

Prey capture and caste-specific payload capacities in the European paper wasp *Polistes dominulus*

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Abstract Here, we present a detailed ethogram for the foraging behavior of the eusocial paper wasp, *Polistes dominulus*. The animal's foraging process can be sub-divided into four main stages: (1) approach, (2) attack, (3) butchering, and (4) balling. Although considerable behavioral variation exists within each stage, an analysis of more than 20 individual foraging bouts reveals a single “common path” leading from prey approach to its transportation back to the nest; elucidating this path and separating it into distinct stages is useful when identifying targets for future ethological studies. Of particular interest here is the balling phase, i.e., the preparation of a bolus of flesh for transportation back to the colony. Using an experimental approach, we show that foundresses can carry significantly heavier payloads than workers, suggesting a foraging advantage during the initial stages of colony development. We also show that wasp body mass is significantly positively correlated with payload capacity in foundresses, a relationship not seen among workers or late reproductives. This correlation suggests a beneficial adaptation of foundresses for combating early season pressures associated with the foundation of a new colony.

Keywords Invasive species · Foraging · Eusociality · Foundress · Worker caste

Introduction

Primitively eusocial paper wasps of the genus *Polistes* are common predators of caterpillars and other arthropods (Nannoni et al., 2001). Both reproductive females and sterile workers forage for prey species amid vegetation located near nest sites, attack the prey, and then carry it back to the nest for distribution to larvae (Gamboa et al., 1978). While reproductives do most of the hunting in the weeks following colony foundation, the foraging burden shifts to workers once they emerge (Reeve, 1991).

Polistes dominulus, a distinctive black and yellow paper wasp native to Europe, is a relatively new invader on the North American continent (Liebert et al., 2006). Since its first sighting near Boston in the late 1970s, the species has spread across at least two-thirds of the United States. While genetic analyses strongly suggest that this spread has been facilitated by multiple introduction events (Johnson and Starks, 2004; Liebert et al., 2006), the species' versatile diet, colonization flexibility, and short development time have probably all contributed to its rapid spread (Cervo et al., 2000; Liebert et al., 2006, 2008).

As a group, *Polistes* wasps are well known for their roles as model organisms in studies of the evolution of eusociality (see, e.g. Reeve et al., 2000; Nonacs et al., 2006). As primitively eusocial insects, these wasps lack the dramatic physiological caste differences seen in honey bees and ants (Gadagkar, 1996; but see Hunt and Amdam, 2005), thus representing a sort of “intermediate form” between solitary and fully eusocial insects. Indeed, reproductives and workers are best distinguished by behavior, rather than by morphology. Females fall into one of three castes: foundresses, the early reproductives that initiate or help to initiate nest construction; workers, early offspring that soon take over most of the off nest tasks of colony maintenance;

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and late season reproductives, late offspring that, once inseminated, retreat to hibernacula before emerging as the next season's foundresses (West-Eberhard, 1969; Reeve, 1991; Starks and Turillazzi, 2006).

Although *Polistes* wasps are frequent subjects of behavioral ecology research (Starks and Turillazzi, 2006), little is known about the specifics of their foraging behavior. While Nannoni and colleagues followed hunting wasps on their search for prey, they did not rigorously track the behavioral sequences of those hunting trips. They did show that foragers feed their larvae with the malaxated flesh of caterpillars and other insects captured during the hunt, but provided few details of specific behaviors associated with the foraging process (Nannoni et al., 2001). Other studies have also followed hunting patterns and females' interactions with other foraging wasps. For example, *Polistes* wasps are known to return to areas of past hunting successes (Dew and Michener, 1978), and the contents of *Polistes* worker foraging bouts have been analyzed (Elisei et al., 2010). It has also been observed that *Polistes* will steal prey items already caught by smaller wasp species such as *Polybia* (Raveret Richter, 1990). Still, these studies include few details regarding the actual behavior associated with prey capture, and little data exist regarding behavior leading up to, and immediately following, the hunting process.

