

A role for thermoregulation in the *Polistes dominulus* invasion: a comparison of the thermoregulatory abilities of the invasive wasp *P. dominulus* and the native wasp *P. fuscatus*

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Abstract Social insects are excellent invaders that have had negative impacts on native species and humans. Many invasive species move from warmer to cooler climates. For these species, thermal adaptations may both be important for their ability to invade and to limit their invasion range. The invasion of *Polistes dominulus* into North America provides an example of a primitively eusocial invader from a warmer climate. We studied the differences in thermoregulation between *P. dominulus* and the native *P. fuscatus*. We found that, during flight, thorax temperature in *P. fuscatus* was less affected by ambient temperature than thorax temperature of *P. dominulus*. We also found that *P. dominulus* and *P. fuscatus* showed different patterns of warming after removal from a cold environment. Unlike *P. dominulus*, live *P. fuscatus* never fully cooled down in a cold environment. *P. fuscatus* also reached their relative minimum flight temperatures earlier than *P. dominulus*, but *P. dominulus* maintained higher elevated temperatures for longer. These differences in thermoregulatory ability suggest that the lower winter survival of *P. dominulus* could be offset by a greater thermal tolerance during flight, while the lower thermal tolerance of *P. fuscatus* in flight is offset somewhat by better thermoregulatory ability.

Keywords Exotic species · Hymenoptera · Eusociality · Thermoregulation

Introduction

Since the process of globalization began, many exotic species have found their way to new habitats around the world, including over 50,000 species in the USA alone (Pimentel et al., 2004). Of all invaders, social insects can be particularly effective because a single female can bring the sperm of one or more males (Moller, 1996). This means that one social insect invasion event can have the genetic impact of several invasion events in other species. In some cases, social factors such as unicolonialism (the mutual tolerance of interconnected neighboring colonies) following a genetic bottleneck can also help invasive eusocial insects to out-compete natives (e.g., Starks, 2003).

Eusocial insects are group living animals with overlapping generations, reproductive division of labor and communal brood care (Wilson, 1971). Although eusociality has played an important role in many biological invasions, the invasion of *Polistes dominulus* to North America is the first time that the invasion of a primitively eusocial insect has been studied in detail (see Liebert et al., 2006). Workers in primitively eusocial insects are totipotent, meaning that all females can mate and produce offspring (Wilson, 1971). Therefore, in primitively eusocial species, an isolated worker could potentially form a new colony, which could have a significant effect on the spread of an invasive species. *P. dominulus* was first found in the USA in Massachusetts in 1978, and has since spread rapidly throughout the USA and Canada (Johnson and Starks, 2004; Liebert et al., 2006). *P. dominulus* has been a very successful invader, and this

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may be due in large part to its high production of reproductives (Gamboa et al., 2002).

There are many features of *P. dominulus* biology that may facilitate production of more reproductives than native congeners, but an important one is that *P. dominulus* colonies produce workers earlier in the season (Pickett and Wenzel, 2000; Gamboa et al., 2002). After temperate *Polistes* gynes emerge from hibernation, they found nests alone or in associations of a few foundresses (see Reeve, 1991) or wait and adopt abandoned nests (Starks, 1998, 2001). In the early founding period, prior to worker emergence, foundresses must forage for themselves and for the developing brood. This period has a high risk of nest loss, and the sooner that workers emerge, the better is the colony's chance of surviving (see Reeve, 1991). Finally, the earlier production of workers in *P. dominulus* provides those workers with more time to forage for and rear a large workforce, thus producing a large brood of reproductives.

Polistes dominulus are particularly successful in cities (see Liebert et al., 2006), which has allowed them to spread throughout New England, in regions previously dominated by *P. fuscatus*. As befits the name, nests of *P. dominulus* are commonly found on the eaves of buildings and other human habitations. Both urban environments and proximity to heated buildings provide a slightly warmer environment than the surrounding climate (Landsberg, 1981). While *P. dominulus* is found in most parts of central and southern Europe, it is of highest abundance in Mediterranean Europe and northern Africa (see Cervo et al., 2000), which are warmer and have milder winters than many areas of North America where *P. dominulus* is now found (The Weather Channel, 2010). *P. dominulus* gynes do not appear to survive hibernation as well as *P. fuscatus* gynes (Gamboa et al., 2004), which may limit their invasion success in areas with particularly harsh winters. Indeed, many gynes are lost during this overwintering period (Starks, 2001; Gamboa et al., 2004).

