

Thermal effect of dark cocoon caps in paper wasp nests (Hymenoptera, Vespidae, *Polistes*): An adaptation to cold climates

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Summary

The paper wasp, *Polistes riparius* that dwells in cold regions exhibits a behavioral habit darkening of the surface of its cocoon caps. In this study, I investigated the thermal effect of the dark cocoon caps by using model nests under outdoor and indoor conditions. Thermoregulation by the foundresses was also observed in the field. The surface color of the cocoon caps in the field nests was brownish and 28% of lightness. Model nests with cocoon caps were prepared and the cocoons were painted in different grades of lightness. When the temperature of model nests was measured in the outdoor condition, the nests with darker caps exhibited higher temperatures than those with the lighter caps. The difference in temperature among the models was higher under windy conditions and lower under calm conditions. The association of higher temperature with darker caps was confirmed by measurements in the indoor condition, and strong wind was observed to decrease the higher temperature induced by the thermal effect of the dark cap. Finally, I concluded that the darkening of the cocoon caps is related to thermoregulation in the cocoon cells and that it is an adaptive measure in cold regions.

Keywords: Paper wasp, lightness of cocoon caps, nest thermoregulation, adaptation to cold climates

Introduction

In insects, the color of its body surface is ecologically important, and it plays an important role in functions such as courtship, mimicry, and thermoregulation. The body surface color has two thermal features, absorption of thermal energy from the sun and emission of heat to avoid overheating of the body. In small insects, such as flies, bees and wasps, the body temperature is easily influenced by changes in the environment, and the body surface color is sometimes determined depending on their habitats (Cloudsley-Thompson, 1999). In hot climate areas, such as tropics and desert, the body surface color of small insects is pale or light to prevent overheating of the body (Cloudsley-Thompson, 1999), while in cold regions such as the Arctic zone, their body is almost black to retain more heat (Danks, 1983). On the other hand, some

nocturnal beetles with a large body mass found in the tropics are almost black and this allows them to emit heat efficiently during the flight (Heinrich, 1995).

However, the role of surface color in thermoregulation of the nests of these animals is not well understood. The nests of some paper wasps (*Polistes*) have been reported to exhibit a thermoregulatory surface darkening (Hozumi & Yamane, 2001a). The nests of paper wasps are composed of plant materials and a proteinous oral secretion. The oral secretion contains substances such as glue is a water repellent, and turns gray or brownish when dried. The wasps often smear the oral secretion on the surface of their nests to maintain the nests against rain (Kudô, et al., 1998); this secretion confers the dark color of nests. Such darkening of the nests would contribute to efficient absorption of sunlight and consequent increase in its temperature (Heinrich, 1993; Hozumi & Yamane, 2001a). On the other hand, the color of the nests of the tropical paper wasps such as *Polybia* and *Apoica* is pale or light yellow (Richards & Richards, 1951), probably for reducing the absorption of the sunlight in the hot tropical climate (Yamane, personal communication).

It has been suggested that the cocoon caps of social wasps also regulate the temperature of the brood cells. The caps insulate the cells from the outer environment (Spradbery, 1973). In vespine nests, the contiguously arranged cocoon caps automatically generate heat by their thermoelectromotive force depending on the thermal environment (Kirshholm & Ishay, 2000; Ishay et al., 2002). Another method of thermoregulation with regard to darkening is suggested in some paper wasps. In the nests of *Polistes riparius* Yamane et al. dwelling in the cold regions in Japan (Yamane & Yamane, 1987), the wasps darken not only the surface of the nests but also the cocoon caps (Yamane & Kawamichi, 1975). A similar darkening behavior is also observed in the nests of *P. biglumis bimaculatus* (Geoffroy in Fourcroy), which dwell in the high mountainous region of the Alps (Lorenzi & Turillazi, 1986). These authors believed that under a cold climate, darkening of cocoon caps is an adaptive behavior to increase the cell temperature by absorption direct absorption of early morning sunlight; however, the ecological significance of the dark cocoon caps has not been investigated.

