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Polistes metricus queens exhibit personality variation and behavioral syndromes

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Abstract

Consistent differences in behavior between individuals, otherwise known as animal personalities, have become a staple in behavioral ecology due to their ability to explain a wide range of phenomena. Social organisms are especially serviceable to animal personality techniques because they can be used to explore behavioral variation at both the individual and group level. Despite the success of personality research in social organisms generally, and social Hymenoptera in particular, social wasps (Vespidae) have received little to no attention in the personality literature. In the present study, we test *Polistes metricus* (Vespidae; Polistinae) paper wasp queens for the presence of repeatable variation in, and correlations ("behavioral syndromes") between, several commonly used personality metrics: boldness, aggressiveness, exploration, and activity. Our results indicate that *P. metricus* queens exhibit personalities for all measured traits and correlations between different behavioral measures. Given that paper wasps have served as a model organism for a wide range of phenomena such as kin selection, dominance hierarchies, mate choice, facial recognition, social parasitism, and chemical recognition, we hope that our results will motivate researchers to explore whether, or to what degree, queen personality is important in their research programs.

Key words: behavioral syndromes, personality, social insects, temperament, wasps.

Any casual observer of animal behavior can attest that no 2 animals behave precisely the same way. Behavioral differences within a species that persist across either time or context are known as animal personalities, and behavioral syndromes occur when 2 or more personality traits appear linked (Sih et al. 2004; Dingemanse and Reale 2005). For a long time, scientists had written off personality variation within a species as constituting merely noise around an adaptive mean, and instead focused largely on behavioral differences between species. However, the past several decades have given rise to numerous studies highlighting the importance and predictive power of animal personality research that it can no longer be ignored. The study of personality is alluring because many personality traits are important in accounting for seemingly maladaptive behavior within a population, such as superfluous prey killing (Maupin and Riechert 2001) and precopulatory cannibalism

(Johnson and Sih 2005; Pruitt and Riechert 2009). Additional studies have shown that individual personality is often linked with key life-history parameters (Wolf et al. 1999, 2007; Pruitt and Riechert 2012; Wolf and Weissing 2012; Juette et al. 2014; Modlmeier et al. 2015; Canestrelli et al. 2016), further indicating the importance of personality in driving a variety of ecological outcomes.

Social or group-living organisms provide particularly interesting case studies for the animal personality research paradigm (Jandt et al. 2013; Bengston and Jandt 2014). This is due to the fact that one can quantify personality at multiple levels: the *individuals* within the group, and the emergent behavior of the *entire group* itself relative to other such groups. Social organisms exhibiting personality variation span an ever-widening range of taxa such as birds (Schoepf and Schradin 2012; Aplin et al. 2013, 2014), fishes (Dyer et al. 2009; Magnhagen 2012; Rasmussen and Belk 2012), mice

(Schoef and Schradin 2012), and various arthropod species (Modlmeier et al. 2012; Holbrook et al. 2014; Shearer and Pruitt 2014; Wright et al. 2015, 2016). The social Hymenoptera—ants, bees, and wasps—have been of great interest to early ethologists as well as modern behavioral ecologists due to their stunning efficiency and complex division of labor along morphological and behavioral castes (Oster and Wilson 1978). Our understanding of these insect societies has increased substantially under animal personality research (Jandt et al. 2013) and, conversely, these taxa have been instrumental in their ability to test general personality theory (Bengston and Dornhaus 2014). For instance, in honeybees, colonies exhibit strong differences in defensive, foraging, and undertaking behavior that also predict colony productivity and winter survival (Wray et al. 2011). In *Temnothorax* ants, colonies that harbored more intracolony variation in brood care and exploration were more productive (Modlmeier et al. 2012). Taken together, considering intraspecific variation at both the individual and group level appears to enhance the predictability of a variety of behavioral and ecological phenomena in social insects.

