.44	0.10	1	On tree
12	ON	9	3	56	54	27.21	5.43	0.10	1	On tree
13	ES	12	5	87	145	26.89	5.43	0.10	2	Beneath the eave
14	ES	13	4	56	86	27.09	5.44	0.09	1	On tree
15	ES	13	4	55	48	26.87	5.40	0.10	1	Beneath the eave
16	ON	13	4	87	128	27.11	5.40	0.10	1	Inside of house
17	ES	13	5	55	101	26.91	5.38	0.09	1	In abandoned house
18	VN	9	3	56	44	27.10	5.38	0.10	1	On tree
19	ES	13	5	88	109	26.77	5.40	0.10	1	In abandoned house
20	ES	13	3	88	112	26.66	5.40	0.09	1	Under rocky cliff
21	ES	10	3	32	44	27.07	5.43	0.10	1	Under rocky cliff
22	ON	10	3	55	136	26.79	5.42	0.10	1	In abandoned house
23	ON	10	4	55	68	27.13	5.42	0.09	1	Under rocky cliff
24	ES	13	4	55	88	26.76	5.44	0.09	1	Under rocky cliff
25	ES	12	4	57	59	27.14	5.43	0.09	1	Inside of house
26	VN	10	4	56	77	27.12	5.40	0.09	1	Inside of house
27	VN	7	3	33	24	27.00	5.37	0.10	1	On tree
28	ES	13	5	87	120	26.60	5.37	0.10	1	Beneath the eave
29	ON	8	3	33	33	26.83	5.43	0.10	1	On tree
30	ES	11	5	87	152	26.87	5.41	0.10	1	Under rocky cliff
31	ON	13	4	88	147	26.98	5.38	0.10	1	In abandoned house
32	VN	11	3	89	68	27.00	5.38	0.10	1	Under rocky cliff
33	ON	13	4	90	112	26.75	5.37	0.10	3	Under rocky cliff
34	VN	12	3	89	105	26.59	5.37	0.09	1	In abandoned house
Min–max Means		7–13 10.82 ± 2.21	3–5 3.76 ± 0.78	30–90 58.41 ± 24.11	24–152 76.23 ± 42.11	26.59–27.21 26.90 ± 0.19	5.37–5.44 5.41 ± 0.02	0.09–0.10 0.09 ± 0.004		

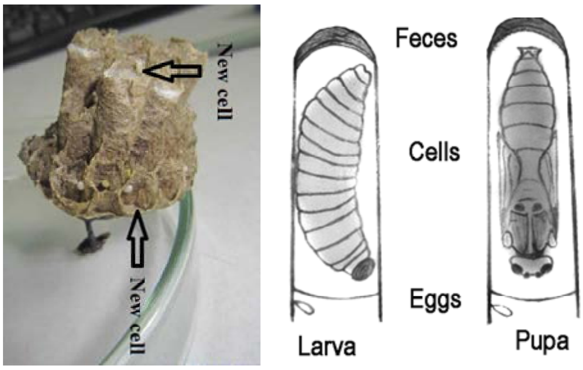

Fig. 4. New cell sites built and egg sites laid.

Рис. 4. Новые построенные ячейки и ячейки с отложенными яйцами.

0.10 mm thick, an average 0.09 ± 0.04 mm. Distance between opposite sides of a hexagon relatively constant regardless of position (= width) ranged from 5.37 to 5.44 mm, an average 5.41 ± 0.02 mm. The height of the cell ranged 26.59–27.21 mm, an average 26.90 ± 0.19 mm (table 1).

New cells were built by the following two sites: beside old cells (from the edge of comb), and beyond the top of cocoon (Fig. 4).

Size of development stages. There are two development stages in lifespan of *P. olivaceus.* They are immature stage (including egg, larva, and pupa) and mature stage (including adults: the queen, worker, and male) (table 2).

Immature stage: *Egg* (Fig. 5a): was ivory white, slightly curved and narrowed at the base. The size was 2.1–2.3 mm in length, an average 2.19 ± 0.08 mm; 0.8–1.0 mm in width, an average 0.92 ± 0.07 mm.

Larva (Fig. 5.b–c): was 1.90–19.1 mm in length, an average 8.95 ± 5.76 mm; and 0.9–6.6 mm in width, an average 3.31 ± 1.76 mm. Because there was a mistake in measurement process of the width of the cephalic capsules, the larva instars were not determined. But with measurement of 293 individuals of larvae, it can be grouped in the following five levels: the first is 2.5–3.0 mm in length and 9–12 mm in width; the second 3.2–4.5 and 17.0–22.0 mm; the third 7.0–8.5 and 2.8–3.5 mm; the fourth 12.1–14.0 and 40–50 mm; and the last 17.0–19.0 and 5.5–65 mm. This can be implied that the larva of *P. olivaceus* has five instars.

