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Overwintering Habits of the Social Wasp, *Parapolybia crocea* Saito-Morooka, Nguyen & Kojima, 2015 (Vespidae: Polistinae: Ropalidiini)

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Abstract

Overwintering behavior and relatedness between females within an overwintering cluster of social wasps, *Parapolybia crocea*, were examined. The overwintering cluster consisted of both related and unrelated females, including gynes and workers. They interacted frequently and moved between neighboring hibernation sites before entering hibernation.

Intruduction

Insects living in winter exhibit various mechanisms to avoid lethal damage (Asahina, 1991; Sinclair, 1999; Sinclair et al., 2003). For example, overwintering congregations have been observed in ladybirds (e.g., Holecova et al., 2018), honeybees (Owens, 1971), and stink bugs (e.g., Lee et al., 2014). Social paper wasps, *Polistes*, also spend winter in overwintering clusters in temperate regions (e.g., Allen et al., 1982 for *Po. exclamans*; Dapporto & Palagi, 2006; Dapporto et al., 2004, 2005, 2006 for *Po. dominula*; Gibo, 1980 for *Po. fuscatus*; Yoshikawa, 1963; Matsuura, 1980, 2000 for *Po. chinensis*, *Po. japonicus*, *Po. rothneyi* and *Po. jokahamae*; Pham, 2014, 2021 for *Po. orivaceus*). After mating, gynes congregate in hibernation sites, such as fallen bamboo canes (Matsuura, 2000), gaps in artificial buildings (Yoshikawa, 1963; Matsuura, 1980, 2000), nests (Pham, 2014, 2021), and the abundant nests of vespine species (Yoshikawa, 1963; Gibo, 1980; Matsuura, 1980, 2000). They are inactive during winter until the following spring. *Polistes japonicus*, *Po. jokahamae* and *Po. rothneyi* sometimes form interspecific overwintering clusters (Yoshikawa, 1963; Matsuura, 1980, 2000), consisting of thousands of individuals (Matsuura, 2000).

The genus *Parapolybia* belongs to the tribe Ropalidiini, which is mainly distributed in the tropics and subtropics of the Old World but also found in temperate East Asia (van der Vecht, 1966; Saito-Morooka et al., 2015), where it overwinters in clusters (e.g., Matsuura, 2000; Pham, 2016 for *Pa. varia*; Hiura, 1960; Sugiura et al., 1983; Yamane & Maeta, 1985; Matsuura, 2000; Saito-Morooka, 2014 for *Pa. crocea*). The overwintering sites of *Parapolybia* are humid and enclosed, usually tree hollows dug by beetle larvae (Hiura, 1960; Matsuura, 1980; Sugiura et al., 1983; Saito-Morooka, 2014), holes in the ground (Matsuura, 1980, 2000; Yamane & Maeta, 1985), fallen bamboo canes (Matsuura, 2000), and the roofs of human houses (Pham, 2016). The number of individuals in an overwintering cluster usually ranges from dozens to thousands (Matsuura, 1980; Yamane & Maeta, 1985); occasionally reaching approximately 6000 (Matsuura, 2000). In contrast to the interspecific clusters in *Polistes*, the overwintering cluster of *Parapolybia* consists of a single species (Matsuura, 2000; Saito-Morooka, 2014). Therefore, an overwintering cluster of *Parapolybia* species may consist of genetically related individuals.

I observed the overwintering behavior of *Pa. crocea* and investigated the caste of and the genetic relationships among females within an overwintering cluster using molecular markers. The overwintering habits of *Parapolybia* were discussed.

Materials and Methods

Study sites and wasps

Parapolybia wasps were collected from their hibernation sites in the Forest Park of Mito City, Mito (36°25'N, 140°22'E; site A, 17 clusters), Ibaraki Botanical Garden, Naka (36°29'N, 140°26'E, site B, 2 clusters), Forest of Hitachiomiya City, Hitachiomiya (36°39'N, 140°16'E, site C, 1 cluster), and Seminar House of Ibaraki University, Daigo (36°49'N, 140°23'E, site D, 5 clusters) in Ibaraki Prefecture from October 2009 to April 2010; and the Campus of Rissho University, Kumagaya (36°06'N, 139°22'E, site E, 1 cluster) and NOURIN park, Fukaya (36°06'N, 139°17'E, site F, 1 cluster) in Saitama Prefecture in October 2012 (Table 1), Japan.

