Insect. Soc. (2010) 57:157–162
DOI 10.1007/s00040-009-0062-9

Insectes Sociaux

RESEARCH ARTICLE

Thermoregulation in the primitively eusocial paper wasp, *Polistes dominulus*

S. A. Weiner · C. T. Upton · K. Noble ·
W. A. Woods Jr. · P. T. Starks

Received: 8 June 2009 / Revised: 13 November 2009 / Accepted: 1 December 2009 / Published online: 20 December 2009

Abstract Regulation of wing muscle temperature is important for sustaining flight in many insects, and has been well studied in honeybees. It has been much less well studied in wasps and has never been demonstrated in *Polistes* paper wasps. We measured thorax, head, and abdomen temperatures of inactive *Polistes dominulus* workers as they warmed after transfer from 8 to ~25°C ambient temperature, after removal from hibernacula, and after periods of flight in a variable temperature room. Thorax temperature (T_{th}) of non-flying live wasps increased more rapidly than that of dead wasps, and T_{th} of some live wasps reached more than 2°C above ambient temperature (T_a), indicating endothermy. Wasps removed from hibernacula had body region temperatures significantly above ambient. The T_{th} of flying wasps was 2.5°C above ambient at $T_a = 21$°C, and at or even below ambient at $T_a = 40$°C. At 40°C head and abdomen temperatures were both more than 2°C below T_a, indicating evaporative cooling. We conclude that *P. dominulus* individuals demonstrate clear, albeit limited, thermoregulatory capacity.

Keywords Hymenoptera · Flight · Temperature · Thermoregulation · Hibernation

---

S. A. Weiner (✉) · W. A. Woods Jr. · P. T. Starks
Department of Biology, Tufts University,
163 Packard Avenue, Medford, MA 02155, USA
e-mail: susan.weiner@tufts.edu

C. T. Upton
Department of Biology, Williams College,
Williamstown, MA 02167, USA

K. Noble
Department of Biology, Smith College,
Northampton, MA 01063, USA

Introduction

Polistes paper wasps are an important model system for the study of the evolution of eusociality and insect dominance hierarchies (West-Eberhard, 2006). *Polistes* are considered primitively eusocial because they do not seem to have physiological caste differentiation (Wilson, 1971; but see Hunt, 2006). This lack of caste differentiation, as well as general ease of study, has led to the use of *Polistes* for testing theories about the evolutionary origins and maintenance of eusocial behavior (e.g. Field et al., 1998; Reeve et al., 2000; Hunt, 2006; Nonacs et al., 2006). While much work has been done on the behavioral ecology of this system some very important basic physiology remains unknown.

While some work has been done in nest thermoregulation in *Polistes* species (Steiner, 1930), our understanding of their individual thermal behavior remains limited. Many large insects (>50–200 mg) in several orders maintain high thorax temperatures (T_{th}) during flight (reviewed in Heinrich, 1993), and some social insects maintain elevated temperatures in the nest (reviewed in Heinrich, 1993). Thermoregulation is clearly important in some highly social insects, whether at the level of the nest (army ants: Franks, 1989; termites: Korb, 2003), the individual (yellow jackets: Kovac and Stabentheiner, 1999), or both (bumblebees and honeybees: reviewed in Heinrich, 1993). Elevated flight temperatures have also been shown in several wasps, including yellow jackets (Coelho and Ross, 1996) and cicada killers (Coelho, 2001). The latter has also been shown to warm prior to flight (Coelho, 2001). To date, however, work with wasps has been done only in large, strongly endothermic wasps (yellow jackets: Kovac and Stabentheiner, 1999; Coelho and Ross, 1996; cicada killers: Coelho, 2001). *Polistes* are relatively small wasps, and so are expected to be, at most, only weakly endothermic.

Understanding individual thermoregulation in *Polistes* will provide background for researchers studying important questions about thermoregulatory behaviors, such as whether *Polistes* maintain elevated brood temperatures, as do bumblebees (Heinrich, 1972) and honeybees (Heinrich, 1985) and whether they use behavioral fever to combat infection (Starks et al., 2000). Here, we investigated whether *P. dominulus* workers, both flying and non-flying, have the capacity to elevate wing muscle temperatures above ambient temperature, and, if so, whether they also display mechanisms for preventing endothermic overheating during flight.