Despite the fervor surrounding personality research in social organisms, personality studies in social wasps (Vespidae) remain conspicuously absent from the literature. We believe this is an oversight, as social wasps have served as model organisms for the study of dominance hierarchies and social interactions (Pardi 1948; Turillazzi and Pardi 1977; Strassmann 1981; Cervo et al. 2008b; Zanette and Field 2009; Jandt et al. 2014), facial recognition (Tibbetts 2002; Tibbetts and Lindsay 2008; Sheehan and Tibbetts 2010; Green et al. 2013; Cervo et al. 2015), kin selection and reproductive skew (Field et al. 1998, 2006; Gamboa 2004; Liebert and Starks 2006), social parasitism (Sledge et al. 2001; Cervo 2006; Cervo et al. 2008a), mate choice (Izzo and Tibbetts 2012; Beani et al. 2014), and even chemical recognition (Dani 2006; Dapporto et al. 2007; van Zweden and d'Ettorre 2010). Many if not all of these lines of research may be heavily influenced by, and could, therefore, benefit from, incorporating an animal personality framework. Additionally, Vespid wasps evolved eusociality independently from bees and ants (Johnson et al. 2013), and comparative studies on personality variation may, therefore, spark novel insight into discussions surrounding the evolution of eusociality.

Polistes metricus (Vespidae; Polistinae) is a paper wasp native to North America, and can be found in the central and eastern United States as well as Southern Canada. Unlike most paper wasp species that begin nests with multiple foundresses, *P. metricus* predominantly founds nests solitarily (Bohm and Stockhammer 1977), and thus undergoes a transition from solitary to social living during its lifetime unlike many other paper wasps that are social throughout their lives. Additionally, this species has been known to reutilize old nests from the previous season (Starr 1976), as well as sharing and maintaining multiple active nests (Gamboa 1981), sometimes even with other *Polistes* species. In the present study, we test for the presence of personality variation and behavioral syndromes in *P. metricus* paper wasp queens using several commonly used personality metrics: boldness, aggressiveness, exploration, and activity. These personality metrics have proved useful for a wide variety of systems, and it is our hope that this study may serve as a basis for future personality studies in social wasps.

Materials and Methods

All experimental *P. metricus* foundresses were collected on the same day in the early Spring in May 2014 from 2 sites in Western Pennsylvania in the United States: the University of Pittsburgh's Pymatuning Laboratory of Ecology (PY; 41°37′22.80″N, 80°27′16.62″W) and the Powdermill Nature Reserve (PM; 40°9′36.98″N, 79°16′17.30″W). The queens ($n = 59$) were taken from their recently founded nests and transported back to the laboratory at the University of Pittsburgh where we measured head width and wing length, both of which are highly correlated with body size and mass (Eickwort 1969). The queens were given new combs from the same site. Giving the queens new nests is somewhat of an artificial condition, but was required because the queens did not successfully build their own nests from scratch in the laboratory. However, *P. metricus* queens commonly adopt new foreign or previously used nests in the wild. Therefore, our results should be viewed in the context of this limitation. Before queens were introduced to their new nests, we removed the eggs, and the queens and nests were placed in a $30 \times 30 \times 30$ cm nest box with an aluminum frame and chiffon siding on all walls, save for the front, which is covered with clear plastic for easy observations. This material allows light to permeate throughout the entire container. Wasps were fed an *ad libitum* diet of greater wax moth larvae *Galleria mellonella* and sugar cubes, and were given fresh water every week. The wasps were kept on a 16:8 h light:dark cycle using incandescent halogen bulbs (Inger et al. 2014), and the temperature was maintained at approximately 25 °C. All behavioral assays (boldness, aggressiveness, and exploration/activity) were performed under incandescent lighting between 10 AM and 3 PM. Each behavioral assay trial, except for the first boldness assay (approaching a rival), was performed one at a time over 4 consecutive days, with 1 trial per day. Therefore, each trial was performed 24 h apart, and no assays overlapped with another. The first boldness assay was performed once every 72 h, as it took some time to collect new "rival" dummy wasps. Exploration/activity assays were performed first, followed by boldness assays (approaching a rival), and then on-nest boldness and aggressiveness assays. The wasps were tested in random order for each trial. Wasps were given 24 h to acclimate to the laboratory prior to all trials, and all experiments, from beginning to end, took a total of 21 days to perform.

The short time frame was chosen because we wanted to properly assess queen personality early in the founding phase when all nests are nearly equal in size and contain mostly eggs. Given that paper wasp queens tend to become more aggressive as nests approach the worker emergence phase, we wanted to take an early snapshot of queen personality before other factors such as nest contents have an opportunity to significantly influence their behavior.