Pupa (Fig. 5d): was 19.5–22.4 mm in length, an average 21.02 ± 0.81 mm and 5.1–5.8 mm in width, an average 5.43 ± 0.18 mm.

Mature stage: *the queen* (Fig. 5f): the body is extensively yellow or orange in colour and few black markings on the thoracic sutures. Thoracic sterna and coxae are yellow. The queen was a medium large wasp with the size ranged 23.0–25.4 mm in length, an average 24.3 ± 0.73 mm; and 5.3–6.4 mm in width, an average 5.82 ± 0.29 mm.

Worker (Fig. 5e): was with colour similar to that of queen and the size ranged 16.9–20.5 mm in length, an average 19.3 ± 0.75 mm; and 3.6–4.6 mm in width, an average 4.23 ± 0.23 mm.

Male: was with the size from 27.1–28.6 mm (n = 3) in length and 7.1–7.5 mm (n = 3) in width. Male has thus the

Table 2. Size of developmental stages

Таблица 2. Размер стадий развития

Development stages		*P. olivaceus*	
		Vietnam	Hong Kong
Egg	Length	2.1–2.3 (2.19 ± 0.08, n=68)	
	Width	0.8–1.0 (0.92± 0.07, n=68)	
Larva	Length	1.9–19.1 (8.95 ± 5.78, n= 293)	
	Width	0.9–6.6 (3.31 ± 1.76, n= 156)	
Pupa	Length	19.5–22.4 (21.02 ± 0.81, n= 69)	
	Width	5.1–5.8 (5.43 ± 0.18, n= 69)	
Worker	Length	16.9–20.5 (19.3 ± 0.75, n=73)	14–17
	Width	3.6–4.6 (4.23 ± 0.23, n= 73)	
Queen	Length	23–25.4 (24.30 ± 0.73, n= 25)	16–18
	Width	5.3–6.4 (5.82 ± 0.29, n=25)	
Male	Length	27.1–28.6	18–20
	Width	7.1–7.5	

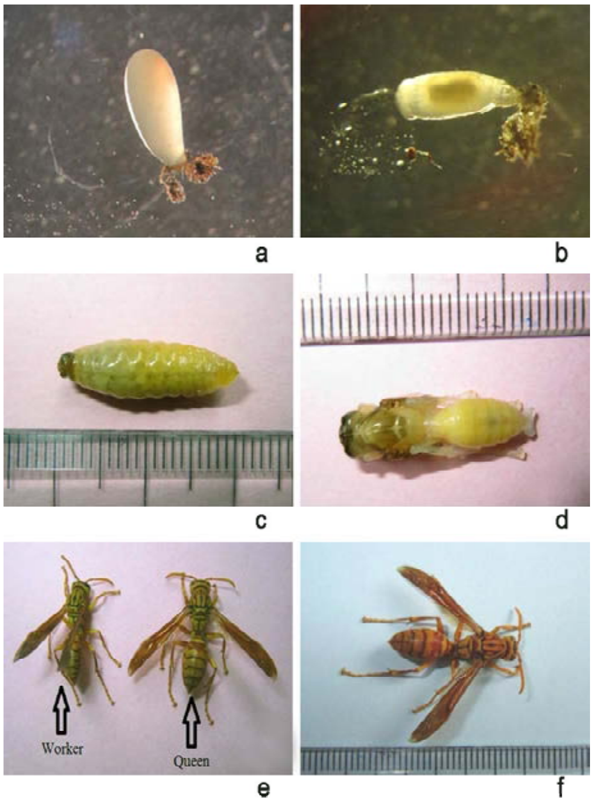

Fig. 5. Development stages of *P. olivaceus*. 1 — egg, 2–3 — larva, 4 — pupa, 5 — worker and queen, 6 — queen

Рис. 5. Стадии развития *P. olivaceus*. 1 — яйцо, 2–3 — личинка, 4 — куколка, 5 — рабочая и королева, 6 — королева.

Table 3. Compositions of nests of *P. olivaceus*
Таблица 3. Состав гнезд *P. olivaceus*

Nest No.	Total of cells	Egg	Larva	Pupa	Adult	Total of empty cells
7	34	16	11	4	3	3
8	37	15	12	5	3	5
10	278	19	49	13	24	197
13	311	9	48	10	30	233
14	89	40	31	11	9	7
15	55	24	19	7	7	5
17	137	48	64	15	14	10
19	225	28	39	11	20	147
20	176	51	69	13	17	43
21	40	17	12	5	4	6
24	93	33	41	10	11	9
25	65	29	22	9	7	5
28	262	22	38	10	24	192
30	378	6	19	4	33	349

biggest size. The size of workers is always smaller than that of the queen. Barthelemy [2009] produced size of worker, queen, and male of this species in Hong Kong as follows: 14–17, 17–18, and 18–20 mm respectively. So in Vietnam size of worker, queen, and male is bigger than that of these the same castes in Hong Kong.

