

Yellowjackets (*Vespula pensylvanica*) thermoregulate in response to changes in protein concentration

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Abstract Social insects can modulate body temperature to increase foraging efficiency; however, little is known about how the relative value of protein resources affects forager body temperature. Such regulation may be important given that colony growth is often limited by protein availability. In this paper, we present what are, to our knowledge, the first data for social insects showing that thoracic temperatures (T_{th}) of foragers increase with the protein content of food resources. In an introduced population of western yellowjacket (*Vespula pensylvanica*), we measured T_{th} of foragers collecting high-quality protein (100% canned chicken) and low-quality protein (50% canned chicken, 50% indigestible alpha-cellulose by volume) at different ambient air temperatures (T_a). Wasps foraging on 100% chicken consistently exhibited higher T_{th} compared to wasps foraging on 50% chicken. After correcting for T_a , the mean T_{th} for wasps collecting 100% chicken were 1.98°C higher than those of individuals collecting 50% chicken. We suggest that this mechanism may increase foraging efficiency in this and other social wasp species.

Keywords Foraging · Thermoregulation · *Vespula* · Protein · Wasp

Introduction

In eusocial Hymenoptera, foraging strategies generally balance the energy expenditure of individual foragers with net energetic gains to the colony (Seeley et al. 1991). For example, honeybee (*Apis mellifera*) foragers trade off food value of nectar with the caloric costs of food transport, colony recruitment, and competition (Dyer 2002). The value of carbohydrates in influencing nectar foraging behavior and communication is well known (Pankiw and Page 2000; Kay 2002; Nieh et al. 2003; Scheiner et al. 2004; Nieh and Sanchez 2005). These studies discuss sophisticated behavioral mechanisms that play key roles in colony food gathering. By comparison, the role of protein quality in hymenopteran foraging has received less attention, although protein is essential to colony growth. The few existing studies on this topic all address pollen collection in bees (Pernal and Currie 2001; Pankiw and Rubink 2002; Bertram et al. 2003).

During resource collection, foraging insects incur a metabolic cost in part because flight muscles must achieve a minimum threshold temperature (Coelho and Ross 1996). Variation in ambient air temperature (T_a) can greatly affect the energy expended by foragers to reach this flight threshold. Thus, some wasps and bees alter their metabolic or activity rates to respond to changes in T_a (Heinrich 1993). For example, honeybees exhibit a positive correlation between thoracic temperatures (T_{th}) and T_a over certain ranges of T_a (Schmaranzer and Stabentheiner 1988; Woods et al. 2005). The ability to maintain a positive relationship between body temperature and T_a is a form of thermoregulation (Coelho and Ross 1996).

Foragers can minimize thermoregulatory costs incurred while foraging by varying T_{th} in response to the *carbohy-*

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drate content of food (Heinrich 1984; Dyer and Seeley 1987; Schmaranzer and Stabentheiner 1988; Waddington 1990; Stabentheiner and Hagmüller 1991; Underwood 1991; Kovac and Stabentheiner 1999; Stabentheiner 2001; Nieh and Sanchez 2005; Nieh et al. 2006). Honeybee foragers thermoregulate in response to sugar concentration, maintaining a higher T_{th} in response to more concentrated sucrose solutions compared to less concentrated solutions over the same range of T_a (Stabentheiner 2001). Using a similar approach, Kovac and Stabentheiner (1999) demonstrated that *Vespula vulgaris* foragers adjust T_{th} in response to sucrose concentration. The ability to maintain T_{th} above T_a may reduce the time needed to attain the minimum threshold temperature for flight even at low environmental temperatures (Heinrich 1984; Coelho and Ross 1996). In this way, thermoregulation may facilitate resource exploitation (Kovac and Stabentheiner 1999). In Vespine wasps, T_{th} closely corresponds with activity level; T_{th} decreases during inactivity and increases during high activity (Kovac and Stabentheiner 1999). Although such thermoregulation depends on the behavioural context of the forager (e.g., leaving the nest, entering the nest, or interacting with nestmates; Coelho and Ross 1996), no study to date has examined whether thermoregulatory behaviors also change with the type of resource (such as carbohydrates or proteins).

