**Insectes Sociaux**

# The cost of flight: a role in the *Polistes dominulus* invasion

**S. A. Weiner · K. Noble · C. T. Upton ·
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**Abstract** *Polistes dominulus* is a primitively eusocial paper wasp from Mediterranean Europe that is invasive to North America. In Eastern North America, *P. dominulus* is in competition with *P. fuscatus*. One reason for the success of *P. dominulus* is that their colonies produce more reproductive offspring than *P. fuscatus* colonies. A partial explanation for this difference is that *P. dominulus* foundresses make more foraging trips in the pre-worker period, which likely helps them to rear workers more quickly. In comparing the species, we found that *P. dominulus* had a lower absolute flight metabolic rate, but that *P. fuscatus* had a lower mass-specific flight metabolic rate. In addition, in *P. fuscatus*, wingloading correlated with flight metabolic rate, but that this was not the case in *P. dominulus*. This suggests that *P. fuscatus* is not able to transport large loads inexpensively. Therefore, the lower overall cost of transport of *P. dominulus* may provide an advantage by allowing the foundresses to make more relatively efficient foraging trips. In addition, we compared time in flight by *P. dominulus* and *P. fuscatus* over a range of temperatures and found that while *P. fuscatus* flew well over a broad range of temperatures, *P. dominulus* had a relatively narrow range of optimal temperatures for flight (30–33°C). These differences may help explain both the success and the limitations of the *P. dominulus* invasion.

**Keywords** Eusocial · Hymenoptera · Metabolism · Energetics · Thermoregulation

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## Introduction

From monkeys stealing fruit in Costa Rica (Engeman et al., 2010) to the western corn rootworm in Europe (Carrasco et al., 2010), invasive species have become a major economic and ecological problem in our modern global society. As our global economy continues to spread species around the world, and changing land use and global climate change alter habitats in ways that do not match the conditions under which native species evolved, invasions are expected to become an even bigger issue. Social insects are particularly adept invaders, due to both the sperm storage capabilities of hymenopteran females and the ability of workers to greatly multiply the reproductive output of an individual foundress (Moller, 1996).

*Polistes dominulus* is a primitively eusocial paper wasp native to Mediterranean Europe that has become a very successful invader in North America (reviewed in Liebert et al., 2006). In much of Eastern North America, *P. dominulus* is found alongside a native congener, *P. fuscatus* (reviewed in Liebert et al., 2006). *P. dominulus* has been successful in large part because *P. dominulus* colonies

produce more reproductives than *P. fuscatus* colonies (Table 1, Gamboa et al., 2002). In order to address how *P. dominulus* is able to outproduce *P. fuscatus*, first it is helpful to understand how the colony cycles of the two species differ.

*Polistes dominulus* workers emerge earlier in the summer than *P. fuscatus* workers (Table 1, Gamboa et al., 2004). On *Polistes* colonies, until the first workers emerge, the foundress or foundresses do all the foraging. Foraging is a risky and energetically expensive job, as it involves flight, and for single foundress colonies, requires the foundress to leave the colony undefended. The sooner that the first workers emerge, the less likely a colony is to fail (Reeve, 1991). In addition, the sooner workers emerge, the more workers a colony can rear to help provide for reproductives at the end of the summer. The earlier emergence of workers in *P. dominulus* could partially explain how *P. dominulus* colonies are able to produce more reproductives.

However, this opens the question of how *P. dominulus* colonies produce workers earlier in the season. One partial explanation of this is the fact that *P. dominulus* foundresses make more foraging trips during the pre-worker period (Gamboa et al., 2002). While foraging can be hazardous, early colonies are energy limited (Rossi and Hunt, 1988), and additional foraging trips would likely increase the growth rate of the brood (Mead and Pratte, 2002). One way that *P. dominulus* foundresses might be able to benefit from making more foraging trips is if flight is less energetically costly for them than for *P. fuscatus*. This would allow them to spend less energy to bring back the same amount of food, making foraging more energetically efficient.

In this study, we compare the energetic costs of flight in *P. dominulus* and *P. fuscatus* at a range of temperatures. This allows us to test both whether flight metabolic rate is generally lower for *P. dominulus* and whether *P. dominulus* has a lower cost of transport at the low spring temperatures that foundresses would experience.