Colony size. Colony size is small to medium. The biggest colony size in present study was 33 individuals (nest No. 30). Nests (No. 10, 14, 17, 19, 20, 24, 25, and 28) were being in the emergent stage with many eggs, larvae, and pupae. This can suggest that the colony size of these nests will be much bigger than that of nest No. 30 (more than 33 individuals) and is also able to more than 50 individuals (table 3). Barthelemy [2009] stated that small to medium colonies, rarely exceeding fifty individuals in Hong Kong, although bigger colonies can be found. This present study also agrees with his studies.

Nest protection habits of the queen. As what mentioned in introduction section, *P. olivaceus* is one of the defensive *Polistes* wasps. It will attack anything to come close its nest by its sting. In an observation produced on one nest at Nghia Do, the founding queen perched upon the nest and powerfully clapped the wings with its body being directed towards a house lizard coming to close its nest, and this house lizard had to run away. Also at this place, a flock of black and a flock of red ants were observed moving across near its nest but no any invading action. This shows that this wasp secretes an ant-repellent substance. According to study of Downing and Jeanne [1983], the ant repellent substance was secreted by a gland (called van der Vecht's gland) located in the VI abdominal sternite. In many species of *Polistinae* tufts of hair were observed close to the anterior edge of the VI abdominal sternite in female, serving as storage and as an applying brush, whose function is spreading the ant repellent secretion. In case of *P. olivaceus*, it also secretes this substance around its nest to drive away the flocks of ant. To some snout moths, however, this substance has no effect. A clear evidence to this was showed in a late paper of Pham [2014a, b] (the snout moth *Hypsopygia postflava* was a parasite on the nest of *P. olivaceus*). The nest of *P. olivaceus* collected at Nghia Do, Cau Giay late February, 2014 had appearance of the parasitic moth that it was being in the hibernant stage. This implies that this snout moth had parasitized on the nest of *P. olivceus* in 2013 when the immature stage had been present on the nest.

Cycle of colony. By observation in a period of 4 years, the annual cycle of *P. olivaceus* can be divided into five stages as follows: post-hibernant stage, solitary stage, emergent stage, pre-hibernant stage, and hibernant stage.

Post-hibernant stage. This stage is from hibernaculum departure to nest building, and it lasted about 7 days. Depending on the every year temperature the founding queens are able to appear soon or late. Or in other words the appearance of the queens does not depend on time (late March, early April, or mid April) that it depends on the temperature level. The founding queens usually appear in the beginning of summer, with a temperature level of over 20°C. The results of the observation showed that two queens appeared from 27–31th March, 2011, three from 15–23th April, 2012; six from 29th March to 5th April, 2014 with temperature 24–27 °C, 22–25 °C, 22–29 °C respectively. Pham [2014a]reported that wasps left their hibernaculum 22 – 27th March, 2014 with the temperature level of above 20 °C. No detailed observation was made on behaviors of this species in the post-hibernant stage. 3–5 days after appearance of the founding queens in the field, no

Table 4. The number of nest-left times of the queen
Таблица 4. Количество вылетов королевы из гнезда

Nest number	Stage					
	Eggs+Larvae		Eggs+larvae+Pupae		Eggs+ Larvae+Pupae+Workers	
	Time	Total of cells	Time	Total of cells	Time	Total of cells
1	5–6 5.3	8	-	-	-	-
2	6–7 6.7	18	-	-	-	-
3	6.0 6.0	14	-	-	-	-
4	5–6 5.7	12	7–8 7.3	15	4–5 4.7	16
5	2–3 2.7	7	6–8 7.0	12	4–5 4.3	18
6	-	-	8–9 8.3	20	3–4 3.7	23

new nest was found. It means that the founding queens mainly found the food instead of nest building. Because they need a lot of energy to compensate for the energy that lost in all hibernant stage and also to prepare for the solitary stage.

According to study of Yoshikawa [1963] on *P. jadwigae* in Osaka, the post-hibernant stage begins in middle March, lasting about four weeks until middle April. Yamane [1969] on two *Polistes* wasps *P. snelleni* and *P. biglumis* stated that the founding queens appear in late April probably about two or three weeks after the disappearance of the snow cover. The nest is started in early May in Hakken-zan and in late May in Tsunejizawa and Bankei. Delayed appearance of founding queens and short post hibernant stage are remarkable in Sapporo, apparently caused by severe climatic conditions.