The higher susceptibility of *P. dominulus* to death during winter suggests that thermoregulation may be important to the invasion of *P. dominulus* into North America. On the one hand, *P. dominulus* is less successful than the native congener at overwintering in New England, which should serve to decrease the population size. On the other hand, *P. dominulus* begins foraging earlier in the day than *P. fuscatus* and rears its first brood more quickly (Gamboa et al., 2004). If *P. dominulus* are able to fly at lower air temperatures, they may be able to forage more effectively during nest initiation, which would allow them to more effectively provision their early brood, possibly shortening their development time. *P. dominulus* could potentially fly at lower temperatures either by more effectively maintaining an elevated thorax temperature or by flying at a wider range of thorax temperatures, therefore needing to spend

less energy warming at cold temperatures. In this study, we explored the differences in thermoregulatory abilities between *P. dominulus* and *P. fuscatus*. These differences could help both to explain the success of the *P. dominulus* invasion and to predict its limits.

Methods

Animals

In the summer of 2007, combs and associated adults were collected from 29 nests of *P. dominulus* and 12 nests of *P. fuscatus* found in Waltham, Grafton, and Carlisle, MA. In the summer of 2008, an additional 32 *P. dominulus* and 28 *P. fuscatus* nests were collected from the same sites. The nests were maintained in 0.037 m³ cages on the Tufts campus in Medford, MA, USA. Colonies were kept on a summer light cycle (17L:7D) at ~26°C and provided with wax worms and a 50% sugar water solution ad libitum (Sumana and Starks, 2004). In 2008, colonies were provided with construction paper for nest construction. All individuals tested were females that emerged more than 2 weeks prior to the first male and, thus, were assumed to be workers (Mead et al., 1990). No live individual was used in more than one test, as the 24-h mortality rate from measurement of internal temperature was high (>30%) and the procedure might alter the wasps' ability to maintain temperature.

Temperature measurements

Warm-up measurements

To compare the ability of *P. dominulus* and *P. fuscatus* workers to defend their body temperature during exposure to cold air (~8°C) and to elevate it when returned to normal temperature (~26°C), the body region temperatures of live and dead individuals were measured during the 10 min following their return to laboratory air temperature. Dead wasps were measured as they equilibrated from 8°C to ambient temperature (T_a) to establish a baseline to which living wasps could be compared (e.g., Bishop and Armbruster, 1999). Dead wasps were freeze killed at least 1 h, but <8 h, before use, to prevent desiccation. Live and dead wasps were placed in a plastic bag and kept for 10 min at 8°C. The validation of this procedure was presented by Weiner et al. (2010). After cooling, wasps were moved to a temperature-controlled room kept at $26 \pm 0.6^\circ\text{C}$, while still restrained. Body region temperature was measured by inserting 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). The thorax was measured first, followed by head and

then abdomen. All these measurements were taken within 10 s.

Each dead wasp was measured continuously for 10 min and the temperature was recorded every 30 s (Weiner et al., 2010). Each live wasp was used for only one data point. Temperatures are reported as temperature excess relative to room temperature to compensate for variation in room temperature. An ANCOVA was done on the log of the temperature over time to compare the live wasps to the dead ones. The average of the dead wasp body region temperature for each time point for the appropriate species was subtracted from each live wasp time point. A non-linear regression was used on the cumulative difference between live and dead animals over time to compare the two species. Most of the warming data on *P. dominulus* found in this paper have been reported by Weiner et al. (2010).

Flight measurements

To compare the temperatures of flying *P. dominulus* and *P. fuscatus*, the body region temperatures of individuals were recorded immediately following capture from flight. For each test, the wasp was released in a temperature-controlled room and allowed to fly for 30–60 s (as in Weiner et al., 2010). After a wasp had flown for 30–60 s, it was captured in a net and immediately restrained in the net against a piece of soft foam. Thorax temperature (T_{th}), head temperature (T_h), and then abdomen temperature (T_{ab}) were measured within 10 s using the Physitemp thermometer and probe. Body region temperatures were regressed upon the corresponding T_a values, and the slopes were compared between species and to a slope of 1 (representing region temperature = T_a) using an ANCOVA. The *P. dominulus* portion of this data set has been reported by Weiner et al. (2010).