Methods

Animals

During the summer of 2007, 29 nests of *P. dominulus* were collected from field sites in Waltham, Grafton, and Carlisle, MA, USA. During the following summer (2008), 32 more nests were collected from the same sites. These nests were maintained in 0.037-m^3 cages on the Tufts campus in Medford, MA, USA, and colonies were provided with wax worms and 50% solutions of honey in water ad libitum (Sumana and Starks, 2004). All individuals tested during the summers were females that emerged more than 2 weeks prior to the first male and, thus, were assumed to be workers (Mead et al., 1990). The individuals used for hibernation experiments were gynes overwintering in wooden hibernacula located inside mesh-walled enclosures in Medford, MA, USA. These gynes were produced by colonies collected the previous summer and released into enclosures in October. Enclosures were periodically provided with 50% solutions of honey in water. No individual was used in more than one test, as the 24-h mortality rate from the procedure was high (greater than 30%), and puncturing may have altered the wasps' ability to maintain temperature.

Temperature measurements

Warm-up measurements

To determine whether *P. dominulus* workers elevate their temperatures after removal from a cold environment, we measured the body region temperatures of live and dead individuals over time. Dead wasps were used as comparisons to determine how warm-up differed from equilibration to ambient temperature (T_a) (e.g. Bishop and Armbruster, 1999). Dead wasps were freeze killed at least 1 h, but less than 8 h before use to prevent desiccation. Live and dead wasps were constrained in a plastic bag and kept for 10 min at 8°C. The internal temperature of an empty plastic bag moved from 25 to 8°C reached 8°C within 5 min.

After cooling, and while still restrained, wasps were moved to a temperature controlled room kept at 25.0 ± 0.6°C. Wasps were maintained at this temperature for 0–300 s, before thorax, head, and abdomen temperature (T_{th}, T_h, and T_{ab}, respectively) were measured by inserting into each body region a Physitemp MT 29/1B microprobe thermocouple (diameter 0.33 mm, time constant 0.025 s) connected to a Physitemp BAT-12 thermometer (Physitemp, Clifton, NJ, USA). Thorax was measured first, followed by head, and then abdomen within 10 s. Each dead wasp was measured continuously in one body segment for 10 min, and the temperature was recorded every 30 s. In order to determine whether the thermocouple probe provided a significant heat sink for the dead animals, one time course was done using a separate dead wasp for each elapsed time value for comparison. The results did not differ from the previous averages, so the data were combined. Each live wasp provided only one datum for each body region. Temperatures were reported as temperature excess relative to room temperature (wasp body region temperature minus room temperature) in order to compensate for slight variations in room temperature. An ANCOVA was done on the log of the temperature over time to compare the live wasps to the dead ones.

In order to test for evaporative cooling in dead wasps, wasps that had been freeze-killed were monitored for water vapor loss for 2 h after removal from the freezer. H_2O production was measured continuously by differential open-flow respirometry using a Li-Cor 6262 CO_2/H_2O analyzer (Li-Cor, Lincoln NE, USA) calibrated with a gravimetric mixture (Scott Specialty Gases, Plumsteadville PA, USA) and re-zeroed between measurements (Woods et al., 2005). A flow rate of 250 cc min^{-1} of medical grade compressed air was maintained by Sierra Side-Trak mass flow meters (Sierra Instruments, Monterey NV, USA) and a Sable Systems flow controller (Sable Systems, Henderson NV, USA). Excurrent H_2O concentration was sampled every 6 s; each recorded value represented the mean excurrent H_2O concentration for the previous 6 s as calculated by the Li-Cor unit (see Woods et al., 2005). Respirometry data were collected and analyzed in Datacan V (Sable Systems). The same procedure was repeated with live wasps.

Hibernation measurements

The internal temperatures of hibernating females were recorded in February and March 2009 in order to determine wasps' ability to warm up from hibernation in early spring. Wasps were removed from hibernacula and placed in plastic bags that were maintained at ambient temperature (7–9°C). T_{th}, T_h, and T_{ab} were measured by inserting into each body region a Physitemp MT 29/1B microprobe thermocouple (diameter 0.33 mm, time constant 0.025 s) connected to a Physitemp BAT-12 thermometer (Physitemp, Clifton, NJ, USA). After T_{ab} was measured, T_{th} was remeasured to check for order effects. Some individuals had their internal temperatures measured immediately (within 10 s of removal); the remaining wasps were kept in the plastic bags for periods of up to 5 min. During the period prior to measurement, the bags were rotated constantly to maintain activity. An ANCOVA was used to compare the body region temperatures. A repeated measures ANOVA was used to compare the initial temperature measurements with the post-disturbance measurements.