The wasps were collected in the following four phases (modified from Saito-Morooka, 2014): Phase I, the pre-hibernation phase, in which females temporarily congregate in a nest or on plant leaves from late August to mid-October, shortly after mating and colony break-up; Phase II, the early hibernation phase, in which females alternate between hibernacula from late October to November; Phase III, the late hibernation phase, in which females remain in the hibernaculum from December to March; and Phase IV, the pre-colony founding phase, shortly after the emergence of overwintered females from their hibernacula in April.

The wasps were collected using an insect net during Phase I. In Phases II and IV, females congregating at the entrance of the hibernaculum were collected manually using forceps. In Phases II and III, when females burrowed into the hibernaculum, they were collected by scraping the entrance or creating a hole in a tree and using a long steel wire. The collected wasps were stored in a cool box until dissection. The behavior of the wasps was observed around the hibernaculum trees at site A before the wasps were collected.

Determination of female castes

To determine the presence of fat bodies and sperm, the metasoma of the collected females was dissected in 60 % ethanol under a stereoscopic dissecting microscope within 1 day after collection. The degree of wing wear was also examined. The wings of aged workers were typically heavily worn, whereas the gynes and young workers generally had fresh wings. If the wasps had fat bodies, sperm in their spermathecae, and fresh wings, they were classified as a "gyne", whereas if they had no fat bodies or sperm and worn wings, they were classified as a "worker".

Genetic relatedness between wasps within an overwintering cluster

To estimate the genetic relationships between wasps within the cluster in Phases II–IV, their genetic relatedness was analyzed using microsatellite markers. Genomic DNA was extracted from the wasp legs using standard phenol-chloroform extraction. Voucher specimens were deposited in the Ibaraki University Natural History Collection (IUNH).

Twelve microsatellite loci observed in other polistine wasps were analyzed. Nine microsatellite loci (*Ptab6*, *Ptab148, Ptab149*, *Ptab160, Ptab101*, *Ptab158, Ptab187, Ptab220,* Henshaw, *et al.*, 2001; *Pbe 411*, Strassmann, 1997) had monomorphic or multiple non-specific bands. This made it challenging to identify the target bands (Table 2). Three successfully amplified and polymorphic microsatellite loci (*Ptab188* and *Ptab173*, Henshaw et al., 2001; *RP03*, Ishiguro *et al.* unpublished; Table 2) were used for subsequent genotyping.

For the three loci, each microsatellite fragment was amplified by PCR using forward primers with fluorescence-labeled (6-FAM and VIC dyes, Applied Biosystems, Tokyo, JAPAN) 5′-ends and reverse primers with additional poly-A tail sequences. PCR reactions consisted of template DNA, 0.4 μM of each primer, 0.1 mM dNTPs, 0.15 units of *Taq* DNA polymerase (TaKaRa Bio Inc., Tokyo, JAPAN), and 10× *Taq* buffer in a final volume of 5 μL.

Each amplified fragment was electrophoresed using a fluorescence-labeled size marker (500LIZ size standard, Applied Biosystems) on an ABI Prism 3130x or 310 Genetic Analyzer (Applied Biosystems). Fragment size data were analyzed using GeneScan software (Applied Biosystems). Individual genotyping was performed using GeneMapper ver. 4.0 (Applied Biosystems).

Means of pairwise genetic relatedness between individuals within an overwintering cluster were calculated using Relatedness ver. 5.0.8 (Queller and Goodnight, 1989) based on the genotypes of the individuals. The correlation between cluster size and genetic relatedness was analyzed using R version 4.2.2 (R Core Team, 2022).

Results

Overwintering wasps

In total, 782 females were collected from 27 hibernation sites (*Pa. crocea*, 680 females in 26 hibernation sites; *Pa. varia*, 102 females in 1 hibernation site; Table 1, see also Saito-Morooka, 2014). They were found in hollows on broad-leaf trees (Fig. 1), *Quercus serrata* Murray (17 clusters), *Q. acutissima* Carruthers (1 cluster), and *Prunus jamasakura* Siebold (4 clusters), except cluster A-1, which was found in narrow spaces under woody steps in the forest park (site A). Clusters A-6 and A-7, and A-8, A-15, and A-16 were respectively found in the same tree (Table 1).