Considering nest thermoregulation, I carried out this study on *Polistes* cocoon caps and nests to assess the relationship between the thermal property of the cocoon caps and their surface color. The darkness (hereafter, represented as lightness) of the cocoon caps in *P. riparius* nests was measured and the thermal effect of these caps was investigated using model nests with darkened cocoon caps under the outdoor and indoor conditions. Here, the thermal strategies of the *Polistes* wasps dwelling in cold regions are proposed.

Materials and method

Measurement of the heat absorption rate in cocoon caps

Since the study parameters were not well defined, before examining the thermal effect of the cocoon caps, I investigated the details of surface darkening of cocoon caps in the nests of *P. riparius* at the completion of the pre-emergence period. The nests of *P. riparius* were collected together with immature wasps ($N = 8$) in early July 1999 from Sapporo ($43^{\circ}03'N$, $141^{\circ}20'E$), northern Japan. Using pins, the cocoon caps were removed from the nests carefully, and 57 samples of cocoon caps were obtained, i.e., a mean of seven cocoon caps was obtained per nest. The cocoon caps were cut into small pieces (3×3 mm; Fig. 1), and their lightness (%) was determined as follows. The images of the caps were obtained with an image scanner (EPSON GT-X800) and stored in a Macintosh computer. The images were standardized in D65, i.e., daylight condition, using ColorSync in MacOS 10.3 software (Apple Co.). The color images were then converted to grayscale. On each image, ten points were randomly chosen and their lightness (%) was determined with Photoshop ver. 6.0 software (Adobe Co.). Firstly, the average lightness value of each nest was determined (approximately seven caps per nest). Subsequently, the average lightness value across the eight nests was determined. All the cocoon caps observed were darkened, and the mean ($N = 8$) lightness was 28%. For comparison, the lightness of the cocoon caps in the nests ($N = 5$) of *P. chinensis antennalis* Pérez, a consubgeneric species of *P. riparius*, collected in June 2004 from Ibaraki Prefecture, central Japan, was similarly determined, and it was found to be 87%.

Temperature measurement of the model nest

For evaluating the thermal effects of the cocoon caps, I simulated *P. riparius* nests

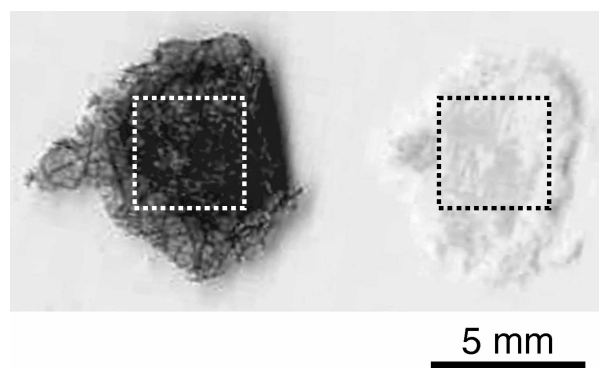


Fig. 1. Cocoon caps of *Polistes riparius* (left) and *P. chinensis antennalis* (right). Squares indicate the area at which lightness was measured (%).

by preparing paper model nests using the same material and surface color because the nests built by wasps vary in the size and shape of combs and in surface color. The models had hexagonal cells with a diagonal diameter of 5.6 mm, which is similar to that of *P. riparius* nests. The model nest was prepared with white tissue paper (thickness <0.1 mm) made from pure wooden fibers, and the surface structure was similar to that of the *Polistes* nests (Hozumi & Yamane, 2001b). In the present study, the model nest had 61 cells that were 40 mm in length; the number and length of the cells of the model was comparable to an average *P. riparius* nest (68 cells, 38 mm in length) at the completion of the pre-emergence period (Hozumi et al., 2008). Dividing walls imitating cocoon caps were attached to seven cells located at the center of the model nests (Fig. 2). The walls were made of the white tissue paper, and the surfaces of the walls were darkened to gray; the lightness was identical to the measured lightness value of the cocoon caps of *P. riparius* (28% lightness; hereafter, PRA). In addition, three other model nests—model nest with white cocoon caps (90% lightness; hereafter, WH), black caps (10% lightness; hereafter, BK), and with no caps (NC) — were also prepared for comparison. In this study, I considered that the thermal effect of the caps of *P. cininsis antennalis* (87%) is comparable to that of the caps in the WH model.