Protein foraging has been examined primarily with respect to pollen foraging by honeybees. Pernal and Currie (2001) demonstrated that *A. mellifera* colonies respond to deficiencies in their pollen reserves by increasing the proportion of foragers collecting pollen rather than by accumulating pollen of higher quality. In this paper, we define protein quality or concentration as the relative proportion of chicken bait that consists of protein. Individual honeybee foragers can evidently assess protein resource quality (Waddington et al. 1998). However, forager sensitivity to pollen quality may not be highly refined because pollen is scraped off the abdomen and packed directly into the corbiculae without first being sampled (Hodges 1984; Pernal and Currie 2001).

In contrast to honeybees, wasp foragers macerate prey, providing them with an extended opportunity to assess protein quality. To examine the role of thermoregulation in protein foraging by predatory wasps, we measured the thermal responses of yellowjacket foragers to varying qualities of protein resources. Because most studies of social wasp foraging address prey preferences, our study is novel in its focus on the behavioral responses of foragers to protein quality. Our results indicate that foraging yellowjackets elevate T_{th} in response to bait concentration. We suggest that yellowjackets, and perhaps other social wasps, may increase their foraging efficiency by modulating T_{th} relative to protein quality.

Materials and methods

Study site and colonies

We performed all experiments in the Hilina Pali region of Volcanoes National Park (HAVO) on the Big Island of Hawaii (19°20.6' N, 155°16.4' W, elevation 994 m). HAVO supports locally abundant, non-native populations of *V. pensylvanica* as well as diverse assemblages of native arthropod prey such as Araneae, Coleoptera, Diptera, and Lepidoptera (Gambino 1992). At these sites, *V. pensylvanica* also actively scavenges vertebrate carrion. We collected data in September 2005 on 134 foragers from four different colonies ($N=31$, $N=33$, $N=29$, $N=41$ wasps, respectively) located in an area of approximately 0.18 km². We tested each colony once per day. Therefore, trials of different protein qualities occurred on separate days but at the same time of day (1000 or 1400) to control for diurnal patterns of activity. Trials were conducted in diffuse sunlight.

Bait composition and experimental setup

We measured T_{th} of *V. pensylvanica* foragers collecting baits with either higher protein content (100% chicken by volume) or lower protein content (50% chicken by volume). Invertebrate species preyed upon by wasps generally consist of 40–70% protein by dry weight (Allen 1989). Lean chicken (Hormel® 98% fat-free chicken breast; 0.3 g fat, 2.7 g protein, 0.0 g carbohydrate) was used as the protein source. Canned chicken is currently used in baiting *V. pensylvanica* at HAVO (Gruner and Foote 2000) and was preferred over ground beef and tuna in our pilot studies. Each 100% chicken bait consisted of 15 cm³ of canned chicken (mean±SD, 28.6±3.4 g). A concentration of 50% chicken by volume was obtained by mixing 7.5 cm³ of chicken with an equal volume of packed alpha-cellulose powder (Sigma, EC 232-674-9), an inert indigestible compound used to vary the protein content of resources for foraging honeybees (Pernal and Currie 2001) and caterpillars (Lee et al. 2004). Alpha cellulose has a low density (bulk density, 110–145 g/l), and thus, we diluted the protein content of the bait by volume instead of by mass. The difference in the consistency of the two bait types is unlikely to have affected foraging responses because grinding meat and altering its texture have no effect on *Vespula* visitation or acceptance of baits (Reid and Macdonald 1986). Although other factors such as weight or odor intensity may also be affected by this dilution process (Waddington et al. 1998), natural prey vary in macronutrient concentration, weight, density, and odor even within the same prey species. We therefore expect foragers to have the ability to assess protein quality in addition to other physical characteristics of their food.