In Phase I, 129 females were found in three clusters (14, 16, and 99 females). Females aggregated in the nests. It was uncertain whether these nests were natal. As a result of dissection, ten individuals in three clusters were classified as "workers" (Table 1). The other females had fat bodies, sperm in their spermathecae, and a lack of wing wear, and were classified as "gyne". No males were found.

In total, 503 wasps were collected during the overwintering period (Phases II and III). Solitary overwintering females were observed at sites A, C, and D (Table 1). Most overwintering clusters contained two or more individuals. The number of individuals found in an overwintering cluster varied from 2 to 192 (n = 18; mean ± SD, 30.44 ± 44.98, median = 11). In Phase II, the females congregated near the entrances of the hibernacula (Fig. 1). The number of individuals decreased daily; however, one to several females usually remained near the entrance (Fig. 1). They showed alert behavior by raising their wings when approached by enemies such as ants, spiders, and humans. When the daytime temperature was above approximately 20 °C, they exhibited more alert and aggressive behavior, such as stinging or chasing enemies. They frequently interacted with each other, performing antennation and grooming. Some individuals collected liquid matter from somewhere near their hibernation site and passed it to others by mouth for hydration. Females frequently move between neighboring hibernation sites. As a result of dissection, nine females from three clusters were classified as "workers" (Table 1). No males were found. Cluster D-1, collected from site D, contained 102 females of *Pa. varia*. This cluster was found in the same tree hollow as the hibernation site of *Pa. crocea*. However, these clusters did not mix with other species in the hollow. In other words, each species exclusively used a different space. During Phase III, the females remained inside the hibernaculum and did not appear at the entrance. They were not in a state of incomplete dormancy, and sometimes shook their bodies slightly in their hibernacula.

In total, 48 females were collected during Phase IV. All females had small eggs in their ovarioles, except for three females collected from A-4, A-10, and A-12. Overwintered females remained at the entrance of the hibernaculum shortly after emergence. They dispersed within a few days.

Genetic relatedness among wasps within the cluster

The mean pairwise genetic relatedness *r* of each cluster varied from -0.293 to 0.552 (Table 1). These values were lower than those expected under the assumption that the cluster contained only related individuals (full-sib and/or half-sib, *r* = 0.75, 0.50). The relationship between cluster size and relatedness was not significant (Pearson's *r* = 0.025).

Discussion

Females of *Pa. crocea* overwintered alone or in clusters at their hibernation site, and the size of the clusters varied. Therefore, the females of this species do not always overwinter in clusters. Most studies on the overwintering behavior of *Parapolybia* have reported that they overwinter in large clusters (Hiura, 1960; Sugiura et al., 1983; Matsuura, 1983, 2000; Yamane & Maeta, 1985; Pham, 2016). However, the potential for some individuals to overwinter alone or in a small cluster may have been overlooked because of the difficulty of finding them. *Parapolybia* wasps prefer closed and humid places, such as hibernacula, hollows in *Quercus* trees, bamboo canes, and holes in the ground (Hiura, 1960; Sugiura et al., 1983; Matsuura, 1980, 2000; Pham, 2016). There may be competition with other organisms for the

Figure 1 - Females of *Parapolybia crocea* congregate at the entrance of their hibernation site (Cluster No.A4, Photo 20091105).

Table 1. Number of adult females (gynes and workers) collected at each hibernation site and mean pair-wise relatedness of each cluster.

Species	Site	Cluster No.	Number of females in each phase					Mean Relatedness
			I	II	III	IV	Total	
Pa. crocea	A	1		16 (4)	1		17 (4)	0.185
		2		5		1	6	0.031
		3		1			1	
		4		27 (3)	1	10	38 (3)	0.036
		5		14	41		55	0.094
		6^{+}		9		2	11	0.178
		7^{+}		6 (2)			6 (2)	-0.130
		8^{++}		11			11	0.167
		9		2			2	-0.293
		10		4		6	10	0.206
		11		4			4	0.552
		12		6	18	16	40	-0.115
		13		1			1	
		14		8			8	0.151
		15^{++}		3			3	-0.133
		16^{++}		2		1	3	-0.231
		17		112	76	4	192	0.040
	B	1				1	1	
		2			55	7	62	0.156
	C	1			1		1	
	D	1*		29			29	-0.035
		2		49			49	0.073
		3	14 (3)				14 (3)	
		4		1			1	
	E	1	99 (7)				99 (7)	
	F	1	16 (1)				16 (1)	
Pa. varia	D	5*		102			102	