The temperature of model nests was measured in the outdoor and indoor conditions. For outdoor measurements, the model nests were placed 1 m above the ground. In each model nest, a copper-constantan thermocouple ($\varnothing = 0.32$ mm) was inserted in the center of the capped cells, i.e., 5 mm from the bottom (Fig. 2). The temperature was measured to the nearest 0.1°C , and the data were stored in a data logger (NR1000, Keyence). The cell temperature, insolation expressed as heat flux (W/m^2 , Medtherm, 64-0.2-16/SW-1C 150), and ambient temperature (T_a) were measured every 1 min. The wind velocity was measured with a digital anemometer (Model DP-70, Hiyoshi) every 10 min. The measurements were carried out from 0630

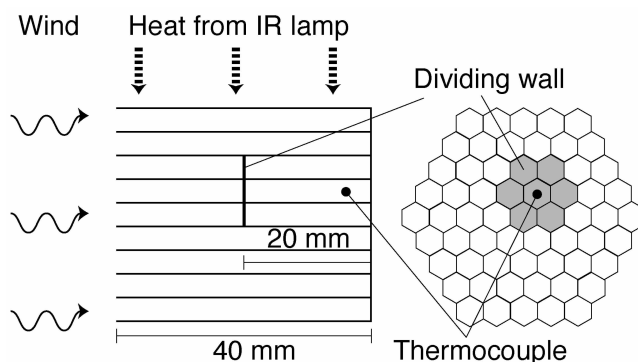


Fig. 2. The scheme of a model nest. Left, cross-section; right, front section.

to 1630 hours on September 13, 2004.

Indoor measurements were carried out in a dark room maintained at 25°C constant temperature. A model nest was set at horizontal cell axes at 1 m above the floor and was heated from above at 900 W/m². Initially, the model was heated until the cell temperature stabilized under still air conditions (approximately 15 min); subsequently, air was blown towards the model such that it could enter the cells for 10 min (Fig. 2). The wind velocity was set at eight levels; 0 (still air), 1, 2, 3, 4, 5, 6, and 7 m/s. The temperature measurements were performed five times for each model nest at each wind velocity, and the values of the five experiments were averaged.

Data analysis

Mann-Whitney U-test was employed to detect the differences between the top and central cell in the field nests of *P. riparius*. No statistical tests such as ANOVA was applied to the temperature data measured with model nests under outdoor and indoor conditions because the temperature data were not independent. However, the thermal effect due to different grades of lightness of the cap color was repeatedly observed, and the values between the outdoor and indoor measurements were inconsistent.

Results

Thermal effect of the surface color on the cocoon caps

On the day of measurement, insolation (mean \pm standard deviation (SD), 511 \pm 378 W/m²) gradually increased from 0700 to 1130 hours, and it largely decreased from 1300 to 1400 due to the cloudy environment (Fig. 3). The wind was strong from morning to noon and calm from afternoon until the measurement was completed. The T_a ranged from 19.6°C to 26.0°C (mean, 23.6°C). The cell temperatures were affected by the changes in insolation, and the temperature was higher in the models with darker cocoon caps (Fig. 3). During early morning (0630– 0730 hours), the temperature was almost similar among all the models, and the nest temperatures gradually increased with the increase in insolation. From 1000 to 1300 hours, the temperature difference (T_d) among the models gradually increased. The cell temperatures decreased in a cloudy environment until the completion of the measurement period. The mean temperatures were 28.2°C (WH), 29.3°C (PRA), 30.3°C (BK), and the T_d was 1°C between the models. The temperature of the NC model was lower than that of the WH model from 0630 to 1100 hours, while the temperatures of these nests were almost similar after 1130 hours under the calm wind condition.