Flight measurements

To determine the temperatures of flying wasps, the body region temperatures of individuals were recorded immediately following capture from flight. For each test, the wasp was released into a variable temperature room and allowed to fly for 30–60 s. No differences in body region temperature were found between flights of 30 s and flights of 60 s (two-tailed *t* test, $T = 0.139$, $P = 0.893$), so these trials were combined. If a wasp attempted to land, the area where she tried to land was tapped several times with a stick. If she persisted in landing, the flight was not used. After a wasp had flown for 30–60 s, she was captured in a net and immediately restrained against a piece of soft foam. Within 10 s of capture, T_{th}, T_h, and T_{ab} were measured by inserting into each body region a Physitemp MT 29/1B microprobe thermocouple (diameter 0.33 mm, time constant 0.025 s) connected to a Physitemp BAT-12 thermometer (Physitemp, Clifton, NJ, USA). A regression line was fitted for the internal temperature of each region relative to T_a and the slopes were compared to a slope of 1 (representing region temperature, T_a) using an ANCOVA.

Results

Warm-up measurements

After being kept at a T_a of 8°C for 10 min, all body regions of dead wasps had reached a temperature of 8°C, while many live wasps maintained slightly elevated temperatures in all body regions (Fig. 1). After 4 min at room temperature (25.0 ± 0.6°C), all body regions of most of the live wasps were at or above T_a (Fig. 1), and T_{th} of all but one of the live wasps was above T_a after 5 min (Fig. 1a). Dead wasps did not reach room temperature until they had been at room temperature for about 7 min. After 20 min, the T_{th} of live wasps had returned to T_a. These data demonstrate that the live wasps were endothermic, since they elevated T_{th} more quickly than the dead wasps (ANCOVA on log transformed data: $F = 1{,}301.187$, $P < 0.0001$; difference contrast: $P < 0.0001$ for all regions) and reached T_{th} and T_h above T_a. Dead wasps did not appear to be subject to significant evaporative cooling, as the water loss in dead wasps did not differ significantly from 0 (one sample *T* test, $t = -1.380$, $P = 0.240$) and was significantly lower than the water loss in live animals (independent sample *T* test, $t = -5.592$, $P = 0.001$).

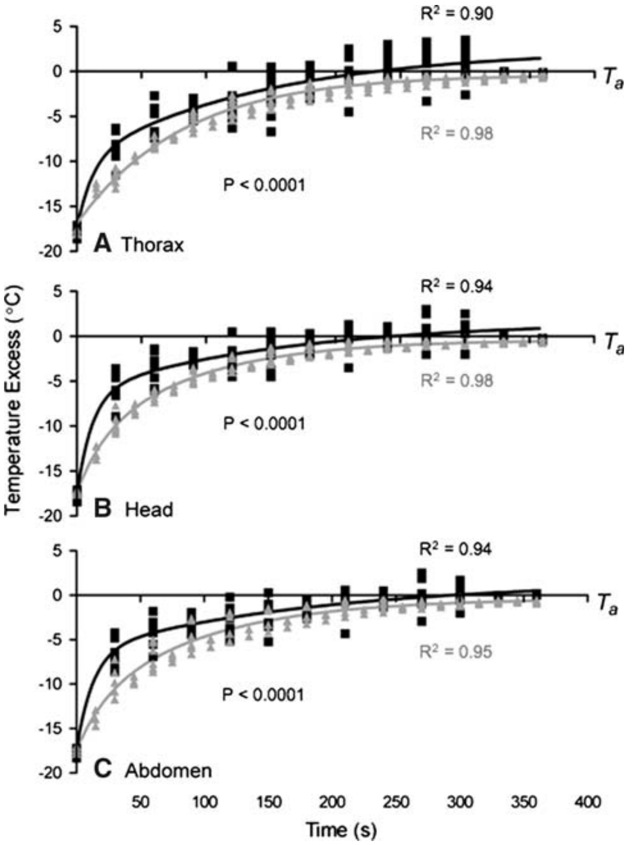

Fig. 1 Time course of body region temperatures of live and dead *P. dominulus* after transfer from 8 to 25°C. Temperature values are relative to ambient temperature (25°C). Each *black square* represents the temperature of a single body region of a single wasp each of whose regions were measured only once. The *points* have been fitted with two phase exponential decay *curves*. Thorax (**a**), then head (**b**), then abdomen (**c**) temperatures were measured for each wasp. *Gray triangles* represent one dead wasp monitored continuously ($n = 6$). *P* values indicate the difference between live and dead wasps