To polistine wasps, climatic conditions (mainly the temperature) are hence causes of delayed or premature appearance of the founding queens.

Solitary stage. This stage is from nest building to emergence of first worker, and it lasted about 50 days. Unlike in most polistine wasps studied in Neotropical zone such as *P. simillimus*, *P. versicolor*, and *P. lanio* Asiatic polistine species only found their nest by a single female, and it is called haplometrotic foundation. These species can here be mentioned such as *P. snelleni*, *P. biglumis*, *P. chinensis antennalis*, and *P. fadwigae*. In six nests observed and 14 nests collected in the present study, no foundation by more than one female or pleometrotic foundation.

After a female (a founding queen) chose a fit site it started to build its nest. After about 2–3 days for completing the petiole, the first cell was emerged. The number of nest-left times of the queen for foraging food, drinking water, or taking nest materials depended on brood and the number of cells (table 4). In eggs + larvae stage (the first stage), the queen left the nest 2–7 times/day; in eggs + larvae + pupae stage (the second stage), 7–9 times/day; and eggs + larvae + pupae + workers stage (the third stage), 3–5 times/day. In the second stage the number of nest-left times of the queen is, hence, the highest in comparison with that of two the other stages. Because in this stage, the queen has to do many things such as laying eggs, nest building, foraging food and water, rearing brood when the number of cells and brood are increasing. To the third stage, the number of nest-left times of the queen decreases because the queen cedes some roles to workers such as foraging food, nest building, rearing brood.

The nest-left time of the queen varies and depends on her purpose (with 164 observation times). If she came the nest away for taking water it was only 2–3 minutes, but for foraging food or taking nest materials it was a maximum of about 75 minutes (observed on the nest No. 3 in the first stage).

The development time of the immature stages was eggs ranging 6–7 days, an average 6.5 ± 0.50 days; larvae 26–28 days, an average 27.1 ± 0.67 days; and pupae 13–15 days, an average 13.8 ± 0.80 days. The total period (from the laid egg to the emerged adult) was from 45–50 days, an average 47.5 ± 1.99 days. These values in comparison with those obtained for Nearctic, Neotropic, and Palearctic species (table 5) showed that *P. olivaceus* had the shortest egg stage. The development time of larval stage of *P. olivaceus* was very similar to that of Neotropic species (*P. erytrocephaius* and *P. simillimus*), and the development time of pupal stage of *P. olivaceus* was also very similar to that of Nearctic species (*P. exclamans*) and Palearctic species (*P. dominulus*). The total of development time of the immature stage of *P. olivaceus* was close to that of Nearctic species (*P. dorsalis*, *P. exclamans*, and *P. fuscatus*) and different from that of Neotropic species (*P. cinerascens*, *P. erythrocephalus*, *P. lanio lanio*, *P. simillimus*, and *P. versicolor*) and Palearctic species (*P. dominulus*). This difference may be expounded as the difference in local climate, natural habitat, food available, foraging efficiency, or natural enemy.

The hatched egg rate ranged from 82.5–87.8 %, an average 84.7 % (n = 198), the survivorship rate of larva and pupa was 80–83.3 %, an average 81.9 % (n = 230), and 87.5–100 %, an average 95.8 % (n = 42) respectively (Fig. 6). To *P. simillimus*, Giannotti (1997b) showed a rate of mortality of 18.2 % for the egg stage, of 50.7 % for the larva stage, and of 11.3 % for the pupa stage.

Table 5. Comparative data on developmental time of the immature stages among some *Polistes* wasps
Таблица 5. Сравнительные данные по времени развития незрелых стадий у некоторых ос *Polistes*

Fauna region	Species	Egg	Larva	Pupa	Total
Indo-Australia	*P. olivaceus*	6.5	27.1	13.8	47.5
Nearctic	*P. dorsalis*	14.0	17.2	17.4	48.6
	P. exclamans	13.4	19.7	14.7	47.8
	P. fuscatus	13.0	15.3	22.2	47.8
Neotropic	*P. cinerascens*	13.0	23.7	22.2	58.6
	P. erythrocephalus	17.1	26.6	23.8	67.5
	P. lanio lanio	20.8	40.6	22.6	87.5
	P. simillimus	10.2	25.3	18.7	51.9
	P. versicolor	10.0	20.9	18.4	49.4
Palearctic	*P. dominulus*	10.0	16.0	13.0	39.0

These can be understood as the survivorship rate of egg, larva and pupa stage are 81.8 %, 49.3 %, and 88.7 % respectively. So the survivorship rate of immature stage of *P. olivaceus* is higher than that of *P. simillimus*. To the egg stage, eggs either were lost by falling cells out or were eaten by the queen herself. However, eggs that were fallen cells out were unusual to see because eggs are often attached very solid to the wall of cells. Most of eggs were eaten by the queen as a form to take nourishment or to clear rotten eggs. For both larva stage and pupa stage, either they were eaten by the queen (it is as a form to substitute for foraging activity when climatic conditions are unfavorable) or they were mainly caused by a parasite of other insects. In the case of larvae or pupae parasitized the queen also ate them as an activity to clear the nest or to avoid spread of disease or of parasites.