Another neglected research area concerns the impact of body mass on foraging success among *Polistes* females. Among solitary apoid wasps, larger females have greater foraging success in both *Sphecius grandis* (the western cicada killer wasp) and *Trypoxylon politum* (the organ pipe mud dauber) (Hastings, 1986; Molumby, 1997). Furthermore, previous studies have shown that larger females have greater fecundity in several other wasp and bee species (Kim, 1997; Molumby, 1997). While it remains unclear what advantage larger size might provide to *Polistes* females, studies have demonstrated intriguing body size differentials; *P. annularis* queens, for example, are significantly larger than their subordinates (Strassmann, 1983).

The ecological importance of *P. dominulus* foraging—presumably a key link in the arthropod-to-vertebrate food chain—also remains largely unexplored. Within Galápagos Island ecological communities, the successful introduction and spread of *P. versicolor* may have led to shifting pressures within the islands' delicate native ecosystems. Several vertebrate species, notably Darwin's finches (subfamily Geospizinae), appear to be in direct competition with these invasive wasps, with at least one study suggesting a direct role in the decline of the islands' Mangrove Finch (*Cactospiza heliobates*) populations (Grant and Grant, 1997).

The impact that *P. dominulus*, another introduced and spreading non-native species, may have on North American native fauna is still an area of active research, but initial studies suggest a potential for disruption. When Armstrong

and Stamp (2003) compared colony productivity between *P. dominulus* and its native congener *P. fuscatus*, they found the non-native species to be more opportunistic in its foraging and, as a consequence, ultimately capable of greater colony output. It is important to know the details of the species' foraging behavior because it could help us to better estimate the effect of that behavior on native ecosystems.

Here, we illuminate the process by which prey items are obtained during the foraging trips of *P. dominulus* females. We monitored subjects throughout the foraging process, carefully recording specific behavioral states and transitions between those states. We also examined the impact of body mass on foraging success by means of an experimental study of flight payload capacity across individuals of different size classes and castes.

Methods

Colony collection and maintenance

Beginning in June 2005 and continuing into that fall, we collected 78 colonies of *P. dominulus* (nests and wasps) from field sites located in central and northeastern Massachusetts and transported them to the International Social Insect Research Facility (ISIRF) at Tufts University. We housed 40 of these colonies in four previously existing, wood-framed screen enclosures (2.4 m long × 2.7 m wide × 2.0 m tall; 10 colonies per enclosure). These enclosures were planted with native vegetation and outfitted with suspended feeding sites containing 1:1 honey water solution and waxworms (*Galleria mellonella*) ad libitum. The remaining colonies ($N = 38$) were transferred to individual portable screen boxes (22 cm × 24 cm × 60 cm), also supplied with honey water and waxworms, and kept indoors on a light:dark cycle synchronized with local sunrise and sunset.

Females present on the nest before the first workers appeared were identified as foundresses; these identifications were later confirmed using behavioral observations. Workers were identified by their later emergence dates, their smaller size, and their frequent trips off the nest during foraging bouts. Foundresses were marked with Testors enamel paint, which was reapplied throughout the season as needed; workers were not marked. Behavioral observations began only after colonies had recovered from the disturbances associated with nest relocation and the wasps were seen actively initiating foraging bouts on their own.

Field observations of prey capture and butchering

Our preliminary observations revealed that the behavioral repertoire of hunting *P. dominulus* workers consists of 12

stereotyped behaviors: walking without antennation (W), walking with antennation (Wa), flying (F), grooming (G), stationary antennating (A), initial biting (Bi), biting (B), prey pulling (P), prey repositioning (R), cutting (C), separating (S), and malaxating (M) (see also Raveret Richter and Jeanne, 1991; Raveret Richter, 2000). The last seven of these behaviors involve the killing and butchering of prey; “cutting” is characterized by a sequence of quick, shallow bites, while “separating” refers to the division of the prey into portable chunks; “malaxating” occurs when the foraging wasp chews its prey into a portable ball, while “repositioning”—a behavior previously unreported in *Polistes* wasps—involves a quick realignment of the wasp’s body parallel to that of its prey.