Exploration/activity assay

To measure individual exploration and activity levels, single queens ($n = 52$) were placed into a small plastic cylinder that was then placed over the opening of a $29 \times 16 \times 4$ cm exploration arena. This arena contains 10 compartments that the wasp can enter without hindrance (Figure 1). We allowed the wasps to enter an opening located at the center of the exploration chamber. Once the wasp entered the arena, we started a timer and we allowed the wasp 10 min to freely explore the arena. While in the arena, we recorded the number of novel chambers entered (as a measure of exploration) and the proportion of time the wasp remained active (activity). We define activity as walking or flying. These assays were performed 4 times on each queen, and the values from each trial were averaged for our final measure of both exploration and activity. The arena was cleaned with 70% ethanol and dried after every trial, and fumes were allowed to dissipate for ~2 min between each trial.
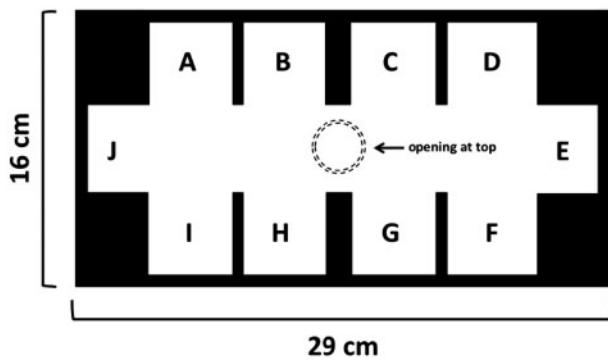
Figure 1. A 10-chambered exploration arena for wasps. Dimensions: LWH = 29 × 16 × 4 cm.

Boldness assays

Boldness—the propensity to engage in risky behavior—was assessed using 2 independent behavioral assays. The first boldness assay measured the latency for an individual queen to approach and feed in the presence of a rival (Boldness I). Queens were starved for 48 h and then placed in a small circular arena (diameter = 12 cm, height = 4 cm) with a dead, previously frozen *P. metricus* "dummy" foundress mounted on a 1-cm³ sugar cube, forcing the hungry queen to interact with the dummy or "rival" to feed. Dummy wasps were taken from a population >150 km from the focal wasps to ensure they were unrelated and never interacted previously. Dummy wasps were frozen ≤24 h prior to all trials. Boldness was measured as the latency to begin feeding after the first antennation of this "guarded" resource. It is important to note that clypeal or "face" pattern variation is minimal or nonexistent in *P. metricus*, and seemingly does not play a role in individual recognition or dominance such as in *P. dominula* and *P. fuscatus* (Sheehan and Tibbetts 2010, 2011), and so was not considered here. Antennation is defined as physically inspecting, via direct contact with the antennae, the food source guarded by the wasp dummy. Wasps that fed more quickly were considered bolder, and longer latencies were associated with shyer individuals. Trials were terminated after 5 min. Dummy wasps were used on no more than 5 focal wasps before they were discarded to ensure a fresh hydrocarbon profile. Dummy wasps were assigned randomly and included as a random variable in our models. Dummy wasps did not vary greatly in size (wing length: mean = 15.01, $\sigma = 0.85$; head width: mean = 3.94, $\sigma = 0.30$). We performed this boldness assay on each queen once every 72 h for a total of 4 trials. Final boldness scores were calculated by averaging the boldness scores from each of the 4 trials.

The second boldness assay was performed while queens were perched on their nests. Only queens on nests containing only eggs (i.e., no larvae yet) were tested to control for behavioral variation (specifically boldness or aggressiveness) that may be associated with having higher valued assets to defend (Clark 1994). For this assay, queens were prodded anteriorly to the clypeus with a small plastic brush up to 10 times, simulating molestation from a foreign rival or predator. A prod test was chosen as our prod represents a general antagonistic stimulus that is standardized for all queens. The use of dummies was avoided because we would have to take into account many attributes of the dummy such as size and head width. Additionally, the dummy's hydrocarbon profile may erode or be contaminated with other chemicals from the focal wasp. This would require changing out the wasp dummy after several trials, and it is difficult to acquire such a large number of dummies for this purpose,