Because of many works that the queen has to do as nest building, caring brood, laying eggs, foraging food, protecting nest, the rate of cell construction of the queen in this stage was 0.3 cells/day. The ratio 0.8 cells/day for the pre-emergence stage (only foundressees) and 7.4 cells/day for the emergence stage were reported to *P. simillimus* by Giannotti (1997b). There is clearly a difference in the rate of built cell per day between these two species. This difference is due to the number of the foundresses. Whereas this number is two to *P. simillimus*, *P. olivaceus* is only one. When there was not any cocoon, the queen built the peripheric cells of the nest, and immediately laid one egg in. These peripheric cells were not, however, fully completed immediately, they were gradually completed following growth of larvae. When cocoons emerged, the queen built both the peripheric cells and cells contained pupae (in this case, it is called simultaneous use of a single cell by two successive broods) (Fig. 4). To cocoon cap cells, however, it was usually 3–4 days after cocoons emerged the queen laid eggs in because it is as a suitable calculation for emergence of workers.

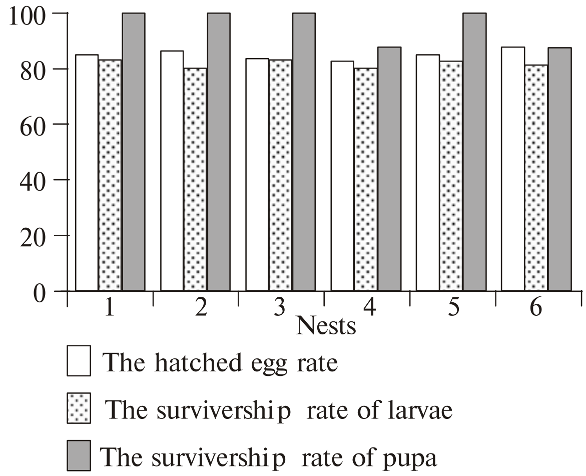

Fig. 6. Survivorship rate of the immature stages of *P. olivaceus*.
Рис. 6. Выживаемость незрелых стадий *P. olivaceus*.

In this stage, in days with severe weather conditions (high temperature and low humidity) the queen often left the nest to take water. Water was put into some cells in form of mall drops that they were not able to fall cells out. And the queen sometime beat its wings to cool the nest.

Emergent stage. This stage is from emergence of first worker to emergence of last worker, and it lasted about 170 days. Many questions have not yet been answered such as the lifespan of workers? the death of queen? roles of workers, the queen, males and young females? foraging habits of workers? and so on. Obtained observations in this stage are as follows: by six nests observed at Nghia Do, Cau Giay, Hanoi in 2012, the first workers emerged from mid to late May with 6/6 nests having more than 10 cells. After emerged workers, the queens were seldom to join for cell construction and to go out for foraging food. The proofs of these are the number of nest-left times of the queen reduced from maximum of 9 times in the solitary stage to maximum of 5 times in this stage (see Table 4), and workers often

Table 6. Hibernaculum of *P. olivaceus* and other wasps
Таблица 6. Зимняя спячка *P. olivaceus* и других ос

Species	Hibernaculum	Source
P. olivaceus	The nest, under the surface of the ground, and slits between tree trunk and tree bark	Pham 2014a and the present paper
P. annularis	Crevices of rocks	Rau 1942
P. chinensis, and *P. jadwigae*	Vacancies under roof tiles and above the ceiling	Yoshikawa 1963
P. dominulus	Former nest sites	Pardi 1951
North American *Polistes*	Rotting woods and under the surface of the ground	Michener & Michener 1951

brought food for the queen. The main role of the queens was to lay eggs and to lead other castes. Taking care of brood was almost to be ceded to workers.

One nest collected at Dong Minh Commune, Tien Hai District, Thai Binh Province in 22 June, 2013 without the queen, pupae or any sign of cells that contained cocoons. This nest was with 43 cells, including 7 workers, 20 eggs, and 12 larvae. The colour of this nest is darker than that of other nests. Two nests near to this nest were collected with all of queens and workers. It is affirmed that this nest is reused and maybe females from one or all two adjacent nests or from other nests come in this orphaned nest to found a new colony. It means the females are reproductive but the queen can have using some substance or dominant activities to inhibit reproduction of these females on the same nest. When these females escape the nest they can absolutely oviposit.