Between 13 June and 22 July 2005, we spent 70 h observing individual hunting bouts ($N = 21$) carried out by *P. dominulus* workers at special prey arenas (transparent plastic dishes supplied with two waxworms each), located on or near vegetation growing inside the screen enclosures. Using the above list of stereotyped behaviors, we constructed individual ethograms for each of these bouts, combined these into a single ethogram, and calculated the probabilities of specific transitions between behaviors. Enclosure studies similar to this have been performed in this lab (Starks, 1998, 2001, 2003); while it is possible that observing foraging behavior within the confines of an enclosure may have restricted the behavioral repertoire, we believe the enclosure provided reasonable resources to study general foraging behavior expressed by *P. dominulus* in the wild.

Determining the relationship between body mass and maximum payload capacity

Between 10 July and 21 October 2005, we tested the maximum weighted flight capacities of foundresses ($N = 48$), workers ($N = 44$), and late season reproductive females (“late reproductives”; $N = 14$) by attaching weighted tethers (“payloads”) to their bodies and observing subsequent attempts at sustained flight (see Dillon and Dudley, 2004 for a similar method used in Neotropical orchid bees). Each payload consisted of a thin thread, approximately 30 cm long, passed through a series of polystyrene beads weighing between 1.0 and 1.5 mg; as these beads were removable, we were able to make adjustments to the payload mass during subsequent flight trials.

To prepare the wasps for payload attachment, we placed them individually into BD Falcon™ 50 ml conical tubes and chilled them on ice for 5–10 min. Once each wasp was immobilized, we positioned it on its dorsal side and passed the looped, weighted thread around its thorax with the knot positioned between the prothoracic and metathoracic legs; we then turned the wasp over and secured the loop in place

with a small drop of hot wax (KerrLab, Bellewax™ Sticky Wax) on the dorsal surface of the thorax.

Once we had secured the wasp to its payload, we placed both under a transparent plastic cup located beside a portable electric heater; when the wasp became active (i.e., began to buzz, walk, groom itself, or climb on the inner surface of the cup), we removed the cup and encouraged the wasp to fly, either by holding it close to a light or by gently releasing it into the air. If the wasp proved incapable of sustained flight (~ 7 s of lift), we removed one of the polystyrene beads from the payload and repeated the process.

Once a wasp achieved sustained flight, we chilled it on ice for 5–7 min and removed the payload and the hardened wax. We then weighed both the wasp and the payload separately using an Ohaus portable balance (accurate to 0.01 g) and a Mettler AT20 balance (accurate to 10^{-7} g), respectively.

Data analysis

Differences among the mean body mass of foundresses, workers, and late reproductives were analyzed using a one-way ANOVA with Tukey’s post hoc analysis. Differences among the maximum payload capacities of the three castes (when controlling for body mass) were analyzed using a two-way ANOVA with Tukey’s post hoc analysis. The relationship between body mass and payload capacity for each of the three castes was examined using linear regression. Given that heterogeneity of variance occurred in both datasets (body mass and payload capacity), the following transformations were performed prior to analysis: $[\text{body mass}]^{-1}$; $1/[\text{payload}]^3$. Two outlying individuals were removed from the worker caste sample prior to data analysis. Statistical tests were performed using R (Version 2.15.0, General Public License).

Results

Prey capture and butchering

The aggregate analysis of individual hunting bouts led us to divide each bout into four main stages: (1) approach (all behaviors preceding the initial bite), (2) attack (all behaviors between the initial bite and the beginning of cutting behavior), (3) butchering (all behaviors after cutting but before separation begins), and (4) balling (all behaviors between separation and sustained flight away from the hunting site) (Figs. 1, 2, 3).