Results

Warm-up measurements

Live *P. dominulus* and *P. fuscatus* individuals differed significantly from dead conspecifics in their warming patterns (ANCOVA on log-transformed data, *P. fuscatus*: $F = 71.264$, *P. dominulus*: $F = 83.998$, $p < 0.0005$ for both species). Both species eventually reached temperatures above the ambient. The warming patterns of the two species (relative to dead conspecifics) differed from each other (non-linear regression: thorax, $p = 0.008$; head, $p = 0.097$; abdomen, $p < 0.001$; Fig. 1). These results indicate that both species show endothermy. Since the patterns of warming relative to dead conspecifics differed between the species, our data suggest that the rates of warming differ in

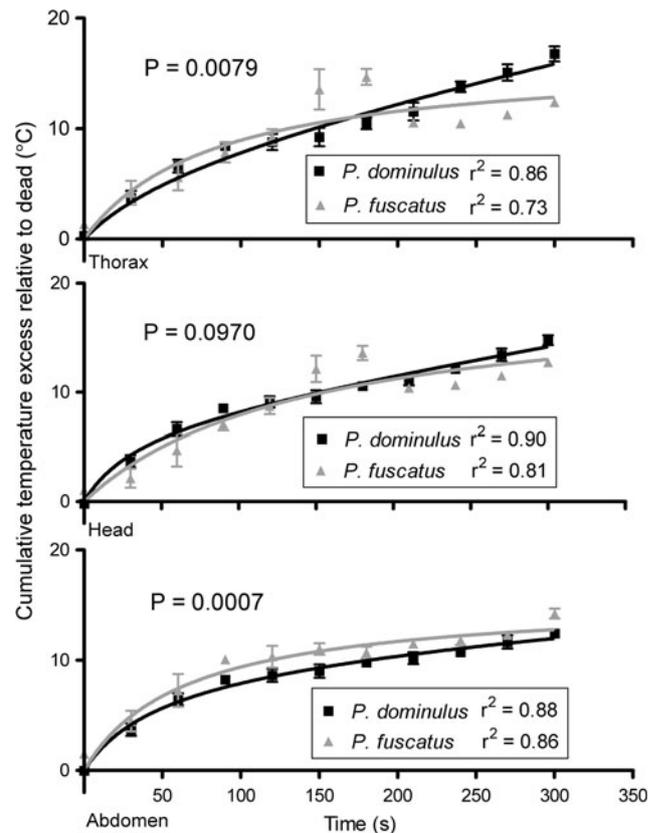


Fig. 1 Time course of cumulative body region temperature excess of *P. dominulus* and *P. fuscatus* after transfer from 8° to 26°C. Temperature values are relative to the average temperature of a dead animal of the same species under the same conditions. Each point is cumulative, representing the total excess temperature since removal. Points indicate means and error bars show standard deviation. Each time point represents eight *P. dominulus* and six *P. fuscatus*

ways that are not fully explained by body mass. If the differences were due only to body mass, the patterns of warming for live animals relative to dead conspecifics would be similar between the species. This difference suggests that active warming patterns differ between the species.

Flight measurements

P. dominulus did not initiate flight below ~22°C, while *P. fuscatus* initiated flight at temperatures below 20°C, although these flights did not last for the full 30 s. The slopes of regressions for all body regions of both species were significantly different from 1 (95% confidence intervals of slopes from regression for *P. dominulus*: thorax = 0.88 ± 0.04 , head = 0.79 ± 0.03 , abdomen = 0.78 ± 0.03 ; *P. fuscatus*: thorax = 0.75 ± 0.08 , head = 0.74 ± 0.06 , abdomen = 0.78 ± 0.07 , Fig. 2). The slopes of body region temperature on T_a during flight differed significantly between species (Fig. 2, ANCOVA, thorax: $p = 0.002$;