## Methods

### Animal care

In the summer of 2009, 19 *P. fuscatus* colonies and 22 *P. dominulus* colonies were gathered from field sites in Waltham, Carlisle and Grafton, MA. The colonies were maintained in 0.037 m$^3$ cages on the Tufts campus in Medford, MA. Colonies were provided with wax worms and a 50% solution of sugar in water, as well as construction paper for nest-building. All individuals tested emerged during the summer from these colonies. No individual was used in more than one test.

### Flight measurements

For each measurement, one individual was placed in a respirometry chamber, inside a transparent temperature control chamber set up outside, in the shade (Woods et al., 2005). Temperature was raised by means of a warm air blower whose output was ducted by 3.2 cm PVC tubing through a fitting in the floor of the cabinet and directed away from the respirometry chamber; a 5 cm aperture in the top Plexiglas panel of the cabinet served as an exhaust (Woods et al., 2005). The respirometry chamber was a 1L Pyrex Erlenmeyer flask lined with fluon to discourage landing. Flight was encouraged by tapping or moving the flight

**Table 1** Differences between *P. dominulus* and *P. fuscatus* in North America

| Trait | P. dominulus | P. fuscatus | Source |
|---|---|---|---|
| Genetic diversity | High | Presumed high | Johnson and Starks (2004), Liebert et al., (2006) |
| Native location | Europe | North America | Liebert et al., (2006) |
| Aggressiveness | Low | Moderate | Silagi et al., (2003), Curtis and Stamp, (2006) |
| Colony productivity | High | Moderate | Gamboa et al., (2002, 2004) |
| Timing of first workers | Early | ~6–7 days later | Gamboa et al., (2002, 2004) |
| Worker size | ~80 mg | ~100 mg | Personal observation |
| # of foraging trips per day | 28.5 | 15.3 | Liebert et al., (2006) |
| Duration of foraging trips | 781 s | 468 s | Liebert et al., (2006) |
| Nectar stores | More nectar | Less nectar | Silagi et al., (2003) |
| Colony usurpation | Rare | Frequent | Gamboa et al., (2004) |
| Winter survivorship | Low | Moderate | Gamboa et al., (2004) |
| Flight thermoregulation | Low | Moderate | Weiner et al., (2011) |
| Warming | Warmer | Faster | Weiner et al., (2011) |
| Immune function | Weaker | Stronger | Wilson-Rich and Starks, (2010) |

chamber (Woods et al., 2005). Animals that tried to land were discouraged by tapping the flight chamber, but those that persisted in doing so were not prevented. All periods of flight were recorded, and only the longest flight was used for each animal.

$CO_2$ 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. Air scrubbed of water and carbon dioxide by soda lime-Drierite-soda lime columns was flowed at 860 cc min$^{-1}$ through the respirometry chamber. Excurrent $CO_2$ concentration was sampled every 6 s; each recorded value represented the mean excurrent $CO_2$ concentration for the previous 6 s as calculated by the Li-Cor unit (see Woods et al., 2005). Air temperature ($T_a$) inside the chamber was monitored to ±0.1°C using a Physitemp BAT 12 field thermometer (Physitemp Instruments, Clifton, NJ, USA) with its sensor inserted through the chamber stopper.

Respirometry data were collected and analyzed in Datacan V (Sable Systems International, Las Vegas, NV). Behavioral observations were synchronized with respirometry data taking into account time lag and washout properties of the respirometry system as determined by bolus injection (Bartholomew et al., 1981). We used the standard Z transform implemented in Datacan V. Flight metabolic rate (FMR) was calculated as the amount of CO2 produced during flight, and mass-specific FMR was calculated by dividing FMR by the wasp's body weight.

Flight speed

The flight speed of *P. dominulus* was measured by releasing foragers and timing their return to the area of their nest. Six colonies were founded naturally in wasp boxes arrayed behind a fence. Returning foragers were captured in a net and carried 10 m away from the fence while stored in a 50 mL Falcon tube. They were released and allowed to exit the tube without additional disturbance. The time it took each wasp to reach the fence was recorded. Only wasps that took a relatively straight path back to the fence were included in the data. This result was compared to previous work showing size-related differences in speed among closely related animals in order to calculate an expected speed for *P. fuscatus* (McNeill, 2002).