Most hunting bouts (95.2 %) began with a wasp approaching its prey on foot. During the majority of these walking approaches (71.4 %), the wasp either antennated while

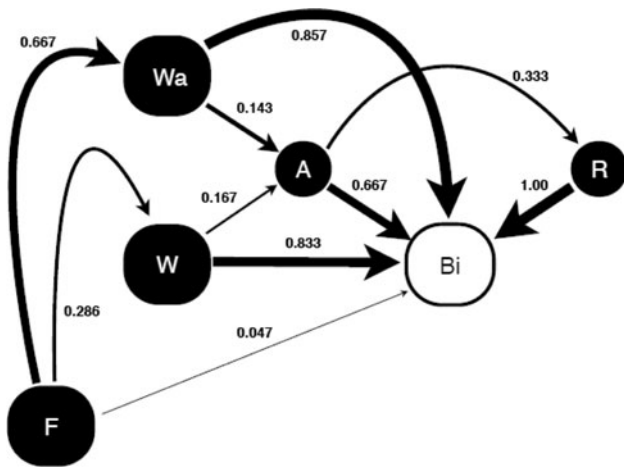


Fig. 1 The approach phase of *P. dominulus* hunting behavior (black) leads to the initial bite (Bi) of the attack phase (white). Possible behaviors include: walking without antenation (W), walking with antenation (Wa), flying (F), stationary antenation (A), pre-bite repositioning (R), and initial biting (Bi). Numbers are the approximate probabilities of specific behavioral transitions and arrow size represents these approximations

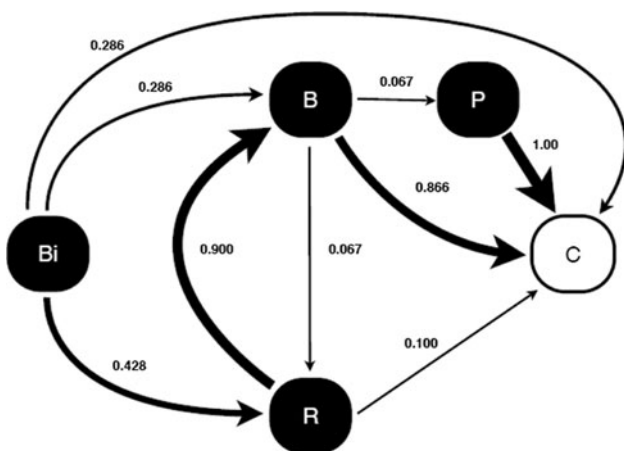


Fig. 2 The attack phase of *P. dominulus* hunting behavior (black) leads to cutting (C) and the initiation of the butchering phase (white). Possible behaviors include: initial biting (Bi), follow-up biting (B), prey pulling (P), axial repositioning (R), and cutting (C). Numbers are the approximate probabilities of specific behavioral transitions and arrow size represents these approximations

walking or stopped and engaged in stationary antenation prior to the initial bite. While these initial bites were often aimed at the anterior half of the waxworm, bite location was highly variable; initial biting may represent a compromise between the need to deliver a precisely aimed attack and the need for a quick and decisive offense. Once the initial bite occurred (officially marking the transition to the attack stage) many wasps would reposition themselves, moving over the waxworm to align their body axes parallel to their prey's and in the same anterior-posterior direction (42.8 %). Straddling the waxworm, or at the very least

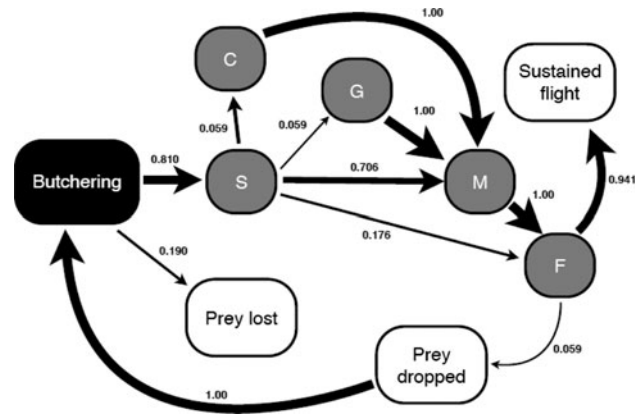


Fig. 3 The balling phase of *P. dominulus* hunting behavior (gray) follows the butchering phase (black). Possible behaviors include: flying (F), grooming (G), cutting (C), separating (S), and malaxating (M). Separation of prey is the only necessary step on the pathway from butchering to prey transport. Numbers are the approximate probabilities of specific behavioral transitions and arrow size represents these approximations