especially because so many were used during the "approach a rival" boldness test. Boldness was calculated as the number of "attacks" required before the wasp fled her nest (Boldness II). Each attack consisted of prodding the wasp anteriorly with the brush and holding the brush in place for 2 s before removing it. Once removed, we waited an additional 2 s before initiating another prod. Queens that held their ground after frequent prods were considered bolder, and queens that readily abandoned their nests were considered shyer. Boldness was, therefore, scored on a 1–10 scale for each individual trial corresponding to the number of prods necessary before nest abandonment, which was then averaged over 4 trials. It should be noted that this assay might also be consistent with the proactive–reactive behavioral trait, and not boldness per se. Correlations with this trait and between others such as exploration and activity would potentially lend more support for the proactive–reactive interpretation. The brush was wiped down with a 70% ethanol-soaked paper towel and air-dried between each trial to remove any residual chemical cues from previous trials.

Aggressiveness assay

Aggressiveness was measured concurrently with the second boldness assay ("prodding"). During each prod, it was noted whether or not the queens responded aggressively toward the brush. Aggressive responses included active biting and stinging. Aggressiveness was calculated during each trial as the proportion of prods to which the queen responded aggressively. This proportion was averaged over 4 trials to arrive at our summative measure of an individuals' aggressiveness.

Statistical methods

We tested for the repeatability across trials of individual queen personality using generalized linear mixed model (GLMM) (Poisson distribution and log-link function) with head size as a fixed effect, individual wasp ID nested within site ID, and dummy wasp ID (for Boldness I test) as random effects, and starting nest size, egg numbers, and trial number as fixed effects. Our predictor variables were the latency to feed (Boldness I), the number of prods before fleeing (Boldness II), proportion of observed aggressive encounters, exploration, and activity time. The proportion of total variation attributable to between individual differences provides an estimation of repeatability (Boake 1989; Falconer and Mackay 1996), which is a measure of how consistent individuals are in their behavior over multiple trials. Repeatability estimates and 95% CI were estimated using maximum likelihood, and the significance of the repeatability estimates was retained regardless of the error distribution modeled. Correlations between boldness, aggressiveness, activity, and exploration were analyzed using Spearman rank correlation tests using the average of each individual's response for each behavioral metric. All statistics were performed using JMP version 10 (SAS Institute, Cary, NC).

Results

Repeatability of behavior

All behaviors tested showed high repeatability, indicating the presence of between-individual differences in behavior. Boldness, measured as the latency to feed in a threatening environment (from a sugar cube guarded by a dead queen), was highly repeatable [$r = 0.93$; $n = 53$, 95% CI (0.62, 1.56)]. Similarly, boldness measured as the number of aggressive encounters before nest
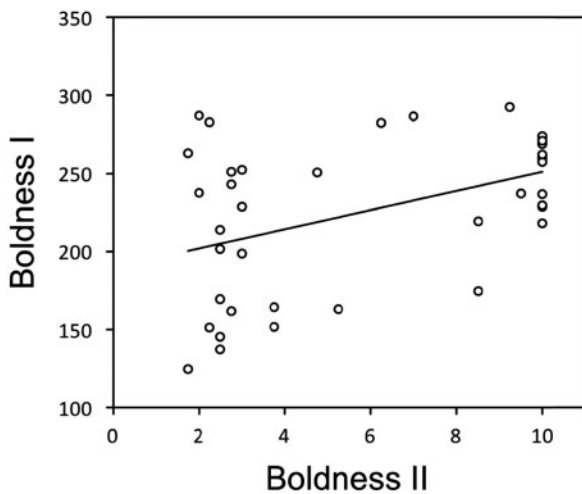
Figure 2. Relationship between both boldness assays: the number of encounters before retreat (Boldness I), and latency to approach a rival (Boldness II) shows that both are significantly correlated, providing mutual corroboration that both boldness assays are measuring the same personality trait. Note that Boldness II latency scores have been subtracted from the maximum value to make higher values correspond to higher boldness.