Individual wasps foraged at protein bait stations, each of which consisted of a single bait on a blue circular plastic dish (14-cm diameter) placed on an ice pack ($12.1 \times 19.1 \times 1.9$ cm). The ice pack ensured that bait temperature remained relatively constant throughout the trial and provided a sufficiently low background temperature against which to measure the T_{th} wasps. The mean temperature of the bait achieved by this process was $21.2 \pm 1.8^\circ\text{C}$, while T_a ranged from 21.1°C to 29.0°C . Because of air flow and wasp movements during foraging, the ice pack had a negligible effect on wasp body temperature.

We measured surface T_{th} to the nearest 0.1°C with an infrared thermometer (Radio Shack, cat #220-0325, spot size of 5 mm). Temperature measurements were accurate to 2.0°C , but they were all precise and repeatable to within 0.2°C as compared with a reference mercury thermometer. Thermal measurements were taken with the infrared thermometer placed within 5 mm of the thorax. Ambient temperature data were measured to the nearest 0.1°C with a digital temperature probe (Pyrex model 7738). Processing T_{th} were measured while foragers processed the chicken into a ball. To collect control T_{th} (non-processing temperatures), we placed a domed wire screen (11.1-cm diameter \times 3.7-cm height; 0.1-cm mesh spacing) over the bait to prevent wasps from contacting chicken. Trials lasted between 45 and 60 min depending on wasp activity. Trials ended after data were collected for at least 15 individual foragers per colony per day.

Thoracic temperature measurements

Before each trial, we stimulated colony foraging activity by placing 30 cm^3 of 100% chicken on the ground 20 m away from a nest entrance. After 15–20 min, we removed this initial bait to ensure that it did not affect the body temperatures of foragers during the trial. We waited 20–30 min after removal of the initial bait before placing experimental bait stations at the same locations as the initial baits.

We measured ambient temperature and chicken temperature at approximately 15-min intervals throughout the trial. Each wasp was uniquely marked on her abdomen with acrylic paint (Duncan Craft, RM# 0010788) for individual identification (Gambino 1990). In each trial, temperatures were taken from 15–20 different foragers that were provided with either 100% or 50% chicken by volume.

Pilot studies showed that wasps were unable to imbibe detectable quantities of liquids from baits during short time periods (10 s). We observed that 93.2% of foragers (68 of 73) produced no regurgitate after processing 100% chicken bait for 10 s; this observation indicates that 10 s is too short of a time interval for liquids from the bait to be consumed and metabolized. Thus, in the current study, we measured body temperatures within 3 s of initiation of bait processing

to ensure that any observed changes in temperature were not caused by metabolic activity. Repeat temperature measurements (mean \pm SD, 2.82 ± 1.84) of individual wasps were taken on successive visits to the bait. We used the mean T_{th} per individual in all statistical analyses.

Statistical analyses

Only individual wasps for which we had both control and processing temperature data were included in the analyses ($N=134$ wasps). We report mean \pm SD. We performed three analyses of covariance (ANCOVAs). In the first ANCOVA, we assessed whether colony (2, 3, 4, and 5), protein quality (100% and 50% chicken), and T_a (covariate) affected T_{th} . In the remaining ANCOVAs, we analyzed how these same independent variables affected the following dependent variables: (1) non-processing T_{th} (control temperatures) and (2) the mean differences between the control and processing temperatures of the thorax. JMP In v. 5.1 (SAS Institute) statistical software was used for all analyses.

Results

Foraging wasps visiting the baits for the first time circled bait stations aerially before landing. Yellowjackets orient towards odor plumes emanating from food resources (Hendrichs et al. 1994), and we observed that low flying foragers on their first approach flew in a zigzag pattern into the wind, apparently following the scent plume created by the bait. After initial location and exploitation of the bait, all returning foragers flew directly to and from the bait station. As more wasps visited the bait, foragers had a greater chance of interacting. Although aggressive behaviors such as buzzing, pouncing, and grappling may increase body temperatures, we observed minimal aggression among foragers irrespective of bait type (100% or 50% chicken), colony, and T_a .