Wingloading

The right wings were removed from the wasps, and photographed under magnification. Images were converted to binary files in ImageJ. If necessary, "unsharp mask" in Adobe Photoshop was first used to clarify the distinction between the wings and the background. Then, the wings were measured using "analyze particles" in ImageJ. The animal's weight divided by the recorded wing size was reported as wingloading (Dudley, 2000).

## Results

In both *P. dominulus* and *P. fuscatus*, ambient temperature ($T_a$) was significantly associated with time in flight (Fig. 1). In *P. dominulus*, the flights of the longest duration occurred at a $T_a$ of 30–33°C, while in *P. fuscatus*, flight time increased with $T_a$ up through our highest temperature measurements at 37°C (nonlinear regression comparison, $F = 2.679$, $p = 0.033$, Fig. 1). Despite this correlation of time in flight with $T_a$, no correlation was found between $T_a$ and $CO_2$ production in either species (linear regression, *P. dominulus*: $r^2 = 0.008$, $p = 0.498$; *P. fuscatus*: $r^2 = 0.030$, $p = 0.309$, Fig. 2).

The average flight speed of *P. dominulus* was $3.84 ± 0.89$ m s$^{-1}$. Our observed flight speed for *P. dominulus* matched predicted flight speeds based on previous work in other animals. The predicted maximum flight for *P. dominulus* based on size would be 4.3 m s$^{-1}$, or about 12% greater than our measurement (McNeill, 2002). We were not able to get direct flight speed measurements for *P. fuscatus*. However, these calculations predict that *P. fuscatus* would have a flight speed of 3.2% higher, or 3.96 m s$^{-1}$.

When the total rate of $CO_2$ production of both species in flight (absolute flight metabolic rate = FMR) was compared, *P. fuscatus* produced more $CO_2$ than *P. dominulus* for the same period of flight (Mann–Whitney $U = 994$, $p = 0.001$, Fig. 3a). However, when mass-specific $CO_2$ production was considered, *P. dominulus* produced more
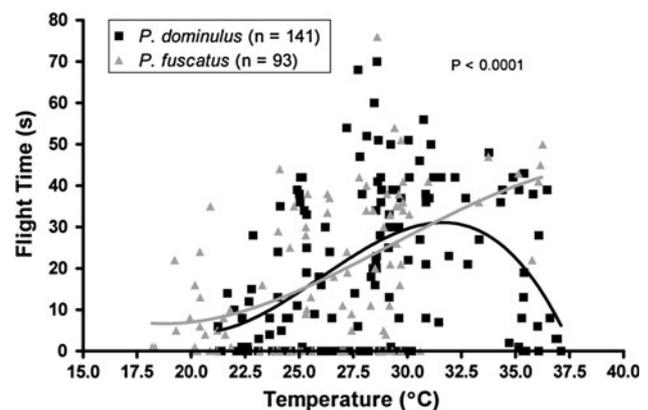