Hibernation measurements

Animals removed from hibernacula had internal temperatures above ambient in all body regions (Fig. 2; repeated measures ANOVA, T_{th}: $P < 0.05$, T_h: $P < 0.05$, T_{ab}: $P < 0.01$, repeated T_{th}: $P < 0.01$). After remaining out for

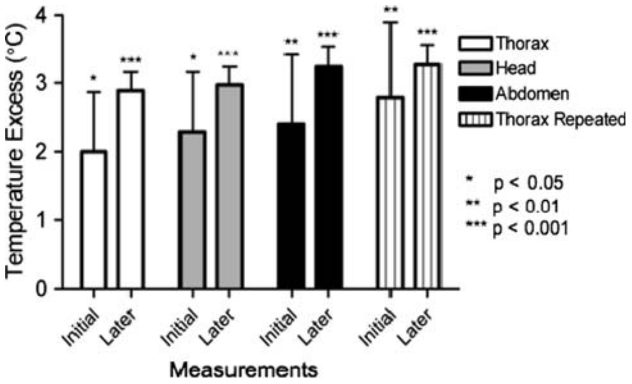

Fig. 2 Temperature excess of body regions of hibernating wasps. The *bars* show the mean and standard error of the recorded temperature. The initial measurements were taken within 10 s of removal from the hibernacula; the post-disturbance measurements were taken after at least 30 s of disturbance. The thorax repeated *bars* indicate a second measurement of thorax temperature taken after the other measurements. *Asterisks* indicate a significant difference from ambient temperature

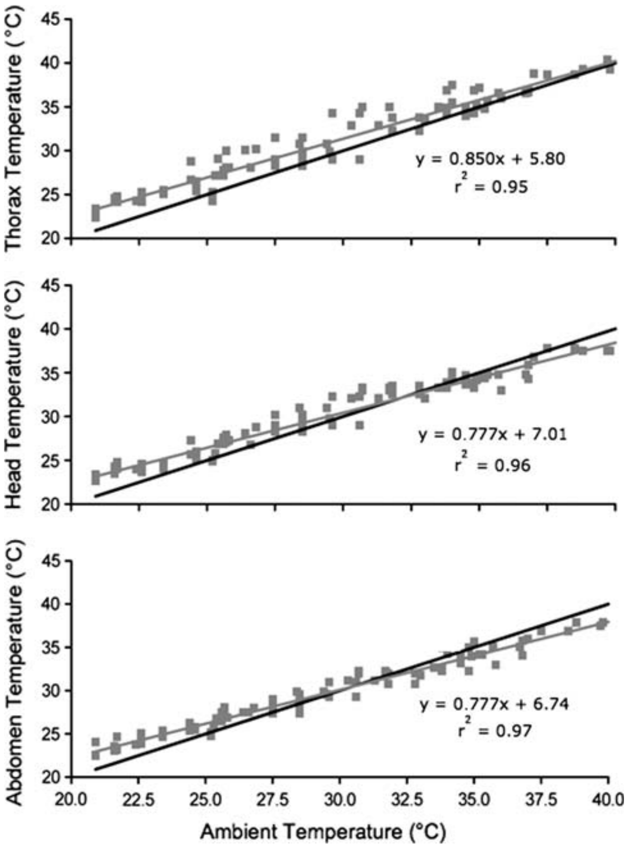

Fig. 3 Body region temperatures of *P. dominulus* workers captured in flight. Each *point* represents the temperature of one region of one wasp. Thorax (**a**), then head (**b**), then abdomen (**c**) temperatures were measured for each wasp. Data for each region were fitted with a linear regression. The slope of each line differed significantly from the slope of $T_{\text{region}} = T_{\text{a}}$ (shown as a *black line*) (ANCOVA $P < 0.0001$)

30–300 s, animals warmed up slightly, but not significantly (repeated measures ANOVA $P > 0.05$ for all regions). Time after removal did not correlate significantly with body region temperature (linear regression $P > 0.05$ for all body regions). This indicates that, at least in the early spring, many individuals maintained a slightly elevated body temperature in the hibernacula, and that, in addition, they warmed up further upon removal.