Three males emerged on the nest from mid to late June. One was on the nest No.13 in June 20, 2012, one on the nest No.19 in June 18, 2013, and one on the nest No.28 in June 21, 2014. Because the size of males is bigger than that of workers, cells that contain the male pupae are higher than other cells and are visible. These cells were usually sited at the centre of the comb.

The decline stage lasted from mid September to late October. In this stage, because of the death of the queen, neither the cell was built nor egg was laid, and many workers died.

Pre-hibernant stage. This stage is from emergence of last worker to hibernation of the wasps, and it lasted about 50 days (from late October to early December). In this stage, the nest was without any egg, larva, or pupa, and the number of wasps also reduced because of death of many workers. Activities of the wasp entirely depended on weather conditions because this time the temperature was being down. In low temperature days, wasps stayed the nest and did not almost move. Restricting movement of wasps may be to save energy for the hibernant stage. When it was warm and sunny they would leave the nest either for taking food and water or for having a warm. The number of nest-left times of wasps was just 1–2. The observation did not record for any case of wasps back the nest with food or water.

Hibernant stage. This stage is from starting hibernation to leaving hibernaculum of the wasps, and it lasted about 80 days. By five nests observed (three at Nghia Do, Cau Giay; two at Co Nhue, Bac Tu Liem, Hanoi), the wasps started to leave the nest from the beginning of December to the end of January next year. They found and stayed their hibernaculum until late March or early April [also see Pham 2014a]. Its hibernacula were found on the nest, in a rotten tree trunk 15cm under the surface of the ground, or in slits between tree trunk and tree bark. In other *Polistes* species, hibernant sites are also reported as showed in Table 6.

The colony cycle of *P. olivaceus* lasts about 8–10 months (average 270 days). The colony cycle of some other *Polistes* species studied regarding lifetime of colonies reported as follows: *P. cinerascens* 199.3 days (from 100 to 338 days) [Giannotti, 1997a], *P. versicolor* 154.8 days [Gobbi, Zucchi, 1985] or 177.0 days [Gobbi et al., 1993], *P. simillimus* 277.0 days [Gobbi et al., 1993], and *P. lanio lanio* 388 days [Giannotti, Machado, 1994b]. The colony cycle of *Polistes* wasps is hence much dependent on habitats, climatic conditions, food resources, or natural enemies (predators and parasitoids).

Acknowledgments

The author is grateful to Mr. Nguyen Van Thanh, Mr. Tran Anh Tuan, Mrs. Nguyen Thi Linh, and Mrs. Nguyen Thi Lan Anh, 19 Group, Nghia Do Precinct, Cau Giay District, Mr. Pham Quang Tuan and Mr. Le Van Nhan, Co Nhue 1 Precinct, Bac Tu Liem District, Hanoi Capital, for providing facilities to carry out observation at their home; also to Mrs. Nguyen Thi Thuy, Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Hanoi, Vietnam (IEBR) for her help in creating favorable conditions for study.

References

Barthelemy C. 2009. A provisional identification guide to the social vespids of Hong Kong (Hymenoptera: Vespidae) http://www.insectahk.com/HK-Vespids.Rev.M%20web.pdf (2015.03.26).

Boiiartg E. 1942. Notes on some feeding and hibernation habits of California *Polistes* // The Pan-Pacific Entomologist. Vol.18. No.1. P.30–31.

Carpenter J.M. 2003. On “Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps” // American Museum Novitates. Vol.3389. P.1–20.

Cervo R., Zacchi R., Turillazzi S. 2000. *Polistes dominulus* (Hymenoptera, Vespidae) invading North America; some