**Fig. 1** Longest time flown by $T_a$ for *P. dominulus* and *P. fuscatus*. Each point represents the longest flight recorded for one individual. The curves are third order polynomials. *p* value is for the comparison between the two polynomials
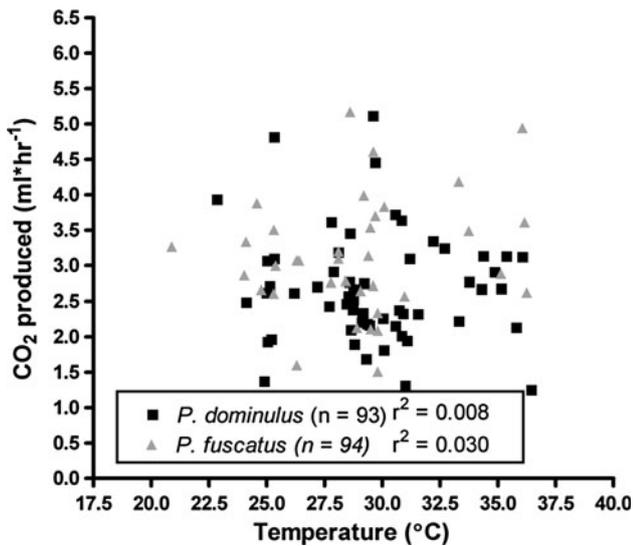
**Fig. 2** Rate of energy use in *P. dominulus* and *P. fuscatus* relative to temperature. Each point represents the energy rate of the longest flight recorded for one individual. Only flights over 25 s are shown. A linear regression was performed on the data
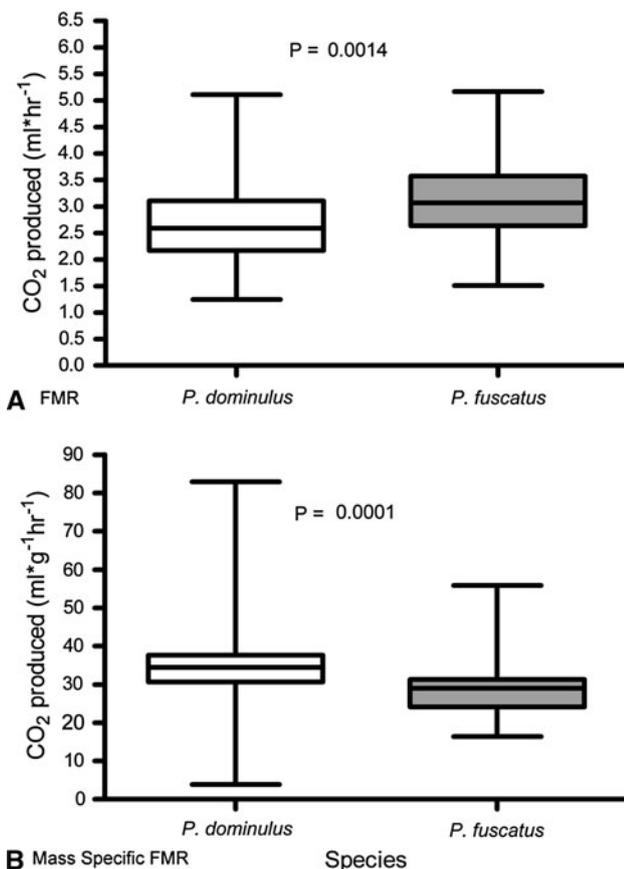


**Fig. 3** Flight metabolic rate for *P. dominulus* and *P. fuscatus*. Absolute flight metabolic rate is shown in (**a**) and mass-specific flight metabolic rate is shown in (**b**). Only the longest flight was used for each individual. Only flights over 25 s are included. (Mann–Whitney *U* Test, FMR: $U = 994$, Mass-specific FMR: $U = 386$)

$CO_2$ than *P. fuscatus* per gram of body mass (Mass-Specific FMR, Mann–Whitney $U = 386$, $p = 0.0001$, Fig. 3b).

We used the measured speed for *P. dominulus* and 3.96 m s$^{-1}$ for *P. fuscatus* (calculated based on McNeill, 2002), and calculated the cost of transport to be $2.5 \times 10^{-3} \pm 7.1 \times 10^{-4}$ ml g$^{-1}$ m$^{-1}$ for *P. dominulus* and $2.1 \times 10^{-3} \pm 5.6 \times 10^{-4}$ ml g$^{-1}$ m$^{-1}$ for *P. fuscatus*. However, the total cost of flying a given distance would be $1.9 \times 10^{-4} \pm 5.5 \times 10^{-5}$ ml m$^{-1}$ for *P. dominulus* and $2.3 \times 10^{-4} \pm 6.1 \times 10^{-5}$ ml m$^{-1}$ for *P. fuscatus*. To address how this might apply in foraging, we looked at flight metabolic rate (FMR) relative to wingloading. We found that wingloading was relatively similar between the two species, but that FMR production correlated strongly with wingloading in *P. fuscatus*, but there was no significant correlation between FMR and wingloading in *P. dominulus* (ANCOVA, $F = 3.843$, $p = 0.295$, Fig. 4).

## Discussion

In this study we found that while *P. dominulus* had a lower absolute FMR, *P. fuscatus* had a lower mass-specific FMR. The lower total flight energy use could be an advantage for *P. dominulus* allowing the foundresses to use less energy on each foraging trip. However, since *P. fuscatus* is larger and has a lower mass-specific FMR, *P. fuscatus* foundresses might be able to cheaply carry larger foraging loads. If so, they would actually be more efficient foragers.

