

How do fighting ability and nest value influence usurpation contests in *Polistes* wasps?

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Abstract Most research on animal contests has focused on the factors that influence the intensity and outcome of aggressive contests within nonsocial species, while relatively little is known about contests in social taxa. Here, we examine contests among queens of the social paper wasp, *Polistes dominulus*. Queens use multiple reproductive strategies, including nesting alone, usurping established colonies, and cooperatively joining other queens. We stage contests between a nesting queen and a challenger to test how resource value (RV) and resource holding potential (RHP) influence (a) who occupies the nest at the end of the contest and (b) the extent of conflict between the queen and challenger. We found that RHP, as measured by individuals' facial patterns and body size, influenced the outcome of the contest. Challengers with high RHP were more likely to successfully usurp the nest than challengers with low RHP. Interestingly, queens with relatively high RHP were more likely to form a cooperative association with the challenger than queens with lower RHP, suggesting that queens may evict individuals that are an aggressive threat. RV influenced the intensity of conflict. There was more aggressive conflict over large nests than over small nests. Overall, social taxa have complex contest dynamics with important parallels to contests in nonsocial taxa. Studying contests in social taxa provides an important perspective on the factors

that influence individual decisions about conflict versus cooperation.

Keywords Eviction · Dominance · Badge-of-status · Conventional signal · Quality signal · Conflict · Cooperation

Introduction

Animal societies are a complex mixture of cooperation and conflict. Even within apparently cooperative societies, there is often conflict over relative shares of resources and reproduction (Keller and Reeve 1994; Tibbetts and Reeve 2000; Ratnieks et al. 2006). Species with facultative cooperation have some of the most interesting social dynamics because individuals have the option of reproducing on their own or cooperating with others. The range of reproductive options available to each individual has generated interest in the factors that influence individual reproductive decisions (Reeve and Ratnieks 1993). For example, why do certain individuals cooperate while others compete or reproduce independently? Thus far, relatively few studies have examined the factors that influence individual decisions about cooperation versus conflict.

Most research focuses on the population-level costs and benefits of cooperation, instead of examining individuals while they are making decision about whether or not to cooperate (Gamboa 1978; Shreeves et al. 2003; Tibbetts and Reeve 2003; Liebert et al. 2005). These broad, population-level studies have identified a range of important costs and benefits associated with cooperation, but they are not as useful for understanding how individuals make cooperative decisions.

Although contests within social species have received little attention, there is a rich literature examining decision-

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making during contests in nonsocial species. A number of theoretical and empirical studies have examined the factors that influence the intensity and outcome of aggressive conflict over resources like territories, food, and mates (Parker 1974; Enquist and Leimar 1987; Elwood et al. 1998; Arnott and Elwood 2008). The length and intensity of conflict is often influenced by resource value (RV); contests over valuable resources are longer and more intense than conflicts over less valuable resources (Enquist and Leimar 1987). In addition, the outcome of aggressive conflict is often influenced by the relative abilities of the combatants. Individuals with higher resource holding potential (RHP) typically win the contests (Parker 1974; Taylor and Elwood 2003, but see Elwood et al. 1998). Overall, there has been a long history of theoretical and empirical research on animal contests that has identified key parameters that influence conflicts in many species. However, contest dynamics can vary substantially from species to species and we are still learning about the factors that account for the variation across taxa.

Contests in facultatively social species likely have many similarities with contests in nonsocial species. However, the additional option of cooperation may influence the dynamics of conflict by altering the relative costs and benefits of the strategies. The relative costs and benefits of conflict vs. cooperation are likely to vary with a species' ecology as well as the specific RHP of the individuals involved in the contest (Keller and Reeve 1994; Gunnels et al. 2008; Tibbetts and Reeve 2008). As a result, contest dynamics in facultatively social species may vary from species to species and between different pairings within a species.