hypothesis for its rapid spread // Insectes Sociaux. Vol.47. P.155–157.
Downing H.A., Jeanne R.L. 1983. Correlation of season and dominance status with activity of exocrine glands in *Polistes fuscatus* (Hymenoptera: Vespidae) // Journal of Kansas of Entomological Society. Vol.56. No.3. P.387–397.
Gadagkar R., Joshi N.V. 1982. Behabiour of the Indian social wasp *Ropalidia cyathiformis* on a nest of separate combs (Hymenoptera: Vespidae) // Journal of Zoology of London. Vol.198. P.27–37.
Gamboa G.J., Grieg E.I., Thom M.C. 2002. The comparative biology of two sympatric paper wasp, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae) // Insectes Sociaux. Vol.49. P.45–49.
Giannotti E. 1997a. Biology of the Wasp *Polistes (Epicnemius) cinerascens* Saussure (Hymenoptera: Vespidae) // Anais Da Sociedade Entomológica Do Brasil. Vol.26. No.1. P.61–67.
Giannotti E. 1997b. Notes on the biology of *Polistes simillimus* Zikán (Hymenoptera, Vespidae) // Annals of the Society Entomology of Brasil. Vol.26. P.41–49.
Giannotti E., Machado V.L.L. 1994a. The seasonal variation of brood stages duration of *Polistes lanio* (Fabricius, 1775) (Hymenoptera, Vespidae) // Naturalia. Vol.19. P.97–102.
Giannotti E., Machado V.L.L. 1994b. Colonial phenology of *Polistes lanio lanio* (Fabricius, 1775) (Hymenoptera, Vespidae) // The Revista Brasileira de Entomologia. Vol.38. P.639–643.
Giannotti E., Mansur C.B. 1993. Dispersion and foundation of new colonies in *Polistes versicolor* (Hymenoptera, Vespidae) // Annals of Society Entomology of Brasil. Vol.22. P.307–316.
Gobbi N., Zucchi R. 1980. On the ecology of *Polistes versicolor versicolor* (Olivier) in southern Brazil (Hymenoptera, Vespidae, Polistinae). I. Phenological account // Naturalia. Vol.5. P.97–104.
Gobbi N., Zucchi R. 1985. On the ecology of *Polistes versicolor versicolor* (Olivier) in southern Brazil (Hymenoptera, Vespidae, Polistinae). II. Colonial productivity // Naturalia. Vol.10. P.21–25.
Gobbi N., Fowler H.G., Chaud Netto J., Nazareth S.L. 1993. Comparative colony productivity of *Polistes simillimus* and *Polistes versicolor* (Hymenoptera: Vespidae) and the evolution of paragyny in the Polistinae // Zoologische Jahrbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere. Vol.97. P.239–243.
Harris A.C. 1979. Occurrence and nesting of the yellow oriental paper wasp, *Polistes olivaceus* (Hymenoptera: Vespidae), in New Zealand // New Zealand Entomologis. Vol.7. No.1. P.41–44.
Hermann H.R., Dirks T.F. 1975. Biology of *Polistes annularis* (Hymenoptera: Vespidae). I. Spring Behavior // Psyche. Vol.82. P.97–108.
Jeanne R.L. 1975. The adaptiveness of social wasps nest architecture // The Quarterly Review of Biology. Vol.50. P.267–287.
Jeanne R.L. 1979. The construction and utilization of multiple combs in *Polistes canadensis* in relation to the biology of a predaceous moth // Behavioral Ecology and Sociobiology. Vol.4. P.293–310.
Jeanne R.L., Morgan R.C. 1992. The influence of temperature on nest site choice and reproductive strategies in *Polistes* wasps // Ecological Entomology. Vol.17. No.2. P.135–141.
Joan E., Strassmann K., Meyer D.C. 1983. Gerontocracy in the social wasp, *Polistes exclamans* // Animal Behaviour. Vol.31. P.431–438.
John M.N. 1971. Nesting habits and nest symbionts of *Polistes erythrocephalus* Latreille (Hymenoptera Vespidae) in Costa Rica // Revista de Biologia Tropical. Vol.18. No.1,2. P.89–98.
Karsai I.Z., Pénzes F., Wenzel J.W. 1996. Dynamics of colony development in *Polistes dominulus*: A modelling approach // Behavioral Ecology and Sociobiology. Vol.39. P.97–105.
Khalifa A. 1953. Biological observations on *Polistes gallicus* L. and *Polistes foederata* Koch, with special reference to stylopization // Bulletin of Entomological Society of Egypt. Vol.37. P.392–401.
Klalin J.E. 1979. Philopatric and nonphilopatric foundress associations in the social wasp *Polistes fuscatus* // Behavioral Ecology and Sociobiology. Vol.5. P.417–424.
Landolt P.J., Jeanne R.L., Reed H.C. 1998. Chemical communication in social wasps // Vander Meer R.K., Breed M., Winston M., Espelie C. (Eds), Pheromone Communication in Social Insects. Westview Press, Boulder. P.216–235.
Liebert A.E. 2004. Ground nesting in the paper wasp *Polistes aurifer* (Hymenoptera: Vespidae) // Insectes Sociaux. Vol.51. P.99–100.
London K.B., Jeanne R.L. 1997. Site selection by a social wasp in a nesting association (Hymenoptera: Vespidae) // Journal of Insect Behavior. Vol.10. P.279–288.
Makino S. 1989. Loss of workers and reproductives in colonies of the paper wasp *Polistes riparius* (Hymenoptera:Vespidae) due to the parasitic wasp *Latibulus* sp. // Researches on Population Ecology. Vol.31. P.1–10.
Miyano S. 1980. Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis*, in Central Japan (Hymenoptera: Vespidae) // Researches on Population Ecology. Vol.22. P.69–88.
Pfenning D.W., Gamboa G.J., Reeve H.K., Shellman Reeve J., Ferguson T.D. 1983. The mechanism of nestmate discrimination in social wasp (*Polistes*, Hymenoptera: Vespidae) // Behavioral Ecology and Sociobiology. Vol.13. P.299–305.
Pham P.H. 2014a. Hibernation on the nest of the paper wasp, *Polistes (Gyrostoma) olivaceus* (De Geer) (Hymenoptera: Vespidae) // Biological forum. Vol.6. No.1. P.116–119.
Pham P.H. 2014b. Biological of *Hypsopygia postflava* (Lepidoptera: Pyralidae), a snout moth parasitic on the nest of the paper wasp *Polistes olivaceus* (Vespidae: Polistes) // Biological forum. Vol.6. No.2. P.90–93.
Pickett K.M., Carpenter J.M. 2010. Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera) // Arthropod systematics and Phylogenia. Vol.68. No.1. P.3–33.
Pickett K.M., Wenzel J.W. 2000. High productivity in haplometrotic colonies of the introduced paper wasp *Polistes dominulus* (Hymenoptera: Vespidae; Polistinae) // Journal of the New York Entomological Society. Vol.108. P.314–325.
Post D.C., Jeanne R.L. 1982. Recognition off former nestmates during colony founding by the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae) // Behavioral Ecology and Sociobiology. Vol.11. P.283–285.
Pratte M., Jeanne R.L. 1984. Antennal drumming behavior in *Polistes* wasps (Hymenoptera: Vespidae) // Zeitschrift für Tierpsychologie. Vol.66. P.177–188.
Rau P. 1942. Temperature as a factor inducing the hibernation of *Polistes annularis* // Annals of the Entomological Society of America. Vol.35. No.1. No.94–96.
Reeve H.K. 1991. *Polistes //* Ross K.G., Matthews R.W. (Eds), The Social Biology of Wasps. Cornell University Press, Ithaca. P.99–147
Richards O.W., Richards M.J. 1951. Observations on the social wasps of South America (Hymenoptera, Vespidae) // Transactions of the Royal Entomological Society of London. Vol.102. No.1. P.1–169.
Shellmann J.S., Gamboa G.J. 1982. Nestmate discrimination in social wasps: the role of exposure to nest and nestmates (*Polistes fuscatus*, Hymenoptera: Vespidae) // Behavioral Ecology and Sociobiology. Vol.11. P.51–53.
Tibbetts E.A., Reeve H.K. 2000. Aggression and resource sharing among foundresses in the social wasp *Polistes dominulus*: testing transactional theories of conflict // Behavioral Ecology and Sociobiology. Vol.48. P.344–352.
Tibbetts E.A. 2007. Dispersal decisions and predispersal behavior in *Polistes* paper wasp 'workers' // Behavioral Ecology and Sociobiology. Vol.61. P.1877–1883.