In order to test whether *P. fuscatus* are likely to be able to carry large loads with low energy use, we measured the effect of wingloading on FMR in both species, and found that FMR correlates much more strongly with wingloading in *P. fuscatus*. This suggests that *P. fuscatus* foundresses would not be able to take advantage of their lower mass-specific FMR in order to efficiently carry larger foraging loads. Higher loads would increase their effective wing-
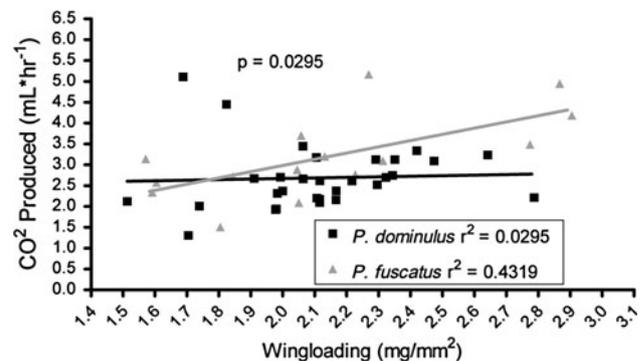


**Fig. 4** Flight metabolic rate for *P. dominulus* and *P. fuscatus* relative to wingloading. Each point represents the energy use rate of the longest flight recorded for one individual. Only flights over 25 s are shown. An ANCOVA was used to compare the results

loading by increasing the flight weight relative to their wing size. This would presumably increase their FMR as well. Instead, the difference in the effect of wingloading suggests that *P. dominulus* may be able to forage at lower energetic cost. During the pre-worker period, this lower energetic cost could allow foundresses to put more energy into rearing offspring, which may partially explain the earlier emergence of workers in *P dominulus*. Indeed, *P. dominulus* store more nectar during the pre-worker period, suggesting that they are more able to gather extra stores, which may protect them against bad foraging periods (Table 1).

While species and wingloading (in *P. fuscatus*) did affect FMR in *Polistes*, temperature did not have an effect. This stands in contrast to what has been observed in honeybees (Woods et al., 2005), and is surprising, since *P. dominulus* has been shown to thermoregulate in flight (Weiner et al., 2010, Table 1). Thermoregulation in flight suggests that there is a range of optimal thorax temperatures. This suggests that there would be a disadvantage to flying outside the optimal range, and a change in FMR could have explained this disadvantage. However, while FMR was not affected by air temperature, time in flight was.

*Polistes dominulus* flew for the longest periods within a temperature range of approximately 30–33°C, while *P. fuscatus* flew longer at higher temperatures, and did not appear to reach a maximum temperature within the temperature range that we tested. In particular, extended flights (of 30 s or more) did not occur at all at the lowest temperatures for either species or at the highest temperatures for *P. dominulus*. These extended flights would be expected to be necessary for foraging, suggesting that temperatures outside the optimal range would affect foraging.

At high temperatures, *P. fuscatus* flew for longer periods than *P. dominulus*, and *P. dominulus* flew for shorter periods than they did at lower temperatures suggesting that *P. dominulus* may have reached thorax temperatures that were too high to maintain extended flight. This is supported by the previous work showing that *P. fuscatus* has lower thorax temperatures during high temperature flight than *P. dominulus*, and that thorax temperature in flying *P. fuscatus* drop below ambient temperature above 35°C, while thorax temperatures in *P. dominulus* do not drop below ambient temperature in flight (Weiner et al., 2011, Table 1). This suggests that, despite its widespread invasive range, *P. dominulus* may not have as flexible a response to ambient temperature as does *P. fuscatus*.

*Polistes dominulus* have shorter foraging flights (Table 1) and a lower absolute FMR. Since our wingloading data suggest that *P. fuscatus* would not be able to carry large loads more cheaply, these results indicate that the likely lower flight costs of *P. dominulus* relative to *P. fuscatus*

could allow more efficient foraging by *P. dominulus* foundresses.

This could help explain the early emergence of workers on *P. dominulus* colonies relative to *P. fuscatus* colonies. However, the differences in the optimal temperature range between the species suggest that *P. dominulus* may not adapt as well to the broad range of temperatures found throughout its invasive range. This may help explain the limits of the invasion and why *P. dominulus* are more often found in cities, which often have less temperature variation. In addition, heated buildings in cities may help protect *P. dominulus* from cold-related mortality. These results present a step toward better understanding the invasion of this eusocial animal, and could, potentially, provide avenues of exploration for better understanding other insect invasions.

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