remaining parallel to it, seemed to limit the potential for prey movement during this critical phase of the attack. This repositioning was often followed (90 %) by a second, presumably more accurate, bite aimed just behind the waxworm's head.

The butchering stage exhibited too much variation, both in behavioral sequence and duration, to map probabilities with any confidence. Instead, all behaviors observed during this stage were pooled into a single catch-all "butchering" behavior. However, the transition into and out of the butchering phase always followed a stereotypical course, beginning with aggressive cutting behavior and ending with the separation of flesh. Interestingly, wasps often seemed to actively avoid their prey's head capsule during this phase, instead cutting and chewing the area immediately behind it. This behavior has also been noted in *P. versicolor* (Parent, 2000).

During the balling phase, females will cut, pull, antennate, and/or reposition their prey, occasionally stopping to groom, until they are able to separate a small chunk of flesh for transport back to the colony. This is apparently the most fraught part of the foraging process, as females occasionally lose their prey entirely during this stage (Fig. 3). At some point during the balling stage, each female wasp attempted sustained flight with her newly separated chunk of prey. If incapable of flight, she returned to the cutting stage, presumably in an effort to reduce the size of the payload (5.9 %). During the balling phase, wasps also seemed to prefer soft tissue to the highly sclerotized head capsule.

Caste-specific correlation between body mass and maximum payload capacity

When comparing mean body mass among the three castes, we found that body mass was a significant predictor of caste

($p < 0.001$, one-way ANOVA). Late reproductives (mean mass = $0.13 \text{ g} \pm \text{SE } 0.005 \text{ g}$, $n = 14$) were also significantly larger than both foundresses (mean mass = $0.10 \text{ g} \pm \text{SE } 0.002 \text{ g}$, $n = 48$, $p < 0.01$, one-way ANOVA, Tukey's post hoc) and workers (mean mass = $0.10 \text{ g} \pm \text{SE } 0.004 \text{ g}$, $n = 42$, $p < 0.001$, one-way ANOVA, Tukey's post hoc) (Fig. 4). No significant difference in body mass was found between foundresses and workers ($p = 0.256$, one-way ANOVA, Tukey's post hoc).

After controlling for body mass [a significant predictor of payload capacity ($p = 0.024$)] using a two-way ANOVA, we found that foundresses were able to carry significantly more massive payloads (mean = $0.0173 \text{ g} \pm \text{SE } 0.0004 \text{ g}$) than workers (mean = $0.0140 \text{ g} \pm \text{SE } 0.001 \text{ g}$) ($p = 0.003$, two-way ANOVA, Tukey's post hoc) (Fig. 4). This relationship was not seen between foundresses and late reproductives (mean tether mass = $0.016 \text{ g} \pm \text{SE } 0.002 \text{ g}$) ($p = 0.086$, two-way ANOVA, Tukey's post hoc) or between workers and late reproductives ($p = 0.973$, two-way ANOVA, Tukey's post hoc).

While difference in body mass was not a significant predictor of payload capacity among groups ($p = 0.375$, two-way ANOVA), body mass was positively correlated with payload capacity within foundresses ($r^2 = 0.338$, $p < 0.001$) (Fig. 5); this relationship was not apparent in workers ($r^2 = 0.034$, $p = 0.242$) or in late reproductives ($r^2 = 0.193$, $p = 0.116$).