Turillazzi S. 1980. Seasonal variations in the size and anatomy of *Polistes gallicus* (L.) (Hymenoptera: Vespidae) // Monitore Zoologico Italiano (Nuova Serie). Vol.14. P.63–75.

Vinícius A.A., Moreira J., Lino-Neto J. 2009. Morphology of the male reproductive system of the social wasp, *Polistes versicolor versicolor*, with phylogenetic implications // Journal of Insect Science. Vol.10. P.1–10.

West Eberhard M.J. 1969. The social biology of Polistine wasps // Miscellaneous Publishcations Museum of Zoology, University of Michigan. Vol.140. P.1–101.

Yamane S. 1969. Preliminary observations on the life history of two Polistine Wasps, *Polistes snelleni* and *P. biglumis* in Sapporo, Northern Japan // Journal of the faculty of science Hokkaido University, Series VI, Zoology. Vol.17. No.1. P.78–105.

Yamane S. 1996. Ecological factors influencing the colony cycle of *Polistes* wasps // Turillazzi S., West-Eberhard M.J. (Eds), The Natural History and Evolution of Paper Wasps. Oxford University Press, Oxford. P.73–98.

Yamane S., Okazawa T. 1977. Some biological observation on a paper wasp, *Polistes (Megapolistes) tepidus malayanus* Cameron (Hymenoptera: Vespidae) In New Guinea // Kontyû, Tokyo. Vol.45. No.2. P.283–299.

Yoshikawa K. 1957. A brief note on temporary polygyny in *Polistes jadwigae* Dalla Torre, the first discovery in Japan. Ecological studies of *Polistes* wasps III // Mushi, Fukuoka. Vol.30. P.37–39.

Yoshikawa K. 1963. Three stages relating to hibernation // Journal of Biology of Osaka city University. Vol.14. P.87–96.

Поступила в редакцию 11.11.2015