This study will use *Polistes dominulus* paper wasps to test decision making during contests in this social species. Nest-founding *P. dominulus* queens use a number of different reproductive strategies that involve varying levels of aggressive conflict vs. social cooperation (Reeve 1991; Roseler 1991). Some foundresses start nests independently, while others cooperatively nest with other foundresses (Pardi 1948). Colony composition remains flexible during the first few months of the colony cycle. Foundresses sometimes cooperatively join groups of foundresses on established nests or usurp established nests by aggressively displacing the original foundresses (Nonacs and Reeve 1995; Gamboa et al. 2004). Late season usurpation and nest joining occurs for many reasons, though it is especially likely to occur after a queen's own colony is predated or parasitized (Cervo and Dani 1996; Starks 2001; Cervo 2006).

Alternative reproductive strategies, such as nest usurpation and joining, are common in many social species (Brockmann 2001). Nest usurpation occurs in most eusocial hymenoptera with independent colony foundation as well as many solitary hymenoptera (Field 1992). Many species

have facultative interspecific nest usurpation where individuals can either reproduce independently or take-over established nests and use the resident workforce to rear their own offspring. Nest usurpation is an important selective force in the paper wasps, as the fraction of usurped nests is substantial, and usurpation battles can be fatal (Field 1992; Cervo 2006). Usurpation also occurs between different species, though we focus exclusively on usurpation within species. Another common alternative behavioral strategy in paper wasps is nest joining. During nest joining, a foreign queen joins an established association and helps cooperatively care for the colony (Gamboa and Dropkin 1979; Nonacs and Reeve 1995). Joining queens may get a share of the colony reproduction and/or the opportunity to inherit the colony if the queen dies (Reeve 1991). Joining and usurpation are important alternative reproductive strategies that are on opposite sides of the conflict/cooperation spectrum. Thus far there has been little research on why some individuals join established nests while others usurp nests.

This study will use staged contests in *P. dominulus* paper wasps to examine the factors that influence social decision making. We will examine how individual RHP and resource value influence individual decisions about whether to fight, flee, or cooperate. We will also test how RHP and RV influence the intensity and outcomes of aggressive conflict. Two measures of individual RHP will be used: body size and facial pattern. Body size is often associated with fighting ability (Turillazzi and Pardi 1977); previous work has shown that *P. dominulus* facial patterns are a badge of status that conveys information about its bearer's fighting ability (Tibbetts and Dale 2004; Tibbetts and Lindsay 2008). Colony size will be used as a measure of RV, as larger colonies produce more offspring and are a more valuable resource than smaller colonies.

Materials and methods

Wasps used in the usurpation trials were collected from sites around Ann Arbor, MI, and transplanted to boxes in the lab. All trials were run using single-queen colonies near the end of the founding stage (mid-June). Trials were completed before workers eclosed. Challenger and queen pairs were collected from sites at least 1 mile apart to ensure the individuals had not previously interacted.

At the beginning of each trial, the queen was removed from her nest, and another wasp (the challenger) was placed on the nest. Challengers were typically foundresses that were collected without a nest. No individuals from multiple-foundress nests were used in the experiment. Wasps were collected early in the morning when they were cool and inactive to ensure that we did not collect

foundresses during foraging bouts. The challenger was allowed to remain undisturbed on the nest for 1 h. Single-foundress queens spend much of their time off the nest foraging, so this method simulates a natural event where a foundress finds and occupies an empty nest. After an hour, the queen was released into the nest box and allowed to return to her nest. Subsequent interactions between the queen and challenger were videotaped for 1 h. Nest ownership typically stabilized within 10 min after the queen and challenger began interacting. At the end of the hour, we recorded whether the queen and/or challenger had possession of the nest. If queen and challenger were both on the nest, they were considered to share the nest. A total of 43 trials were performed.

