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Ambient Temperature Influences Geographic Changes in Nest and Colony Size of *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae)

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Abstract

In some *Polistes* wasps, the foundresses build huge nests during the founding phase to improve the thermal condition of these nests. This implies that *Polistes* wasps change their nesting manner in relation to ambient temperature. To test the hypothesis that nest size increases with latitude, colonies of *Polistes chinensis* were collected from 11 locations. Three nest parameters, the number of cells cell length and index of functional envelope, increased with latitude. The number of cells at the northernmost station was 60, which was 1.5 times more than in lower latitudes. Cell length increased by approximately 4 mm from low to high latitudes, indicating that extra-building in *P. chinensis* is remarkable in adding new cells. The number of first broods was not correlated with latitude, whereas the number of second brood increased with latitude because of the numerous cells built at high latitudes.

Introduction

Climate is a major physical factor that determines the geological distributions and life histories of organisms. Some climates generate different ecological traits among populations of the same species (e.g., Angilletta, 2009). Assessing adaptations to different climatic regimes helps us to understand the major selective pressures affecting organisms and to predict their reactions to global and local climatic changes in the environment (Chown, 2001).

In social insects, ambient temperature is an important physical factor that greatly affects insect activity (Heinrich, 1993). Differences in local ambient temperatures lead to differences in nesting activities (Fucini et al., 2014), rate of development of immature stages (Miyano, 1981), and duration of nesting periods (Yamane, 1969), and intra-specific changes have been reported in the genus *Polistes* (Hymenoptera, Vespidae). *Polistes* paper wasps are independent-founding social wasps. A lone foundress builds an exposed nest and nurses the first brood of larvae until worker individuals emerge (pre-emergence period; Reeve, 1991). After eclosion (post-emergence period), the adult individuals increase colony production and produce as many reproductive gynes as possible (reproduction period). The wasps build an exposed comb, in which the construction of new cells and elongation of cells are commonly related to oviposition and the development of larvae, respectively (Delaeurance's law; Delaeurance, 1957). However, species in different climates exhibit different nest-building activities and colony cycles. Yamane (1972) showed that *P. chinensis* foundresses that inhabit the cool northern areas of Japan (nesting duration 3.5–4 months) build many empty cells just before the emergence of the first adults and elongate the cells beyond the lengths of the pupae. In contrast, in the warm areas of Japan, *P. chinensis* nesting activity is consistent with Delaeurance's law, and the nesting duration is approximately 6 months.

A few previous studies have focused on the intra-specific changes in nest size, in relation to nest thermoregulation; i.e., adaptation to low temperature. Yamane & Kawamichi (1975) found that *P. chinensis* foundresses build larger nests in higher latitudinal regions and concluded that numerous and long cells function as air chambers that improve thermal conditions in the brood-rearing area of the nest, similar to the envelope of a vespine nest (functional envelope). This means

that foundresses build more cells for nest thermoregulation to accelerate the development of the first batch of larvae (first brood) during the pre-emergence period. However, the observations were performed in only 2 locations, and thus further study is needed to understand the relationships between climate and the geographic variation in nest size.

In this study, we set 2 goals. The first was to verify whether nest sizes increase geographically from low to high latitudes as Yamane and Kawamichi (1975) predicted. If *P. chinensis* foundresses change their nesting behavior according to ambient temperature, the number and the length of cells should increase with latitude. We collected *P. chinensis* nests at 11 locations across Japan islands and examined the relationship between nest size and latitude. The second goal was to clarify the relationship between latitude and colony productivity. If foundresses invest more resources in nest building in higher latitudinal regions, the numbers of individuals in the first and second broods would be expected to decrease as a tradeoff. We investigated the numbers of individuals in first broods at 6 locations along a latitudinal gradient and calculated an index of functional envelope. In this study, we also discuss the difference in nesting behavior between lower and higher latitudinal areas.

Material and Methods

Nest parameters

In order to determine the latitudinal differences in nest size among the islands of Japan, a total of 168 nests of *P. chinensis antennalis* were collected at the 11 locations shown in Table 1 and Fig. 1. Two nest parameters, the number of cells and cell length, were measured for each nest. The measurement was performed as follows: number of cells, total number of cells was counted for each nest; cell length (mm), maximum value of the longest cell was measured for each nest with a vernier calliper to the nearest 0.1 mm.

Fig 1. Localities where nests of P. chinensis were collected.