Figure 4 shows the indoor T_d between the models with the cocoon caps, i.e., WH, PRA and BK, and the model with no caps (NC). The temperature tended to be higher

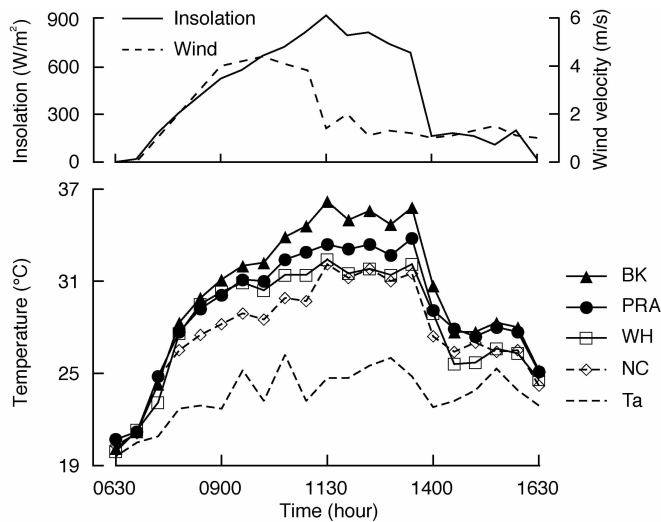


Fig. 3. Temporal changes of environments (upper) and nest temperature (lower); lightness of cocoon caps, BK, PRA and WH had cocoon caps with 10%, 72% and 90% lightness, respectively; NC had no caps.

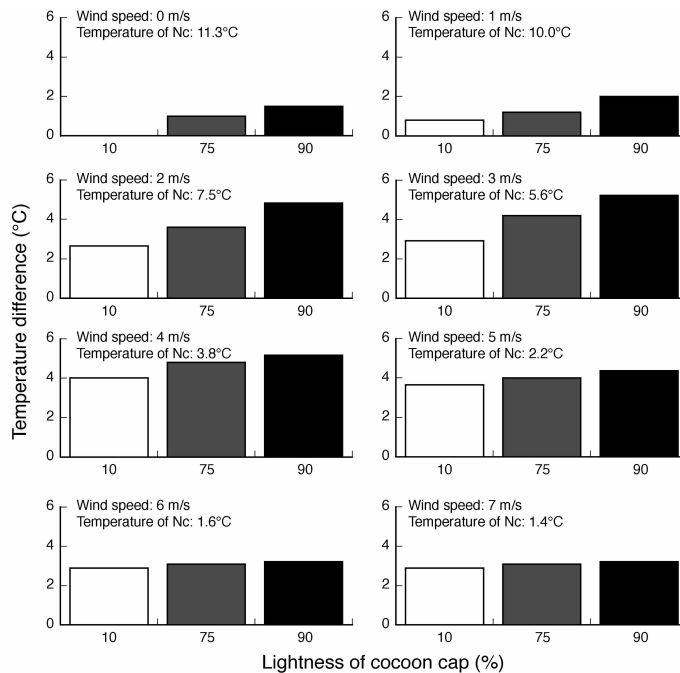


Fig. 4. Temperature difference between models with cocoon caps (BK, PRA and WH) and a model without caps (NC).

in the models with darker caps, and the difference among the models was largest at a wind velocity of 3 m/s; the T_d was 2.7°C, 3.6°C and 4.8°C for WH vs. NC, PRA vs. NC, and BK vs. NC, respectively. The T_d gradually reduced when the wind velocity increased from 5 to 7 m/s, and the T_d among the models were similar (2.9°C– 3.2°C) at 7 m/s. On comparing the WH and NC models, it was found that T_d was zero with still air, while it increased as the wind velocity increased.

Discussion

From the results of temperature measurements with the model nests, two thermal effects of the cocoon caps were observed—the “wind-break” effect by the caps and the “heat absorb” effect due to the darkening of the cap surface. Under both outdoor and indoor conditions, the wind-break effect of the cocoon was observed when air was blown toward the nest. For example, while the temperatures in the WH and NC models were similar under the calm condition, the temperature in the WH model was higher than the NC model when air was blown toward the nest. The heat-absorb effect was observed not only when the model nests received sunlight (or infrared light) but also when the surfaces of the caps were not exposed to sunlight. In addition, the temperature increased due to the thermal effect of the dark cap reduced to the white cap level by the external disturbances, such as wind. The phenomenon can be explained as follows. Due to high heat absorption, the dark surface can retain more heat until a thermal equilibrium is achieved, and the heat is then radiated to both the sides of the cocoon cap, resulting in a higher cell temperature. On the other hand, the heat around the caps can be easily emitted by an environmental disturbance due to the high emission capacity of a dark-colored surface. This explanation is supported from the results of the indoor measurement that revealed that the cell temperature was almost similar in the WH, PRA, and BK models under the high wind velocity (over 5 m/s).