RV was determined by counting the number of cells in each nest. Previous studies have shown that the number of nest cells provides a good measure of the colony's value and eventual reproductive output (Tibbetts and Reeve 2003). Body size and the number of black facial spots were used as the measures of RHP. Before the trials, all queens and challengers were weighed (± 1 mg), and the number of spots on their clypeus was recorded. Previous work indicates that body size and/or facial patterns are associated with dominance in *P. dominulus*. The number of black clypeal spots is a condition-dependent signal of fighting ability that wasps use to assess unfamiliar rivals (Tibbetts and Curtis 2007; Tibbetts and Lindsay 2008). Facial spots are correlated with dominance such that wasps with more spots are typically more dominant than wasps with fewer spots (Tibbetts and Dale 2004). Body size is also correlated with dominance in some populations of *P. dominulus* (Turillazzi and Pardi 1977; Reeve 1991), but not in others (Turillazzi and Pardi 1977; Sullivan and Strassmann 1984).

Videos of queen and challenger interactions were scored to assess length and intensity of conflict over the nest. In particular, we scored the challenger's behavior at the queen's return. Did the challenger flee without conflict or aggressively challenge the queen? The winner of the trials was also scored. An individual was considered to "win" the contest if she was alone on the nest at the end of the trial. In trials where queen and challenger shared the nest at the end of the trial, the winner was the individual that successfully mounted her opponent. Mounts are a stereotyped dominance interaction that are commonly used to assess rank within paper wasp colonies (West-Eberhard 1969). In the few trials where the contestants shared the nest but the contestants did not mount, we did not score a winner. In trials with aggressive conflict over the nest, we scored whether there were grapples or falling fights and the length of these fights. Grapples are intense dominance interactions where two wasps rear onto their hind legs and box/grapple with their front legs while trying to push each other over.

Falling fights occur when grapples become so intense that the two wasps fall off the nest. During a falling fight, the combatants typically try to sting each other (West-Eberhard 1969). Although deaths do occur during falling fights (Klahn 1988; Tibbetts, personal observation), no wasps died during these usurpation trials.

Every trial was independently scored by each author. Observers were unaware of which wasp was the queen versus challenger during tape analysis. In addition, one author (JS) was unaware of the experimental predictions during tape analysis. There was very strong concordance across authors. Minor differences between the authors in time spent grappling was resolved by averaging the values across observers.

Analysis

Categorical data was analyzed using a chi-square analysis. For the chi-squared analyses, *p* values were calculated using the exact test in SPSS v. 16. This analysis compares the observed distribution of data to expected values generated by a 10,000 generation Monte Carlo simulations. Analyses of variance (ANOVAs) were used for comparisons of continuous data (i.e., weight, nest size) across multiple categories. Post hoc comparisons between categories were performed using the LSD post hoc test.

Results

Outcome of contest over the nest

The relative facial pattern of the challenger and queen influenced which individual occupied the nest at the end of the trial. A chi-squared analysis was used to assess whether nest ownership (queen, challenger, both, neither) was associated with which individual had more facial spots. There was a significant association between nest ownership and the relative number of facial spots ($\chi_6^2=15.3$, $p=0.016$). Standardized residuals indicate that the most important factor in this relationship is that challengers with more spots than the queen are more likely to successfully supplant the queen (st. resid.=2.6). Therefore, wasps with facial patterns that signal a higher level of quality than the queen are more likely to successfully usurp a nest than those whose facial patterns signal a lower level of quality than the queen. The results are similar if the few nests occupied by neither individual are excluded from the analysis ($\chi_4^2=10.4$, $p=0.028$, Table 1).