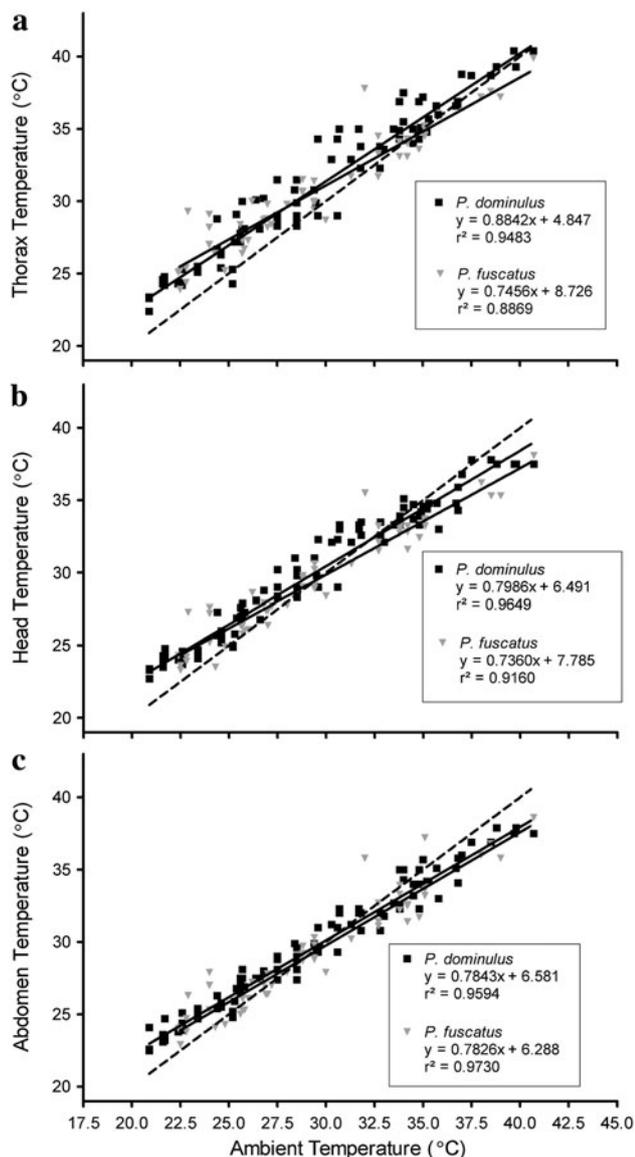


Fig. 2 Body region temperatures of *P. dominulus* and *P. fuscatus* workers captured in flight. Each point represents the temperature of one region of one wasp. Thorax (a), head (b), and then abdomen (c) temperatures were measured for each wasp. Data for each region were fitted with a linear regression. The slope of each line differed significantly from the slope of $T_{\text{region}} = T_a$ (shown as a black dotted line) (ANCOVA, $n = 156$ *P. dominulus*, 50 *P. fuscatus*, $p < 0.0001$)

head: $p = 0.001$; abdomen: slope $p = 0.936$, intercept $p = 0.021$). In particular, the slope of T_{th} on T_a was significantly less steep in *P. fuscatus* than in *P. dominulus* (slope confidence interval, *P. dominulus*: thorax = 0.88 ± 0.04 , *P. fuscatus*: thorax = 0.75 ± 0.08). This indicates that *P. fuscatus* defends a narrower T_{th} range than *P. dominulus*. Weight did not have a significant effect on T_{th} relative to T_a in flight (multiple linear regression, $n = 58$, $t = 0.76$, $p = 0.45$).

Discussion

Our data show that *P. fuscatus* and *P. dominulus* differ in their thermoregulatory abilities in ways that could affect invasion success. Differences in warming behavior following removal from a cold environment may indicate thermoregulatory differences that affect the ability to start a colony early in the season. Live *P. fuscatus* maintained an elevated T_{th} during 10 min at 8°C, unlike live *P. dominulus* and the dead individuals of both species. The ability to maintain an elevated temperature in cold environments could help *P. fuscatus* (whose minimum flight T_{th} is higher than that of *P. dominulus*) avoid being trapped by cool patches in early spring. However, after approximately 3 min in the ~26°C environment, live *P. dominulus* individuals had actually warmed up more than *P. fuscatus*. The ability to warm up relatively quickly and maintain elevated temperatures in response to favorable conditions could allow *P. dominulus* to make more flights in cooler temperatures, such as those that occur during the founding period.

Despite the willingness and ability of *P. dominulus* to maintain elevated temperatures, *P. fuscatus* reached its minimum observed flight temperatures 30 s earlier. The ability to warm up quickly also may help *P. fuscatus* gynes survive the winter by helping them evade predators in early spring or late fall. In flight, T_{th} in *P. fuscatus* was less affected by T_a than the T_{th} of *P. dominulus*, especially at higher temperatures, thus expanding the range of air temperature within which *P. fuscatus* can fly. While the larger size of *P. fuscatus* workers may be important to their thermoregulatory abilities at rest, we found no effect of weight on T_{th} in flight, suggesting that other characteristics are important for allowing them to defend a narrow range of flight temperatures.