Colony composition

Colony composition was investigated at 6 locations (St4, St7, St8, St9, St10, and St11) to determine latitudinal differences among colonies. The content of each cell (egg, young larva, old larva, pupa, or empty) was recorded for all nests immediately after nest collection. For this study, 1st to 3rd instar larvae were classified as young larvae, and 4th and 5th instar larvae were classified as old larvae.

To examine the hypothesis of Yamane and Kawamichi (1975), we defined the index of functional envelope (IFE) to be the nest volume per first brood, i.e., the entire nest volume per total number of individuals in the first brood. Nest volume (ml)

Table 1. Geographic positions and altitudes of localities where *Polistes chinensis* nests were collected.

Station	Locality	Latitude	Longitude	Mean annual temperature (°C)	Date collected	Collector
St1	Fukuoka	33°34'N	130°23'E	17.0	19-21 May 2000	N. Kumano
St2	Tsu	34°43'N	136°30'E	15.9	4-5 June 1997	K. Kudô
St3	Toki	35°21'N	137°11'E	15.8	7-8 June 1997	K. Kudô
St4	Itako	35°56'N	140°34'E	14.5	9-10 June 1998, 10 June 1999	S. Hozumi
St5	Tsurugi	36°27'N	136°37'E	14.3	16-17 June 1997	K. Kudô
St6	Kanazawa	36°33'N	136°39'E	14.6	19 June and 7-8 July 1997	K. Kudô
St7	Tanagura	37°01'N	140°22'E	11.5	8 June 1999	S. Hozumi
St8	Mizusawa	39°08'N	141°08'E	10.7	8 June 1998, 19 June 1999	S. Hozumi
St9	Shichinohe	40°41'N	141°08'E	10.4	4 July 1998, 3 July 1999	S. Hozumi
St10	Kanagi	40°54'N	140°27'E	10.3	4 July 1998, 3 July 1999	S. Hozumi
St11	Okushiri	42°08'N	139°29'E	9.7	21 July 1999, 18 July 2000	S. Hozumi

was estimated as follows: all of the cells were filled with small granular glass beads (diameter 0.1 mm), and the volume of beads was measured with a graduated cylinder to the nearest 0.1 ml (see Yamane et al., 1998). This measurement was repeated 3 times, and the values were averaged.

Statistics

Spearman's rank correlation analysis was used to quantify the relationship between nest and colonial parameters and latitude. All analyses were performed with EZR ver. 1.22 (Kanda, 2013) on a personal computer.

Results

Nest size variation

Table 2 shows the geographical variation in the number and length of cells. Both parameters significantly increased with latitude (Spearman's rank correlation: number of cells, $\rho = 0.6272$, $p < 0.05$; cell length, $\rho = 0.7671$, $p < 0.01$). The number and length of cells were similar (approximately 40 and 22 mm, respectively) from St1 to St8, and the values increased until St11. Cell length also increased significantly, but the range of increase was small; the maximum difference in mean value was 3.9 mm between St10 (23.9 mm) and St1 (20.0 mm).

Table 2. Mean (mean ± SD) number of cells and cell length of *Polistes chinensis* nests collected from 11 localities.

Station	N	Number of cells		Cell length (mm)	
		Mean	Median	Mean	Median
St1	5	38.8 ± 5.3	38.0	20.0 ± 1.4	19.8
St2	14	36.6 ± 5.3	38.5	22.8 ± 1.1	22.7
St3	28	33.0 ± 6.0	33.0	22.0 ± 1.6	22.1
St4	18	37.3 ± 7.6	41.0	21.6 ± 0.9	22.0
St5	10	40.5 ± 7.1	37.0	22.0 ± 1.5	22.8
St6	5	38.0 ± 4.4	38.0	22.7 ± 0.9	21.3
St7	8	39.4 ± 5.4	41.0	21.8 ± 1.7	22.2
St8	20	39.8 ± 6.6	39.0	21.4 ± 0.8	21.5
St9	19	42.9 ± 4.0	43.0	22.9 ± 1.2	23.0
St10	16	45.4 ± 6.8	43.5	23.9 ± 1.4	24.1
St11	25	60.2 ± 15.8	61.0	23.0 ± 2.1	23.5

Colony composition

Table 3 shows the colony composition. The number of individuals in the second brood and the number of empty cells increased significantly with latitude. The number of individuals in the first brood tended to decrease with latitude; however, there was no significant correlation. Nest volume and IFE increased significantly with latitude.