Flight measurements

Slopes of the internal temperatures of all regions against T_{a} were significantly different from 1 (ANCOVA $F = 3{,}201.766$, simple contrast $P < 0.0001$ for all body regions). At the highest T_{a}, both head and abdomen (T_{ab}) temperatures were 2–3°C below T_{a}, and two animals had T_{th} below T_{a} (Fig. 3). This suggests that *P. dominulus* maintains thermal stability in flight at high temperatures by evaporative cooling.

Discussion

In our experiments, we found that *P. dominulus* maintained elevated body region temperature in an 8°C environment and that the T_{th} of live animals rose more rapidly than the T_{th} of dead individuals after being moved to an approximately 25°C environment. After 5 min in the 25°C environment, live wasps had T_{th} values above T_{a}, indicating endothermy (Fig. 1). This was confirmed by the finding that individuals removed from hibernacula during the spring had elevated body region temperatures (Fig. 2). In individuals removed from hibernation, T_{th} was the lowest body region temperature, a surprising result, considering that heat in Hymenoptera is generally produced by the shivering of wing muscles (Heinrich, 1993). However, when T_{th} was remeasured, it was higher than the other body segments. This suggests that warming occurs following (and perhaps in response to) the measurement procedure. We also found that flying *P. dominulus* workers maintained a restricted T_{th} range relative to the range of T_{a}. In particular, T_{th} was more than 2.5°C above ambient where $T_{\text{a}} = 21$°C, and at or below ambient where $T_{\text{a}} = 40$°C (Fig. 3).

Honeybees can fly when T_{th} is between 30 and 45°C (reviewed in Woods et al., 2005) and can maintain these temperatures when T_{a} is between 15 and 46°C. *P. dominulus* individuals are smaller than honeybees, and thus are unlikely to be able to maintain such tight control over internal temperatures (Porter and Gates, 1969; Bartholomew and Epting, 1975). Indeed, the slope of T_{th} on T_{a} in flying honeybees has been reported at between 0.18 and 0.52 (Heinrich, 1979, 1980a, b; Harrison et al., 1996; Roberts and Harrison, 1999; Woods et al., 2005), while in

P. dominulus it was 0.85. However, at the highest T_a values, both T_h and T_{ab} were below T_a, as found in honeybees (Roberts and Harrison, 1999; Woods et al., 2005) and, to a more limited extent, in yellow jackets (Coelho and Ross, 1996). This could be the case only if *P. dominulus* individuals underwent evaporative cooling, whether passive (through open spiracles) or active (through regurgi-tating droplets of fluid). The abdominal cooling could be a passive effect of water evaporation through spiracles opened for increased gas exchange (Hadley, 1994). However, since T_h also drops below ambient temperature, the wasps are most likely regurgitating fluid and allowing it to evaporate in order to actively cool the head (Esch, 1976; Heinrich, 1979, 1980a). In direct sunlight, *Polistes* wasps do sometimes regurgitate droplets of fluid (Weiner, pers. obs.).

The temperature increase in non-flying *P. dominulus* could be due to shivering of the wing muscles, as in honeybees (Heinrich, 1993), but the maintenance of elevated temperatures in hibernation clusters is unlikely to be the result of shivering, since temperature elevation occurred in all body regions. Also, elevated temperatures in hibernation clusters appear to be maintained over extended periods. However, the hibernation clusters generally contained between four and ten individuals clustered very tightly together; as such, small amounts of heat produced by individuals could cause slight increases in the temperature of all individuals in the cluster. Temperature elevation occurred in all regions in the warm-up experiment as well. In this experiment, wasps were moved from a cool environment to a warmer environment; thus, some of the rapid warming observed may have been due to the inspiration of warmer ambient air, although this cannot explain those wasps that had body region temperatures above ambient. Our results raise the question of whether some or all of this temperature increase could be due to a futile cycle as has been observed in bumblebees (Surholt et al., 1991; Staples et al., 2004). While the futile cycle does not appear to be a large part of warming in bumblebees (Staples et al., 2004), the weak temperature elevation observed at low temperatures in *Polistes* could potentially be caused by a futile cycle. Further testing is required to address this possibility.