abandonment was also highly repeatable [$r = 0.81$; $n = 38$, 95% CI (0.49, 1.59)]. Most importantly, these boldness assays corroborate each other, because the wasps that fed without hesitation from a guarded food source were also those that were less likely to abandon their nests after repeated aversive stimuli ($\rho = -0.23$, $P = 0.0044$) (Figure 2). Aggressiveness, measured as the proportion of predator encounters (brush prods) the wasps acted aggressive toward (i.e., bit and stung the poker), was also highly repeatable [$r = 0.88$; $n = 38$, 95% CI (0.53, 1.75)]. Lastly, exploration and activity level showed similarly high repeatability [exploration: $r = 0.88$; $n = 52$, 95% CI (0.66, 1.66); activity: $r = 0.92$; $n = 52$, 95% CI (0.61, 1.56)].

Behavioral syndromes

We tested for correlations across all repeatable behaviors using nonparametric Spearman rank correlation, and Bonferroni correction for multiple comparisons (modified $\alpha = 0.0055$) and found that aggressiveness and at least one of our 2 boldness measures (encounters before retreat) were correlated (latency to approach rival vs. aggressiveness: $n = 38$, $\rho = 0.37$, $P = 0.02$; encounters before retreat vs. aggressiveness: $n = 38$, $\rho = 0.89$, $P < 0.0001$) (Figure 3). This provides evidence for a behavioral syndrome between aggressiveness and at least 1 measure of boldness in *P. metricus*. However, we cannot rule out the possibility that Boldness II and aggressiveness lack independence, given that the assays were performed simultaneously.

Lastly, there existed a strong positive relationship between exploration and activity time ($\rho = 0.93$, $P < 0.0001$), though we are hesitant to call this a behavioural syndrome, as these measures are likely not independent—wasps that are more active will, by random chance alone, enter into more novel chambers than less-active wasps. No syndromes were found between any other behavioral traits (aggressivness vs. activity: $\rho = 0.0035$, $P = 0.98$; aggressiveness vs. exploration: $\rho = 0.046$, $P = 0.77$; activity vs. Boldness I: $\rho = 0.049$, $P = 0.71$; activity vs. Boldness II: $\rho = 0.12$, $P = 0.45$; exploration vs. Boldness I: $\rho = 0.086$, $P = 0.52$; exploration vs. Boldness II: $\rho = 0.097$, $P = 0.54$).
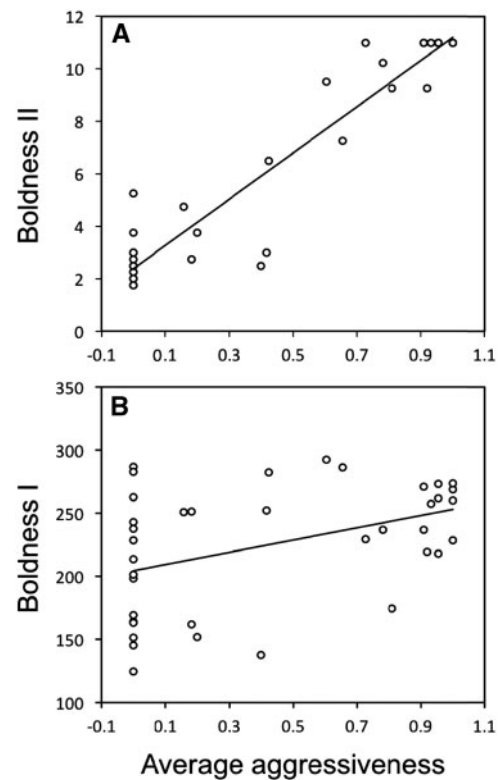

Figure 3. The behavioral syndrome between aggressiveness and (**A**) the number of simulated attacks before retreat (Boldness I), and (**B**) the latency to approach a rival (Boldness II). Note that Boldness II latency scores have been subtracted from the maximum value to make higher values correspond to higher boldness.