Discussion

Our observations reveal the most common foraging pathway of *P. dominulus*. The average foraging approach begins

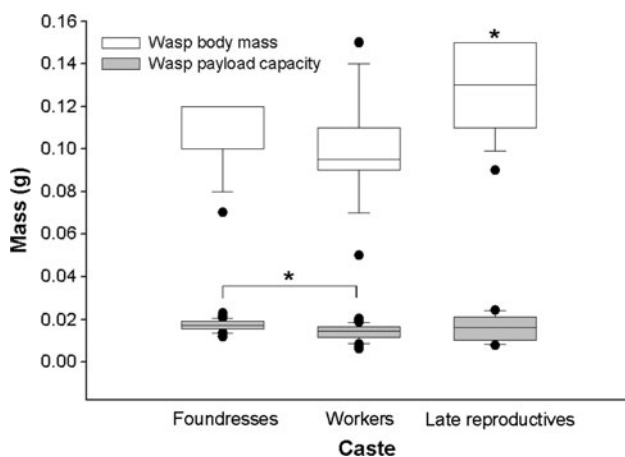


Fig. 4 Boxplots of mean body mass and mean payload capacity for three castes: foundresses ($N = 48$), workers ($N = 42$), and late reproductives ($N = 14$). Late reproductives exhibited a significantly higher mean body mass than either of the other two castes ($p < 0.01$, one-way ANOVA, Tukey's post hoc). Foundresses were able to obtain lift with a higher payload capacity than workers ($p = 0.003$, two-way ANOVA, Tukey's post hoc)

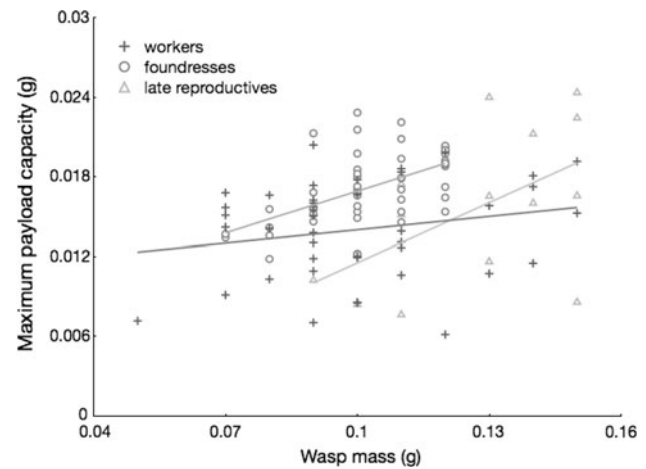


Fig. 5 The relationship between wasp body mass and maximum payload capacity in three castes (foundresses, workers, late reproductives). There was a significant positive correlation between body mass and maximum payload capacity for foundresses ($N = 48$, $r^2 = 0.338$, $p < 0.001$). No such correlation was found among workers ($N = 42$) or late reproductives ($N = 14$)

in flight, followed by walking with antennation and an initial bite to the prey. This initial biting marks the start of the attack phase, which typically includes prey repositioning, biting and cutting. Butchering of the prey follows, ultimately transitioning into a balling phase that consists of the separation and malaxation of prey, followed by sustained flight away from the hunting site. While variations on this behavioral path may exist, the preceding represents a nearly universal common pathway among the wasps observed in this study.

Despite our predictions, we found that significant size differences existed only between late reproductives and the other two castes (Fig. 4). These findings were somewhat unexpected, given that size has been related to reproductive success in other wasp and bee species, and that foundresses have been found to be significantly larger than workers (Molunby, 1997; Strassmann, 1983; Kim, 1997; although see Hughes and Strassmann, 1988). Given that size data were obtained from observations taken over the whole of the season (July to October), however, the absence of specific body mass differences between foundresses and workers may be unsurprising. Haggard and Gamboa (1980) have shown that even though *Polistes* foundresses are the largest females present at the beginning of the season, newly emerging cohorts of workers become ever larger as the season progresses. In other words, even though first emerging workers are smaller than foundresses, size differentials between the two castes become less apparent by the end of the season. (This may be a result of changes in the number of adults providing offspring care as the season progresses: early season workers are reared by only one or a few

foundresses, while late season workers benefit from the attention of multiple adult females on the nest.)