The findings that non-flying *Polistes* increase their body region temperature and that flying *Polistes* stabilize thorax temperature in response to changes in air temperature are important first steps toward a broader understanding of *Polistes* temperature relations, autecology, and social structure. For instance, in our measurements of wasps allowed to warm from 8 to 25°C, body region temperature in non-flying animals eventually returned to ambient temperature, suggesting that elevation above ambient temperature was a response to chilling.

Maintaining an elevated body temperature is costly (Heinrich, 1993), and must be figured into the costs and benefits of many *Polistes* behaviors. For example, *Dolichovespula maculata* and *Vespula vulgaris* elevate temperatures prior to aggressive actions against intruders (Heinrich, 1984). If temperatures are raised prior to aggressive interactions with conspecifics or potential nest predators, these interactions may be more costly than had been previously thought (Weiner et al., 2009).

The data described here provide important background for addressing other questions about thermoregulation in *Polistes*. For example, it is unknown whether any primitively eusocial insect maintains elevated brood temperatures, as do bumblebees (Heinrich, 1972), or engage in behavioral fever, as do honeybees (Starks et al., 2000). In addition, thermoregulatory abilities can affect geographic distribution. *P. dominulus* is a very successful invasive species in North America, having spread throughout most of the Eastern USA as well as parts of California and Canada since their first sighting in Massachusetts in 1978 (reviewed in Liebert et al., 2006). The importance of energetic costs and responses to temperature in the geographic distribution of African honeybees has been well documented (Harrison and Hall, 1993; Harrison et al., 2006). Similarly, the impact of temperature on the range of *P. dominulus* may be important for predicting the full extent and effect of its invasion.

Acknowledgments We thank Jon Harrison for his advice, Robert Stevenson for reviewing a draft of this manuscript and the use of his equipment, and Barry Trimmer for the use of his resources. We would also like to thank Sara Lewis for her assistance with statistics and Ansel Payne for his editing help. Funding was provided by the Tufts University Biology Department, REU site 0649190, the PRAXIS Summer Internship of Smith College, and an Essel Student Fellowship for summer research in neurobiology from Williams College.

References

Bartholomew G.A. and Epting R.J. 1975. Allometry of post-flight cooling rates in moths: a comparison with vertebrate homeotherms. *J. Exp. Biol.* **63**: 603–613

Bishop J.A. and Armbruster W.S. 1999. Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. *Funct. Ecol.* **13**: 711–724

Coelho J.R. and Ross A.J. 1996. Body temperature and thermoregulation in two species of yellowjackets, *Vespula germanica* and *V. maculifrons*. *J. Comp. Physiol. B.* **166**: 68–76

Coelho J.R. 2001. Behavioral and physiological thermoregulation in male cicada killers (*Sphecius speciosus*) during territorial behavior. *J. Therm. Biol.* **26**: 109–116

Esch H. 1976. Body temperature and flight performance of honeybees in aservo-mechanically controlled wind tunnel. *J. Comp. Physiol.* **109**: 265–277

Field J., Solis C.R., Queller D.C. and Strassmann J.E. 1998. Social and genetic structure of paper wasp cofoundress associations: Tests of reproductive skew models. *Am. Nat.* **151**: 545–563

Franks N.R. 1989. Thermoregulation in army ant bivouacs. *Physiol. Entomol.* **14**: 397–404

Hadley N.F. 1994. *Water Relations of Terrestrial Arthropods.* San Diego, CA: Academic Press, 356 pp

Harrison J.F., Fewell J.H., Anderson K.E. and Loper G.M. 2006. Environmental physiology of the invasion of the Americas by Africanized honeybees. *Integr. Comp. Biol.* **46**: 1110–1122

Harrison J.F. and Hall H.G. 1993. African-European honeybee hybrids have low nonintermediate metabolic capacities. *Nature* **363**: 258–260

Harrison F.F., Nielsen D.I. and Page R.E. 1996. Malate dehydrogenase phenotype, temperature and colony effects on the flight metabolic rate in the honey-bee, *Apis mellifera*. *Funct. Ecol.* **10**: 81–88