State-dependent personality

Wasp size (using head width as a proxy) was only significantly correlated with activity and exploration, where larger wasps on average were less active and less explorative than smaller wasps (activity: $F_{1, 52} = 12.1$, $P = 0.0011$; exploration: $F_{1, 52} = 5.18$, $P = 0.027$). Wasp size was not correlated with boldness (latency to approach rival: $n = 52$, $P = 0.65$; encounters before retreat: $n = 38$, $P = 0.21$), or aggressiveness ($n = 38$, $P = 0.32$). Additionally, behavioral differences between queens were not correlated with the size of the nest the queens adopted in the laboratory (latency to approach rival: $n = 52$, $P = 0.98$; encounters before retreat: $n = 38$, $P = 0.62$; aggressiveness: $n = 38$, $P = 0.72$; exploration: $n = 52$, $P = 0.56$; activity: $n = 52$, $P = 0.62$).

Discussion

This study is the first to demonstrate that paper wasp queens (or wasps in general) exhibit consistent differences in behavior across time and context (personality), and correlated personality metrics (behavioral syndrome). It must be noted, however, that behavioral syndromes were only found between traits that were measured in the same trial, and thus future experiments using independent trials should be performed to verify whether the syndromes discovered in our study hold. Additionally, future studies should be careful to remove any traces of apolar compounds left in the arenas that, in this study, may have remained due to the use of a polar solvent. The presence of behavioral differences in *Polistes* wasps found in our study has many potentially important and interesting implications

for their life history and fitness. Though *P. metricus* generally founds nests solitarily, they do also form foundress associations on occasion. Thus, it remains to be determined whether this personality variation correlates with the tendency to form foundress associations, the likelihood of becoming the dominant foundress (the queen) in an association, the likelihood of being usurped by conspecifics, susceptibility to nest parasitism, and overall colony productivity. Additionally, it may be intriguing to find out whether queen personality is related to the differences between queens, foundresses, and workers in how much comb space they occupy as well as how they distribute themselves spatially on the comb (Baracchi et al. 2010). Each of these topics have been rigorously examined using various *Polistes* models, however, we feel that the application of a personality approach has the potential to integrate these topics into a shared explanatory framework.

Polistes wasps have served as prominent model organisms for the study of dominance hierarchies and social interactions (Jandt et al. 2014). Many of these studies have focused on how intracolony aggression mediates dominant–subordinate, foundress–worker, and worker–worker interactions (Eberhard 1969; Strassmann and Meyer 1983; Miyano 1986), yet do not focus on inherent differences in aggressiveness between wasps outside of a social context. A thorough examination of the prevalence of behavioral variation among queens, foundresses, and workers in *Polistes* and other Vespinae presents researchers with an interesting opportunity to delve deeper into the role of intrinsic individual differences in mediating complex social outcomes. Exploring behavioral variation among other social arthropods have proved to be highly insightful, for example, ants (Modlmeier and Foitzik 2011; Hui and Pinter-Wollman 2014; Modlmeier et al. 2014b), bees (Wray et al. 2011), water striders (Sih and Watters 2005; Chang and Sih 2013), social spiders (Pruitt and Riechert 2011; Pruitt and Goodnight 2014; Wright et al. 2014). Moreover, aggressive/bold syndromes, such as the one observed in *P. metricus* here, have been identified in many nonsocial species (Bell 2007), and are often associated with increased dispersal abilities (Clobert et al. 2009), different foraging strategies (Bell and Sih 2007; Chapman et al. 2011), vigilant anti-predator behavior (Huntingford 1976), and even grouping behavior (Aplin et al. 2013). Given that *Polistes* wasps participate in all these behaviors to a great degree, further investigations in this system on how this syndrome and other personality traits influence life history and survival should be rewarding. Notably, *Polistes* might be among the most promising future models for these lines of research, because the repeatability of individual differences in *P. metricus* ($r = 0.81$–0.93) are among the very highest observed for any trait or any taxa measured in either in the lab or field (Bell et al. 2009), though personality traits were measured over a very short-time span in our study that may have inflated our repeatability estimates. Thus, there is compelling evidence that queens exhibit substantial characteristic differences in their behavioral tendencies, and that these individual differences may have consequences on a variety of behavioral and ecological outcomes.

Additionally, given that evidence suggests that paper wasps (and other social Vespidae) evolved eusociality (or primitive eusociality) independently from other eusocial Hymenoptera and Isoptera (Johnson et al. 2013), we feel that comparative personality studies between these taxa could help contribute to the conversation surrounding the evolution of eusociality and insect castes. Recent discoveries in social spiders regarding the presence of "personality castes" suggest that behavioral variation could be an initial step on the path to complete reproductive division of labor (Wright et al.