In cold climatic regions where the nesting period is short, nest thermoregulation plays an important role in accelerating the colonial growth, because the duration of the founding stage influences the number of reproductive gynes under limited nesting periods (Wilson, 1971; Heinrich, 1993). In order to gain heat from the environment, the foundresses of *P. riparius* strive to achieve nest thermoregulation, as a part of nest building. The nest of *P. riparius* is a characteristic structure with extra cells around the broods and darkened cocoon caps (Yamane, 1969, 1971; Yamane & Kawamichi, 1975); both these features increase the nest temperature (Hozumi & Yamane, 2001a, b; Hozumi et al., 2008; this study). From these studies, it is estimated that in a pre-emergence *P. riparius* nest, the cell temperature at the brood area can be increased by 5°C under still air (building extra cells increases temperature by 4°C and darkening of the cocoon cap increases temperature by 1°C), compared to the pre-emergence nests of

P. chinensis antennalis, dwelling in the warm areas of central Japan. On the other hand, the effort invested by *P. riparius* foundresses is commendable, since activities involved in building such nests require great effort in terms of nest materials, such as producing proteinous oral secretion and collecting plant materials. When the effort required for constructing a pre-emergence nest with regard to the amount of oral secretion and plant materials are compared between the two species, *P. riparius* does twice the amount of work done by *P. chinensis antennalis*, and this results in increasing the weight of the nest by four times (Yamane et al., 1998). This simply indicates that the duration of extranidal activities performed by the foundresses of *P. riparius* is four times that of the foundresses of *P. chinensis*. Furthermore, during the pupal substage, the foundresses of *P. riparius* may spent more time for thermoregulatory cooling by fanning and water collection; *P. riparius*, 10.4% and 62.3 times/day, respectively (this study); *P. chinensis antennalis*, 0.5%– 1.8% and 0– 25 times/day, respectively (Kasuya, 1983; Kudô, personal communication). These efforts invested for nest thermoregulation are repaid in the form of accelerated development of the immature wasps and the production of more reproductive gynes within a short nesting period.

It is concluded that the darkened cocoon caps of *P. riparius* is a type of thermal adaptation to cool temperate regions, and the dark caps promote thermoregulation in the cocoon cells via their thermal effect, i.e., high absorption and emission ability. However, some *Polistes* wasps darken the cocoon caps also in hot regions such as tropics (Kojima & Kojima, 1988). It is considered that in addition to thermoregulation, the dark color may act as a protection strategy. In the nests with a gray or brownish surface color, the white cocoon caps exposed to the outside environment may be obvious due to the contrast. It is also possible that in hot climates, this coloration functions to reduce the chance of predation from mammals and birds, rather than thermoregulation, because the wasps are not necessary to achieve high nest temperature due to a high ambient temperature.

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アシナガバチの巣における暗色化した繭の熱的特性

穂 積 訓

寒冷地に生息するトガリフタモンアシナガバチ (*Polistes riparius*) は、繭の表面を暗色化する特徴がある。本研究では、この繭表面の暗色化が持つ熱特性に着目し、巣の模型 (以下、模型巣) を使って野外および実験室で温度を測定して検証した。また、ガリフタモンアシナガバチの創設メスによる温度調節行動についても合わせて調査した。ガリフタモンアシナガバチの繭の表面は黒褐色で、明度は28%であった。実験で用いる模型巣には、明度を4段階に設定した仕切りを繭としてつけた。模型巣の内部温度を野外でしたとき、巣内の温度は明度が低い巣ほど上昇した。模型巣の間の温度差は、風が強いほど小さく、風が穏やかなときほど高かった。実験室の温度測定において、無風条件では明度の低い巣ほど温度の上昇は高くなった。一方、風が強くなると、繭の明度による温度の変化は小さくなった。最後に、これらの結果から、繭の暗色化と温度調節の関係、およびガリフタモンアシナガバチの寒冷地の適応について議論する。

キーワード アシナガバチ, 繭表面の明度, 巣の温度調節, 寒冷な気候への適応