Contest outcome was also associated with the absolute facial patterns of the queen and challenger. The queen's facial patterns was significantly associated with nest ownership ($\chi_6^2=9.79$, $p=0.04$). No cells had a standardized

Table 1 The relationship between the contest outcome and the relative number of facial spots of the queen and challenger

	Individual on nest at the end of the trial		
	Queen	Challenger	Both
Queen more spots			
Count	2	2	5
Standardized residual	-0.5	0.3	0.3
Challenger more spots			
Count	2	5	3
Standardized residual	-0.7	2.3	-0.9
Same spots			
Count	10	1	13
Standardized residual	0.8	-1.6	0.4

residual of greater than abs 2, but numerous cells contributed to the overall significant relationship. In particular, queens with zero facial spots were less likely to end up in a cooperative association (st. resid.=-1.6) and more likely to be successfully usurped by the challenger (st. resid.=1.9) than queens with more facial spots. The results are in the same direction, but not statistically significant after including the few trials where neither individual ended up on the nest at the conclusion of the trial ($\chi_4^2=10.34$, $p=0.1$). There was a nonsignificant association between the challenger's facial pattern and nest ownership ($\chi_6^2=8.3$, $p=0.077$). The largest deviation from random in this comparison is an increased probably of usurper success when usurper had two facial spots (st. resid.=1.3) and reduced probability of queen success when the usurper had two facial spots (st. resid.=-1.2). The results are similar after including the few trials where neither individual ended up on the nest at the conclusion of the trial ($\chi_4^2=11.86$, $p=0.06$). Overall, both the absolute and relative facial patterns of the queen and usurper had some influence on the outcome of aggressive contests.

The relative weight of the queen and usurper had a nonsignificant effect on nest ownership (ANOVA $F_{44,3}=2.66$, $p=0.06$). Post hoc analysis demonstrates that the strongest factor in this relationship is that the queen nested alone when the queen and challenger were similarly sized, but cooperation occurred when the queen was larger than the challenger ($p=0.008$). If the few nests occupied by neither individual are excluded from the analysis, the relationship between the relative weight and nest ownership shows similar patterns, but is statistically significant (Fig. 1, ANOVA $F_{40,2}=4.03$, $p=0.025$).

Although the *relative* weight of the queen and challenger influenced nest ownership, queen and challenger weight were not independently associated with nest ownership (ANOVA challenger weight $F_{44,3}=1.65$, $p=0.33$; queen

weight $F_{44,3}=0.21$, $p=0.88$). Therefore, the relative weight of the queen and challenger has a stronger influence on contest outcome than their absolute weight.

The size of the nest did not influence nest ownership at the end of the trial, as there was no relationship between nest size and whether the nest was occupied by the queen, challenger, both, or neither ($F_{44,3}=1.3$, $p=0.276$).

The outcome of the interaction between the queen and challenger was significantly associated with behavior during the trial. Behavior during a trial fits into one of three categories: (a) the challenger flees from the nest when the queen returns, (b) the queen and challenger fight, or (c) the challenger and queen cooperate without fighting. Overall, these behavioral options are significantly associated with the identity of the individual that ends up on the nest ($\chi_9^2=17.34$, $p=0.008$). The strongest factor in this relationship is that the queen is very likely to end up on the nest alone when the challenger flees (st. resid.=2.2). When the challenger flees, it is unlikely that she will end up on the nest at the end of the trial, alone (st. resid.=-1.4) or with the queen (st. resid.=-1.3). Following an aggressive contest over the nest, it is unlikely that both individuals will abandon the nest (st. resid.=-1.3).

The queen won more contests than the challenger (binomial test $n=31$ $p=0.01$). An individual was scored as winning a contest if she ended up alone on the nest or if she shared the nest but behaviorally dominated her rival with a mount.