In total, 680 *Pa. crocea* females were collected from 26 overwintering clusters and 102 *P. varia* females were collected from a single cluster. The number of females categorized as "workers" is shown in parentheses. + and ++ show hibernation site (tree hollow) found in the same tree. * shows that *Pa. crocea* and *Pa. varia* occupied different spaces in the same hollow of the same tree.

hibernaculum, as wasps have shown intense aggression toward foreign animals approaching it. When wasps are removed from hibernacula, spiders nest, and other organisms (frogs or vespine wasps, etc.) use the space (Saito-Morooka, pers. obs.). The overwintering cluster size of *Pa. crocea* may vary depending on the spatial resources available in the hibernaculum.

When females of *Pa. crocea* congregate in a cluster, it usually consists of unrelated individuals. Relatedness between females within a cluster was not correlated with the cluster size. They interacted frequently with each other and moved between neighboring hibernation sites in Phase II, as reported in *Pa. varia* (Pham, 2016). *Polistes dominula* in Europe also forms overwintering clusters consisting of unrelated individuals (Cervo, 2002; Dapporto et al., 2004, 2005, 2006; Dapporto & Palagi, 2006). In other species, overwintering clusters consisting of a large number of females have been observed and are not considered to be derived from a single colony (Rau, 1930 for *Po. annularis*; Pardi, 1942 for *Po. dominula*; Hunt et al., 1999 for *Po. exclamans*). The presence of a natal nest alters the degree of aggression exhibited by *Polistes* females toward other individuals, and aggressive behavior may decrease in the absence of a nest (Starks et al., 1998; Gamboa et al., 1991). Females of *Polistes* and *Parapolybia* hibernate by migrating from their natal nests to hibernation sites. Therefore, at their hibernation site,

Table 2. Twelve microsatellite loci examined in this study.

Locus	References	Amplicons	Number of alleles	*Ho*	*He*
Ptab6	Henshaw et al. 2001	multi			
Ptab101		multi			
Ptab148		mono	1		
Ptab149		multi			
Ptab158		mono	1		
Ptab160		mono	1		
Ptab173		poly	16	0.60	0.60
Ptab187		mono	1		
Ptab188		poly	14	0.64	0.78
Ptab220		multi			
Pbe411	Strassmann et al. 1997	mono	1		
RP03	Ishiguro et al. unpubl.	poly	11	0.36	0.35

"multi", "mono" and "poly" show multiple nonspecific bands, monomorphic bands, and polymorphic bands, respectively. *Ho*: Observed heterozygosity, *He*: Expected heterozygosity.

Polistes and *Parapolybia* gynes may not be aggressive toward conspecifics or discriminate against non-related members of the overwintering cluster.

Interspecific overwintering clusters have also been reported for *Polistes* species (Rau, 1930, 1931 for *Po. annularis*, *Po. fuscatus,* and *Po. rubiginosus*; Matsuura, 1980, 2000; Yoshikawa, 1963 for *Po. japonicus*, *Po. jokahamae,* and *Po. rothneyi*; Pardi, 1942; Dapporto & Pardi, 2006 for *Po. dominula*, *Po. gallicus,* and *Po. nympha*). In this study, overwintering clusters of *Pa. varia* and *Pa. crocea* were found in the same tree hollow of the hibernaculum. However, these clusters did not mix in the hollow. Overwintering clusters of *Parapolybia* always consist of conspecific adults, as reported by Matsuura (2000). They prefer a specific place, such as their hibernaculum, and are aggressive toward other animals, which may explain why they do not form overwintering clusters with other species.

Some clusters of *Pa. crocea* (collected in Phases I and II) consisted of gynes and workers. Whether workers performed labor at the hibernation site was not determined; however, as they were not observed in the late overwintering period (Phase III), it is likely that only gynes overwintered and became queen candidates. There is no evidence for the existence of a critical morphological caste in *Parapolybia*, but this study suggests that a physiologically differentiated caste is present in *Parapolybia*.

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