We found that late reproductives, whose larger size has been shown to improve their odds of survival over the winter (Cervo et al., 2008), surpassed both workers and foundresses in terms of body mass. Again, this may be unsurprising given the limited energy expenditure required of late reproductives, without a nest of their own to provision, and with ample energy stores for the coming winter, these wasps are likely to weigh considerably more than their worker or foundress relatives. Interestingly, body mass differences among the groups did not prove to be a significant predictor of payload capacity.

While investigating the relationship between caste and payload capacity, we found that foundresses were able to carry significantly heavier payloads than workers (when controlling for body mass) (Fig. 4). On average, foundresses were able to carry 17.1 % of their body mass, while workers were only able to carry 15.37 %. This worker payload capacity is higher than that found in a recent study of foraging behavior in *P. versicolor*, where workers were only able to carry about 10 % of their body mass (Elisei et al., 2010). Elisei and colleagues (2010) provided no information regarding disparities between castes. Comparisons between *P. dominulus* and *P. versicolor* are fraught, however, as Palearctic and subtropical species can differ in terms of colony initiation times (subtropical species may be more phenologically flexible) (Gobbi et al., 2006; Yamane, 1996).

A higher payload capacity for foundresses when compared to workers is not surprising given that foundresses provide for the nest largely on their own during the early weeks of the season (Gamboa et al., 1978), and the ability to carry heavier loads yields a clear survival advantage (Torchio and Tepedino, 1980). Procuring more prey per hunting bout lowers the number of initial foraging trips needed, conserving energy reserves and reducing the inherent mortality risks of foraging trips. This advantage may be even more marked during the beginning of the season, when foundress and worker body mass differences are most pronounced (Haggard and Gamboa, 1980). In fact, the upward trend in worker body mass across the season probably obscures the magnitude of the differences that exist between foundresses and the earliest workers. Future studies that account for this temporal heterogeneity may well strengthen this interpretation of the results.

We predicted a positive correlation between body mass and payload capacity for individuals within all three castes. However, a significant positive correlation was found only among foundresses (Fig. 5). The data for foundresses support earlier findings on digger wasps in which adult body size was positively correlated with the amount of prey females were able to provision (O'Neill, 1985). The absence of a significant correlation in workers and late reproductives,

however, is more suggestive of the relationship seen in Neotropical orchid bees (Dillon and Dudley, 2004). In that case, size and payload capacity are sometimes negatively correlated, apparently because higher body mass hinders the bees' abilities to obtain aerodynamic lift.

Here, the significantly reduced payload capacity of workers when compared to foundresses and lack of a positive correlation in workers may be due to a reduction in individual foraging contributions as colony size grows larger and more workers are available to offer foraging services. This provides a clear contrast to the case of reproductive foundresses, upon whom the entire responsibility for foraging and colony maintenance often falls. The lack of a significant positive correlation in late reproductives ($p = 0.116$) may also be explained by treating these females as a mixed population of the next season's reproductive foundresses and subordinate foundresses, a group whose colony contributions may be similar to workers (Dapporto et al., 2006).

This study is the first of its kind to provide detailed accounts of foraging behavior in *P. dominulus*. We subdivided the foraging process into four main stages: (1) approach, (2) attack, (3) butchering, and (4) balling. Although considerable behavioral variation exists within each stage, a single "common path" is readily apparent. Of particular interest from a behavioral ecology perspective is the balling phase, i.e., the preparation of a bolus of flesh for transportation back to the colony. We found that during the balling phase foundresses can carry significantly heavier payloads than workers. Interestingly, wasp body mass is also positively correlated with payload capacity in foundresses, but not in workers or late reproductives. Physiological differences such as these might be expected between castes in animals that, like *Polistes*, have likely evolved from bivoltine ancestors (Hunt and Amdam, 2005). The foraging advantage displayed here by foundresses is likely beneficial given the early season pressures associated with new colony foundation.

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