As has been demonstrated in the example of the Africanized honeybee, thermoregulation can be important in both allowing and limiting social insect invasions (Harrison and Fewell, 2002; Harrison et al., 2006). The *P. dominulus* invasion resembles that of the Africanized honeybee in several ways: both are social insect invaders from a region with milder winters, both invaders are highly productive during the summers, and both invaders have lower survival than their native or naturalized congener during the winter.

Our data suggest that thermoregulation may be important to explaining the range of the *P. dominulus* invasion. If *P. fuscatus* need to warm up to a higher T_{th} before sustaining flight, despite their ability and willingness to undertake brief bouts of flight at slightly lower ambient temperatures, it may partially explain why they do less foraging in the spring (see Liebert et al., 2006). Making more foraging trips in spring could facilitate the earlier rearing of workers by *P. dominulus* (Gamboa et al., 2004), which shortens the risky preworker period.

P. dominulus, being smaller and from warmer climates, may spend more energy during the winter elevating their temperature to prevent freezing, decreasing their overwinter survival. While *P. fuscatus* maintained slightly elevated temperatures in a short-term cold environment, *P. dominulus* has been observed to maintain elevated temperatures in hibernacula (Weiner et al., 2010). *P. fuscatus* gynes are both better able to maintain these elevated temperatures and also are well-prepared for winter with cryoprotectants (Gibo, 1972; Strassmann et al., 1984). Resting metabolic heat may play a role in elevating hibernacula temperatures, although facultative endothermy would appear to exceed a reasonable energy budget (Masters et al., 1988). While our study was done on workers, caste differences in *Polistes* are small, and there is overlap between workers and reproductives in many traits including size. Therefore, we expect that this study should apply to gynes and foundresses as well; however, future work should look at reproductives to confirm this.

In addition, the maintenance of elevated temperatures in *P. dominulus* upon warming to more moderate temperatures could be costly in certain environments (Rau, 1930). For example, in New England, temperatures during the winter can vary widely, leaving a gyne stranded in cold environments or causing her to use up her energy before resources are available (Table 1). The ability of *P. fuscatus* to maintain elevated temperatures in cold environments could be very beneficial if a foundress encounters spatially or temporally limited cold zones. Indeed, *P. dominulus* foundresses on warm days in early spring have been observed to land on patches of remaining snow and be unable to take off due to the thermal mass (pers. obs.).

P. dominulus has been a very successful invader into North America (see Liebert et al., 2006). The success of this invasion seems to be due, at least in part, to the fact that *P. dominulus* colonies are more productive than *P. fuscatus* colonies (Gamboa et al., 2002). This increased productivity

Table 1 Average High and low winter and summer temperatures for locations in Eastern North America and Mediterranean Europe (The Weather Channel 2010)

	Summer high	Summer low	Winter high	Winter low
Hartford, CT	27.6	15.7	3.3	-7.2
Boston, MA	26.5	17.0	3.9	-4.1
Portland, ME	24.6	13.5	0.9	-9.1
Burlington, VT	25.9	14.3	-1.5	-10.9
Mobile, AL	32.7	21.7	17.0	11.0
Rome, Italy	29.6	15.7	12.6	2.4
Madrid, Spain	30.7	15.2	11.3	1.1
Athens, Greece	31.3	6.9	13.5	7.0

Bold values indicate the lower temperatures to which *P. dominulus* is exposed in New England winters

is likely at least partially because they produce workers earlier (see Liebert et al., 2006). *P. dominulus* may be able to produce workers earlier because *P. dominulus* foundresses make more foraging trips (Gamboa et al., 2002). *P. dominulus* foundresses also make shorter foraging trips, suggesting that their foraging may be more efficient (Gamboa et al., 2002). If *P. dominulus* does not need to maintain as narrow a temperature range and is able to fly at higher T_{th} , the differences in their thermoregulatory behavior may help explain the differences in their foraging patterns. Coupled with the slightly shorter development time of *P. dominulus*, the differences in thermoregulation between *P. dominulus* and *P. fuscatus* may help explain the larger colony sizes of *P. dominulus*, especially in areas with short summers, as in New England.

Our data show that *P. dominulus* and *P. fuscatus* differ significantly in their ability to warm up after removal from cool environments, and in their ability to defend an optimal thorax temperature in flight. These differences may partially explain the high overwintering mortality and the high early season productivity of *P. dominulus*. As such, thermoregulatory behavior is likely to influence invasion patterns in this system.

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