Our results indicate that *V. pensylvanica* thermoregulate in response to processing protein. In the first ANCOVA, there were significant effects of protein quality and colony, but no effect of T_a (Table 1). Wasps collecting 100% chicken exhibited higher mean T_{th} ($31.2 \pm 1.4^\circ\text{C}$) compared to wasps collecting 50% chicken ($30.0 \pm 1.1^\circ\text{C}$; Fig. 1). Although colonies differed in the extent to which foragers adjusted T_{th} to bait type, foragers from all nests consistently exhibited higher T_{th} when collecting from a 100% chicken bait as opposed to a 50% chicken bait (colony 2: $N=31$, $F_{1,29}=36.11$, $p<0.0001$; colony 3: $N=33$, $F_{1,31}=20.89$, $p<0.0001$; colony 4: $N=29$, $F_{1,27}=10.88$, $p=0.0027$; colony 5: $N=41$, $F_{1,39}=5.18$, $p=0.028$).

Before encountering the resource, T_{th} of foragers in 100% chicken trials did not differ from those of workers in

Table 1 Results of the three ANCOVAs that examine the effect of ambient temperature (T_a), colony and protein quality on thoracic temperatures (T_{th})

	T_{th} (processing)			T_{th} (control)			T_{th} (processing)– T_{th} (control)		
	F	df	p	F	df	p	F	df	p
T_a	1.21	1,125	0.27	4.24	1,118	0.042	0.29	1,125	0.59
Colony	8.98	3,125	<0.0001	6.43	3,118	0.0005	1.26	3,125	0.29
Protein quality	40.35	1,125	<0.0001	2.89	1,118	0.092	6.30	1,125	0.013
Colony× protein quality	2.87	3,125	0.04	6.38	3,118	0.0005	0.57	3,125	0.64
Overall model	$F_{8,125}=16.102$			$F_{15,118}=9.94$			$F_{8,125}=2.553$		
			$p<0.0001$			$p<0.0001$			$p=0.013$

the 50% chicken trials. The second ANCOVA demonstrated no statistical effect of protein quality on control T_{th} (Table 1). However, we observed significant effects of colony and the interaction between colony and protein quality that were driven by one trial of one colony that exhibited low control T_{th} .

Thoracic temperature increases were influenced both by forager behavior (processing or control) and by bait type (100% or 50% chicken). When foragers processed meat, their T_{th} increased relative to control temperatures at both protein qualities (Fig. 2). The third ANCOVA showed no effect of colony or T_a on the mean differences between processing and control T_{th} (Table 1). Compared to control foragers, wasps foraging on 100% chicken increased their

T_{th} by $1.7\pm 0.2^\circ\text{C}$, while those foraging on 50% chicken increased their T_{th} $1.1\pm 0.2^\circ\text{C}$ (Fig. 2).

Discussion

Our study demonstrates that foraging *V. pennsylvanica* can adjust T_{th} depending on protein concentration despite the fact that chicken baits are resources from which foragers do not derive any immediate caloric benefit. This finding is, to our knowledge, the first demonstration that foraging Hymenoptera modulate body temperature in response to protein quality. Thoracic temperatures of wasps processing 100% chicken were significantly greater compared to those of wasps processing 50% chicken (Fig. 1). Agonistic interactions among wasps at the bait likely had a negligible effect on T_{th} because aggressive behaviors were not