Intensity of conflict

The best predictor of the length and intensity of aggressive conflict over a nest is the size of the nests. Nests over which there was aggressive conflict about ownership were

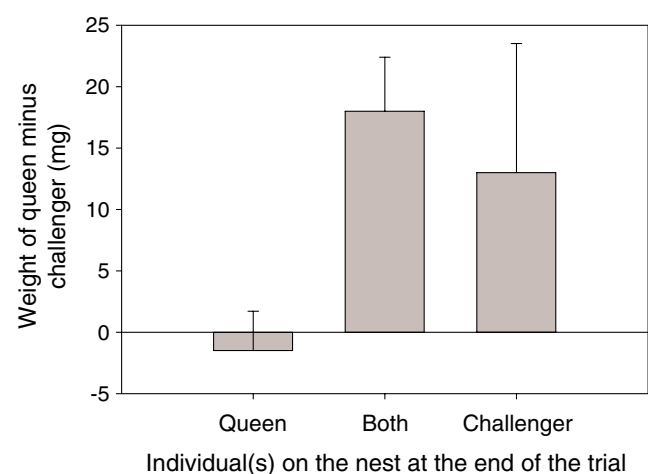


Fig. 1 The relative weight of the queen and challenger (mean + SE) influenced which individual(s) ended up on the nest. The queen was more likely to end up alone on the nest when the queen and challenger were similarly sized, while cooperation was likely when the queen was larger than the challenger

significantly larger than nests over which there was no aggressive conflict ($t_{46}=2.2$, $p=0.03$, Fig. 2). Within trials with aggressive conflict over nest ownership, there was extensive variation in the length of the conflict, from a few seconds of minor boxing to minutes of grappling. There was a significant relationship between time spent fighting (log transformed) and the size of the nest ($R^2=0.11$, $f_{45,1}=5.4$, $p=0.025$). Falling fights are the most intense type of aggression among wasps. During a falling fight, the combatants fall from the nest while grappling and trying to sting each other to death. Nests where interactions escalated to a falling fight were significantly larger than nests where there were no falling fights ($t_{46}=3.5$, $p=0.0001$, Fig. 3).

Aggressive conflict over nest ownership was not associated with the weight or facial pattern of the queen or challenger. There was no significant difference in the weight or facial pattern of challengers or queens that participated in trials with aggressive conflict versus those individuals that participated in trials that lacked aggressive conflict (queen weight $t_{46}=-1.0$, $p=0.32$; challenger weight $t_{46}=0.39$, $p=0.70$; queen spots $\chi_2^2=2.6$, $p=0.27$; challenger spots $\chi_2^2=2.9$, $p=0.24$). There was also no significant relationship between the intensity of the conflict and the abilities of the queen and challenger, as falling fights were not significantly associated with the weight or facial pattern of the usurper or challenger (queen weight $t_{46}=-0.61$, $p=0.54$; challenger weight $t_{46}=-0.29$, $p=0.77$; queen spots $\chi_2^2=2.3$, $p=0.31$; challenger spots $\chi_2^2=0.56$, $p=0.75$).

Discussion

The outcome of interactions between a challenger and queen is influenced by the individuals' resource holding

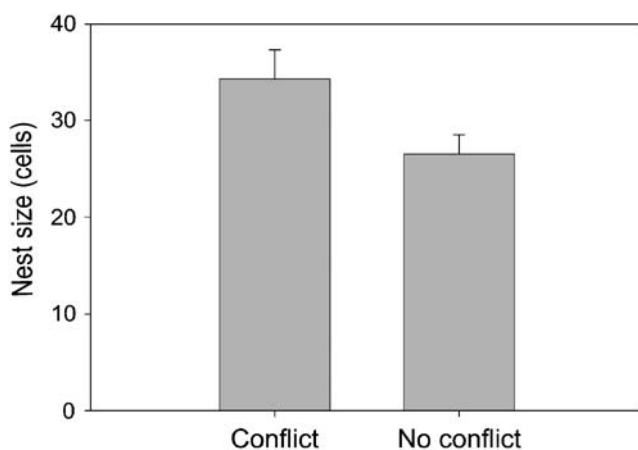


Fig. 2 The mean (+SE) size of nests that produced aggressive conflict compared with the mean size of nests that did not produce aggressive conflict