Heinrich B. 1972. Physiology of brood incubation in the bumblebee. *Nature* **239**: 223–225

Heinrich B. 1979. Keeping a cool head: Honeybee thermoregulation. *Science* **205**: 1269–1271

Heinrich B. 1980a. Mechanisms of body-temperature regulation in honeybees, *Apis mellifera*. I. Regulation of head temperatures. *J. Exp. Biol.* **85**: 61–72

Heinrich B. 1980b. Mechanisms of body-temperature regulation in honeybees, *Apis mellifera*. II. Regulation of thoracic temperatures at high air temperatures. *J. Exp. Biol.* **85**: 73–87

Heinrich B. 1984. Strategies of thermoregulation and foraging in two vespid wasps, *Dolichovespula maculata* and *Vespula vulgaris*. *J. Comp. Physiol. B* **154**: 175–180

Heinrich B. 1985. The social physiology of temperature regulation in honeybees. In: *Experimental Behavioral Ecology and Sociobiology* (Hölldobler B. and Lindauer M., Eds), Sunderland, MA: Sinauer, pp 393–406

Heinrich B. 1993. *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation.* Cambridge, MA: Harvard University Press, 601 pp

Hunt J.H. 2006. Evolution of castes in *Polistes*. *Ann. Zool. Fenn.* **43**: 407–422

Korb J. 2003. Thermoregulation and ventilation of termite mounds. *Naturwissenschaften* **90**: 212–219

Kovac H. and Stabentheiner A. 1999. Effect of food quality on the body temperature of wasps (*Paravespula vulgaris*). *J. Insect Physiol.* **45**: 183–190

Liebert A.E., Gamboa G.J., Stamp N.E., Curtis T.R., Monnet K.M., Turillazzi S. and Starks P.T. 2006. Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. *Ann. Zool. Fenn.* **43**: 595–624

Mead F., Pratte M. and Gabouriaut D. 1990. Influence of a difference in temperature and day-time conditions on the progression of the society life in *Polistes dominulus* Christ reared at the laboratory (Hymenoptera: Vespidae). *Insect. Soc.* **37**: 236–250

Nonacs P., Liebert A.E. and Starks P.T. 2006. Transactional skew and fitness return models fail to predict patterns of cooperation in wasps. *Am. Nat.* **167**: 467–480

Porter W.P. and Gates D.M. 1969. Thermodynamic equilibria of animals. *Ecol. Monogr.* **39**: 227–244

Reeve H.K., Starks P.T., Peters J.M. and Nonacs P. 2000. Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 75–79

Roberts S.P. and Harrison J.F. 1999. Mechanisms of thermal stability during flight in the honeybee *Apis mellifera*. *J. Exp. Biol.* **202**: 1523–1533

Staples J.F., Koen E.L. and Laverty T.M. 2004. ‘Futile cycle’ enzymes in the flight muscles of North American bumblebees. *J. Exp. Biol.* **207**: 749–754

Starks P.T., Blackie C.A. and Seeley T.D. 2000. Fever in honeybee colonies. *Naturwissenschaften* **87**: 229–231

Steiner A. 1930. Die Temperaturregulierung im Nest der Feldwespe (*Polistes gallica* var. *biglumis* L.). *Z. Vgl. Physiol.* **11**: 461–502

Sumana A. and Starks P.T. 2004. Grooming patterns in the primitively eusocial wasp *Polistes dominulus*. *Ethology* **110**: 825–833

Surholt B., Greive H., Baal T. and Bertsch A. 1991. Warm-up and substrate cycling in flight muscles of male bumblebees, *Bombus terrestris*. *Comp. Biochem. Physiol.* **98**: 299–303

Weiner S.A., Woods W.A. and Starks P.T. 2009. The energetic costs of stereotyped behavior in the paper wasp, *Polistes dominulus*. *Naturwissenschaften* **96**: 297–302

West-Eberhard M.J. 2006. Polistine passions. *Ann. Zool. Fenn.* **43**: 387–389

Wilson E.O. 1971. *The Insect Societies.* Belknap Press of Harvard University Press, Cambridge, MA. 548 pp

Woods W.A., Heinrich B. and Stevenson R.D. 2005. Honeybee flight metabolic rate: does it depend on air temperature? *J. Exp. Biol.* **208**: 1161–1173