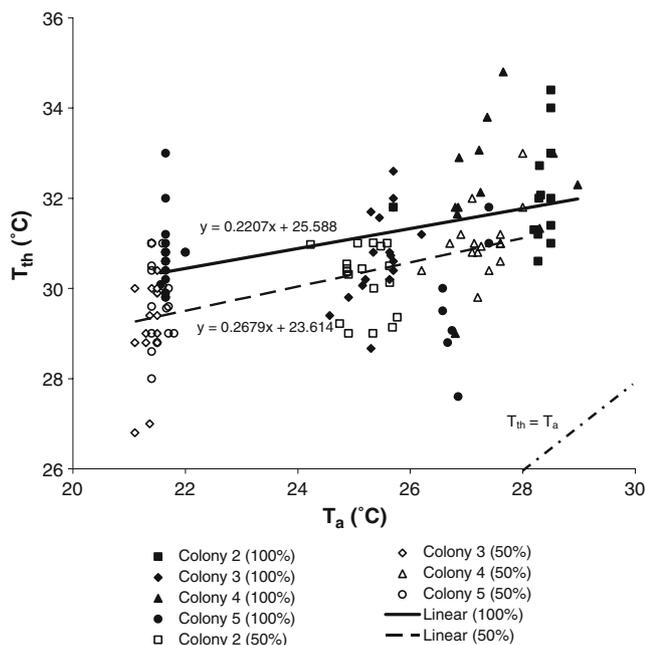


Fig. 1 Change in thoracic temperatures (T_{th}) with protein concentration as a function of ambient temperature (T_a ; $N=31, 33, 29, 41$ wasps from four colonies, respectively). Although T_{th} increase with T_a , T_{th} are significantly greater when wasps forage on 100% chicken compared to when they forage on 50% chicken across all T_a sampled (Table 1)

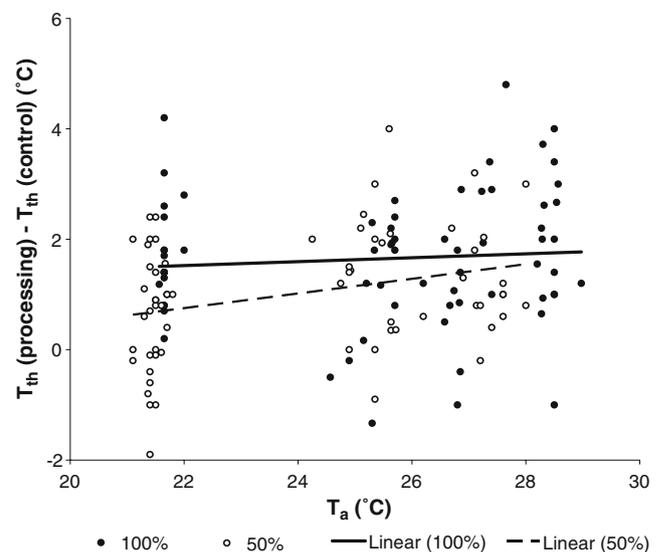


Fig. 2 The difference between processing and control T_{th} as a function of T_a for two different protein concentrations ($N=134$ wasps pooled from all colonies). Across all T_a , differences in T_{th} are greater when foragers collect 100% chicken compared to when they collect 50% chicken (Table 1)

commonly observed at baits. Therefore, we suggest that the observed increase in T_{th} is an active behavioral response to protein quality that may assist in foraging efficiency and contribute to colony fitness.

Most studies on thermoregulation in social insects examine foraging at *carbohydrate* rewards, which can benefit not only workers and brood at the nest but also the forager directly (Heinrich 1984; Schmaranzer and Stabentheiner 1988; Stabentheiner and Hagmüller 1991; Kovac and Stabentheiner 1999; Stabentheiner 2001; Nieh and Sanchez 2005). Our study demonstrates that individual wasps collecting *protein*, a resource from which foragers do not derive any immediate caloric benefit, still adjust the energetics of foraging. Metabolic costs incurred during thermoregulation may be offset by increased colony fitness or by compensation at the nest. The absence of any immediate energetic benefit from the collected protein also suggests that increases in T_{th} do not correspond to higher hemolymph sugar titers in foragers.