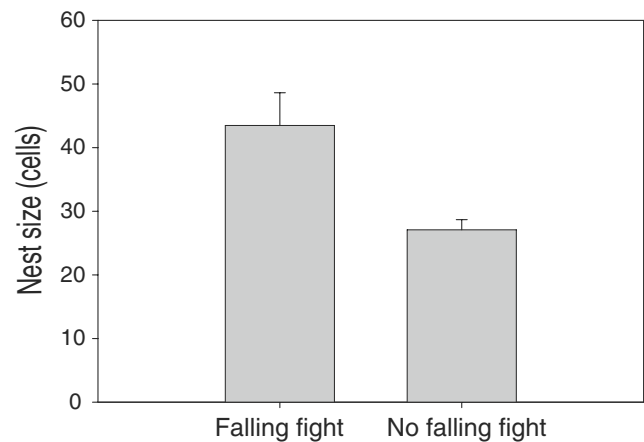


Fig. 3 Contests over larger nests were more likely to end in a falling fight between the queen and challenger than contests over smaller nests. Falling fights are the most intense form of aggression in paper wasps. Bars show mean + SE

potential (RHP). Facial pattern and body size, the two aspects of RHP examined in this study, were significant associated with nest ownership. Challengers with more facial spots than the queen were more likely to successfully usurp the colony than challengers with fewer facial spots than the queen. This result supports previous studies indicating that *P. dominulus* facial patterns are a signal of their bearer's agonistic quality (Tibbetts and Dale 2004; Tibbetts 2008; Tibbetts and Lindsay 2008). In addition, cooperative associations between the queen and challenger were more likely to occur when the queen had higher RHP than when the queen and challenger had similar RHP. Specifically, cooperative associations occurred when the queen was relatively large or when the queen had many facial spots. In contrast, the queen was more likely to end up alone on the nest when the queen and challenger were similarly sized or when the queen had few facial spots. Although this result is initially counterintuitive, it suggests that queens associate with individuals that are not an aggressive threat. Queens may evict threatening individuals rather than allowing them to cooperate. Overall, challengers with high RHP were more likely to successfully evict the queen, while queens with high RHP were more likely to form cooperative associations with the challenger.

The relationship between a challengers' facial pattern and her nest usurpation success provides further evidence that *P. dominulus* facial patterns are signals of their bearer's agonistic abilities. These results also support previous work showing that the black facial patterns in *P. dominulus* are a badge-of-status used to assess rivals during aggressive competition (Tibbetts 2008; Tibbetts and Lindsay 2008). Previous studies have shown that *P. dominulus* facial patterns are associated with agonistic abilities in contexts other than nest usurpation. For example, individuals with more facial spots are more likely to win staged dominance

contests than individuals with fewer facial spots (Tibbetts and Dale 2004). Facial patterns are also associated with dominance in natural associations of *Polistes* cofoundresses (Tannure-Nascimento et al. 2008; Zanette and Field 2009). Interestingly, Cervo et al. (2008) did not find an association between dominance and facial pattern in an Italian population of *P. dominulus*. The basis for the discrepancy between the results of Cervo et al. (2008) and the other studies is not clear. A reanalysis that takes into account the importance of *relative* facial pattern, like that used by Zanette and Field (2009) may yield interesting insights. Further studies of *P. dominulus* facial patterns across their range are important to establish whether the information conveyed by *P. dominulus* facial patterns truly varies from population to population.