2014). Given that paper wasps are only primitively eusocial, meaning that the reproductive division of labor is less discrete than in more "advanced" eusocial taxa such as ants and honeybees (Wilson and Holldobler 2005), personality studies in paper wasps and other Vespidae may prove particularly enlightening in these discussions. For instance, one may explore the extent to which individual differences are associated with task participation, efficiency at various tasks, and propensity to switch tasks. At the colony level, examining within-group behavioral composition may help us to predict inter-colony differences in collective aggressiveness (Hui and Pinter-Wollman 2014; Modlmeier et al. 2014a), brood care (Jandt et al. 2013), or life-history attributes. By conducting such studies in parallel across species with varying degrees of sociality (or eusociality), we may be able to retrace the role of individual behavioral differences as precursors to morphologically based task differentiation. Indeed, such behavioral precursors have already been discovered in ants (Dornhaus 2008; Pinter-Wollman et al. 2012; Lichtenstein et al. 2016) and even social spiders (Wright et al. 2014, 2016).

Our study also hints at the possibility for a more reductionist approach regarding the mechanisms that lead to and help maintain inter- and intra-colony behavioral variation. Most studies have been content with explaining differences in behavior between colonies as resulting from intra-colony differences in behavior. Several mechanisms have been proposed to explain inter-colony behavioral differences, such as differences in the total average behavior of workers, differences in the behavioral distribution of worker behavior, differences in behavioral response thresholds, or purely resulting from external environmental factors (Bonabeau et al. 1996, 1998; Theraulaz et al. 1998; Pinter-Wollman 2012). Furthermore, the social group, as opposed to the individual worker, is often regarded as being the object of selection in many social systems (Holldobler and Wilson 1990; Mayr 1997; Korb and Heinze 2004). We suggest that in some systems, such as ours, where colony life histories are typified by discrete solitary and social stages, the queen herself could be regarded as the object of selection, as her success during the founding stage is necessary for there to even be a colony in the first place. And her behavior may play a role in determining the behavioral composition of her future colony. Once the social group exists, however, the object of selection may then be transferred to the social group as a whole. We feel it is an oversight to ignore the queen's behavior during the founding stage—the most vulnerable period of the colony's life cycle—when considering the underlying mechanisms of both inter- and intra-colony behavioral variation.

To conclude, we have documented a clear signature of personality in *P. metricus* queens, including common traits such as aggressiveness, boldness, exploration, and activity level. This species also exhibits a behavioral syndrome that bears resemblance to those found in a variety of other social and solitary vertebrates (Huntingford 1976; Bell 2005; Dingemanse et al. 2007; Dochtermann and Jenkins 2007; Moretz et al. 2007) and invertebrates (Riechert and Hedrick 1993; Johnson and Sih 2005; Kortet and Hedrick 2007; Reaney and Backwell 2007). The short time frame over which the queens were measured, however, means that we cannot state with certainty that the personality differences observed in our study are maintained throughout the queens' tenure on the nest. Both of these features bode well for *Polistes*' promise as a generalizable model for behavioral syndrome research. This potential is further augmented by the diversity of social structures exhibited within the Vespidae and the reservoir of seminal behavioral research that has already been conducted using these systems. Thus,

Table 1. A summary table of repeatability values and a correlation matrix for each trait tested

Trait	Repeatability (*r*)	Correlations [*P* values and (Spearman's *ρ*)]			
		Boldness I	Boldness II	Aggressiveness	Exploration
Boldness I	0.93	—	—	—	—
Boldness II	0.81	—	—	—	—
Aggressiveness	0.88	0.021 (0.37)	**<0.0001 (0.89)**	—	—
Exploration	0.88	0.52 (0.086)	0.54 (0.097)	0.77 (0.046)	—
Activity	0.92	0.71 (0.049)	0.45 (0.12)	0.98 (0.0035)	**<0.0001 (0.93)**

Notes: The first numbers in the matrix are the *P* values, and Spearman's rho (*ρ*) is to the right in parentheses. Significant *P*-values are in bold.

we encourage wasp researchers to further explore the potential importance of personality in their own research questions.

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