Protein can be eventually converted into metabolic energy (Hunt et al. 2003), and wasps can imbibe some liquid from killed prey (Michener and Michener 1951). However, we observed that foragers primarily tore at the bait with their mandibles and shaped it into a ball rather than directly feeding on it while manipulating the chicken meat. Based on our preliminary studies, wasps did not consume measurable amounts of liquid from chicken bait before our measurement of their T_{th} . Therefore, it seems unlikely that the observed T_{th} changes were due to metabolizing the bait they collected. Although no immediate carbohydrate reward was provided at the meat bait, it is possible that such payment was received upon returning to the nest. In response to being fed protein, vespidae larvae produce a nutrient-rich saliva that is consumed by adults; the nutritive value of this secretion is comparable to that of floral nectar, which is the primary source of nutrition for adult wasps (Hunt et al. 1982). Further investigation may reveal whether larvae adjust the volume or concentration of carbohydrate rewards according to the quality of the protein that they receive.

Although protein resources provide no immediate metabolic compensation for the energetic output necessary to raise T_{th} , wasps may adjust their foraging efficiency (i.e., reduce the amount of time required for flight muscle warm-up) to protein quality. Previous studies of both Vespidae and Apidae suggest that elevated T_{th} enhance the power output of flight muscles and allow for faster foraging and a higher rate of resource exploitation (Esch 1976; Schmaranzer and Stabentheiner 1988; Coelho 1991; Stabentheiner and Hagmüller 1991; Kovac and Stabentheiner 1999). If workers expend energy in proportion to resource quality (Kovac and Stabentheiner 1999), then a greater increase in T_{th} may be expected in response to higher protein

concentration. Similarly, lower T_{th} may help the forager conserve energy while collecting a relatively poor resource. Such flexibility could allow a colony to adjust energy consumption during foraging to the quality of the available protein. This hypothesis is further supported by the result that T_{th} in both meat concentrations increased relative to control T_{th} . Wasps raise their body temperatures when processing any type of protein compared to temperatures during unsuccessful foraging (control temperatures), but the magnitude of this increase in T_{th} is dependent on resource quality.

Vespula wasps also thermoregulate in response to carbohydrate quality. Kovac and Stabentheiner (1999) reported that when sucrose concentrations were doubled, T_{th} of *V. vulgaris* foragers increased between 1.4°C and 1.7°C. In our study, *V. pensylvanica* experienced a comparable 1.2°C increase in T_{th} when protein content was doubled. Although individual foragers increase T_{th} with a twofold increase in resource quality, the degree of thermoregulation (as measured by thoracic temperature excess = $T_{th} - T_a$) (Herrera 1997) may be specific for species or resource. At high T_a (~28°C), *V. vulgaris* exhibited a thoracic temperature excess of 6–9°C, whereas at low T_a (~19°C), thoracic temperature excess was ~16°C (Kovac and Stabentheiner 1999). In our study, we observed a thoracic temperature excess of 5–6°C in *V. pensylvanica* at moderate T_a (~24°C); this value falls below the range reported for *V. vulgaris* and may indicate that wasps may invest less energy in thermoregulation when foraging for protein than when foraging for carbohydrates. Because the present study and that of Kovac and Stabentheiner (1999) occurred at similar times of the year, the disparities observed in thoracic temperature excess are unlikely to be the result of differences in colony cycle. However, the roles of food type, colony need, or interspecific differences in influencing how T_{th} are adjusted remain to be tested. Although we detected a colony effect on T_{th} that was independent of T_a , estimated colony size (Malham et al. 1991), and nest location, it is important to note that foragers from all colonies increased T_{th} in response to increased protein concentration. Our study measured temperatures of foragers only at the bait and not in the nest. To fully contextualize the thermal behavior observed at the resource, future studies should also examine the motivation and behavior of protein foragers once they have returned to the colony.

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