The signal value of animal ornaments often varies between different populations of the same species. For example, tail streamers are a sexually selected signal of quality in European barn swallows (Moller 1988). In North American barn swallows, plumage color rather than tail length is the sexually selected quality signal (Safran and McGraw 2004). The white forehead patch in Swedish pied flycatcher is a badge-of-status, but this forehead patch appears to have no signal value in the Norwegian population of the same species (Dale et al. 1999). Similarly, the information conveyed by the black facial mask and yellow bib in common yellowthroats varies between New York and Wisconsin populations (Dunn et al. 2008). Even the peacock's tail, a classic quality signal (Petrie et al. 1991), appears to have no signal value in some peacock populations (Takahashi et al. 2008). Ornament function even appears to vary from year to year within the same population (Hegyi et al. 2008). Thus far, we know very little about why the variation in ornament function occurs. Understanding the factors that account for the variation in ornament function is an important direction for future research. Therefore, if the signal value of *P. dominulus* facial patterns does vary from population to population, it will be interesting to assess the factors that account for this variation.

Contests over nest ownership are the type of behavioral context expected to favor the evolution of a signal of fighting ability like that found in *P. dominulus*. Signals of fighting ability, such as status badges, allow rivals to quickly assess each other's agonistic ability without engaging in intense competition (Maynard-Smith and Harper 2003; Searcy and Nowicki 2005). Therefore, badges are expected to be particularly important when there is social competition among numerous unfamiliar rivals (Rohwer 1975).

The pre-worker phase of the colony cycle in paper wasps is one such context. During the pre-worker phase, wasps experience many challenges from other foundresses. Many

nests are successfully usurped by foreign foundresses, with measured rates of successful nest usurpation in the *Polistes* ranging from 2% to 61% (Field 1992; Cervo and Dani 1996). Within some *Polistes* populations, intraspecific usurpation rates can be as high as 100% (Gamboa 1978). Each queen likely experiences many more unsuccessful usurpation attempts. In their observations of *P. dominulus* and *P. fuscatus* nests, Gamboa et al. (2004) observed almost one attempted intraspecific nest usurpation every 2 h. Rates of attempted usurpation were higher in *P. fuscatus* than *P. dominulus*, but foundresses of both species experienced numerous aggressive intrusions by unknown queens (Gamboa et al. 2004). Nonacs and Reeve (1995) used intensive census to measure successful nest usurpations in *P. dominulus*, finding daily rates of successful intraspecific nest usurpation of approximately 1% during much of the late founding stage. They also found substantial rates of nest joining by foreign queens. Daily rates of nest joining ranged from 6% in the early nest-founding phase to 1–2% just prior to worker emergence. The substantial rates of nest usurpation and joining indicate that *Polistes* interact with many unfamiliar individuals throughout the founding stage. As a result, signals of fighting ability that allow rivals to quickly assess other's RHP are likely to be important, both for nesting queens and for potential usurpers/joiners.

We found that queens won significantly more usurpation bouts than challengers. Queens tended to prevail when the queen and challenger had similar RHP or when the queen had higher RHP than the challenger. Challengers only prevailed when they had high RHP. One explanation for the queen's greater success during the contests is that the nest is more valuable to the queen than to a challenger. Usurped nests have lower overall productivity than non-usurped nests (Klahn 1988; Cervo and Dani 1996). The reduced productivity of usurped nests may be due to lower work rates by workers that are unrelated to the usurper queen. Usurping queens also eat the eggs and young larvae as soon as they take over a nest (Klahn 1988). This frees colony resources for raising the usurper's own offspring, but also lengthens the time until reproductives are produced. Across taxa, resource holders are often more likely to win contests than challengers (Davies 1978; Krebs 1982). Asymmetries in net payoffs are thought to be an important explanation for this observation (Parker 1974; Davies and Houston 1981; Leimar and Enquist 1984). The asymmetric reproductive payoffs experienced by queens and challengers may be one reason why resident *Polistes* queens are more likely to win contests than challengers.

Control over nest composition

One initially surprising aspect of the experimental results is that cooperation between challenger and queen occurred in

pairings where the queen had relatively high RHP. Cooperation was less likely to occur in pairing where the queen had relatively low RHP. Therefore, the queen may aggressively control nest ownership, evicting challengers that are threatening and allowing nonthreatening challengers to cooperate.