Table 3. Mean numbers of immature individuals (mean ± SD) of *Polistes chinensis* colonies. Index of functional envelope (IFE) was calculated by dividing the nest volume by the number of the first brood. Parentheses indicate median of each value.

	St4	St7	St8	St9	St10	St11	Spearman's rank correlation	
							ρ	Significance
	N=19	N=8	N=19	N=18	N=13	N=24		
First brood	14.6 ± 4.4 (15.0)	14.0 ± 5.6 (15.0)	12.8 ± 5.7 (14.0)	14.2 ± 5.1 (15.0)	12.6 ± 2.3 (12.0)	12.4 ± 4.7 (14.0)	-0.6789	$p=0.1381$
Second brood	19.8 ± 5.6 (21.0)	15.9 ± 5.3 (18.0)	21.1 ± 4.6 (21.0)	23.3 ± 7.0 (23.5)	23.1 ± 8.8 (22.0)	38.5 ± 13.8 (40.0)	0.8407	$p<0.05$
Empty cells	4.1 ± 3.4 (3.5)	7.9 ± 4.9 (6.0)	6.2 ± 4.4 (5.0)	4.6 ± 3.7 (6.0)	9.1 ± 6.8 (8.0)	9.4 ± 6.1 (10.0)	0.8986	$p<0.05$
Nest volume	6.1 ± 1.2 (6.0)	7.0 ± 0.4 (7.1)	6.3 ± 1.3 (6.0)	7.2 ± 1.1 (7.2)	7.2 ± 0.4 (7.2)	8.7 ± 1.5 (8.5)	0.9428	$p<0.05$
Index of functional envelope (IFE)	0.46 ± 0.16 (0.41)	0.59 ± 0.26 (0.49)	0.65 ± 0.45 (0.49)	0.77 ± 0.80 (0.50)	0.59 ± 0.10 (0.58)	0.84 ± 0.42 (0.68)	1.000	$p<0.005$

Discussion

The results of this study confirmed that foundresses in higher latitudinal regions built larger nests, based on the number of cells. The increase in the IFE supports the hypothesis of Yamane and Kawamichi (1975) that the extra cells that enclose first broods may function as thermoregulatory air chambers during the pre-emergence period. Latitude is often closely correlated with ambient temperature, and low ambient temperature is believed to influence the building activities of foundresses.

The building of extra cells is known to increase cell temperatures (Hozumi & Yamane, 2001), which accelerates the rate of development of the first brood. The construction of a large number of new cells not only increases cell temperature but also

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enables the colonies to rear more individuals during the short nesting period. Because cell length greatly affects cell temperature, the thermal effect of the cells could further accelerate development of the immature stages. In this study, the maximum difference in cell length among the locations was only 4 mm. However, even a 4-mm elongation may increase cell temperatures by 1°C when the nest receives solar radiation (Hozumi et al., 2008).

Nest size increased with latitude, whereas the numbers of individuals in the first brood were similar among locations. The numbers of individuals in the first brood were also similar to those reported in other studies, including *P. chinensis* from other areas in Japan (Miyano, 1980; Yamane et al., 1998) and other *Polistes* species (*P. riparius*, Hozumi & Yamane, 2008; *P. biglumis*, Fucini et al., 2014). These results imply that a certain number of first brood individuals (ca. 14) are reared by foundresses during the founding phase, at least in the range of the study areas. However, the numbers of individuals from the second brood and the numbers of empty cells increased significantly with latitude. The foundresses continued to build new empty cells after laying the eggs of the first brood for nest thermoregulation and then began laying eggs to produce as many individuals as possible during the short nesting period. This indicates that *P. chinensis* foundresses at higher latitudes used more resources for nest thermoregulation and production of second broods instead of rearing more first broods.

In conclusion, *P. chinensis* foundresses can adapt to local conditions by altering nest-building activities and colony production, and ambient temperature may significantly influence nesting activities. The building of extra cells is also seen in *P. riparius*, and the building activity (elongation of cells) is influenced by the local ambient temperature (Hozumi & Kudô, 2012). This implies that elongation of cells may occur in *P. chinensis* inhabiting cooler areas. On the building activities of number and length of cells, further studies are needed to assess whether variations in *P. chinensis* populations are due to phenotypic flexibility in response to environmental conditions or to genetic differences.

Acknowledgments

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