Thus far, much research on foundress associations has examined cooperation from the subordinate's perspective (Gadagkar et al. 1988; Field and Foster 1999), but the results of this study suggest that cooperation must also be considered from the perspective of the dominant foundress. The dominant may be favored to evict a high quality subordinate rather than risking losing control of the colony to a threatening subordinate. Although dominance ranks among cofoundresses typically remain stable though the colony cycle, subordinates occasionally take over nests and become reproductive dominants (Reeve 1991; Queller et al. 2000). It is often assumed that the subordinate only takes over if the dominant dies of natural causes. However, foundresses on multiple foundress *P. dominulus* colonies disappear at a higher rate than foundresses from single foundress colonies (Nonacs and Reeve 1995), suggesting that social conflict may play a role in foundress disappearance. Further, the disappearance of the dominant foundress is occasionally preceded by intense aggression between cofoundresses (Tibbetts, personal observation), indicating that subordinates may occasionally overthrow the dominant. Detailed field and lab-based studies of cofoundress behavior at the time of group formation will be important to understand the dynamics of individual decisions during cooperation and to test whether the dominant aggressively controls colony composition.

Eviction is difficult to identify without detailed behavioral observations, so there have been relatively few studies exploring eviction in animal societies. Nevertheless, there is evidence across taxa that dominants aggressively control group membership to reduce threats to themselves or their offspring (Buston 2003; Gilchrist 2006). For example, subordinate gobies that are close to the dominant's size are more likely to be evicted than subordinates that are much smaller than the dominant (Wong et al. 2008).

Length and intensity of aggressive conflict

The length and intensity of contests over nest ownership is influenced by nest characteristics rather than the individual characteristics of the queen and challenger. Contests over larger nests were more likely to produce aggressive conflict between the queen and challenger than contests over smaller nests. Aggressive contests over larger nests were also longer and more intense than battles over smaller nests. Therefore, queens and challengers modify their behavior in response to the value of the nest.

Classic game theoretic models predict that conflict intensity will depend on the value of the contested resource (Enquist and Leimar 1987). Increased conflict during contests over large nests matches this prediction, as larger wasp nests produce a larger workforce and more reproductive offspring than smaller nests (Tibbetts and Reeve 2003). Across species, contests over valuable resources are often more intense than those over less valuable resources (Davies 1978; Gilley 2001). There is also some evidence that individuals within a single species modulate their aggressive intensity from contest to contest, depending on what they are fighting over (reviewed in Arnott and Elwood 2008). However, resource value can be difficult for both rivals to assess. As a result, contest intensity is often based on other parameters, such as challenger's needs (Gherardi 2006), or on one contestant's knowledge about resource value (Bridge et al. 2000). Wasp nests are often left unattended, while the queen forages. As a result, potential challengers have ample opportunity to assess the value of a nest before deciding whether to engage in an escalated contest over ownership. As both contestants have similar information about the nest before engaging in a contest, it makes intuitive sense that both queen and challenger modulate their aggressive behavior based on the nest's value.

Conclusion

The dynamics of contests in the facultatively social wasp *P. dominulus* have important parallels with contests in nonsocial taxa. Queens are more likely to win aggressive contests over nest ownership than challengers, perhaps because of the asymmetry in resource value that is commonly associated with resource ownership. However, challengers can successfully displace the queen and take over the colony. Challengers with relatively high RHP are significantly more likely to displace the queen than challengers with relatively low RHP. Contests over large, valuable nests produce more aggressive conflict than contests over smaller, less valuable nests.

Contest dynamics in *P. dominulus* also differ from the contests in nonsocial taxa. Most importantly, wasps can choose to cooperate rather than evict each other. The results of this study suggest that queens are more willing to form cooperative associations when they have high RHP than when they have lower RHP, suggesting that queens evict challengers that pose an aggressive threat. Overall, research on decision-making during contests provides an important perspective on the factors that influence conflict and cooperation in social species.

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