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REVIEW ARTICLE

Polistes paper wasps: a model genus for the study of social dominance hierarchies

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Abstract *Polistes* are an ideal system to study ultimate and proximate questions of dominance, and to test theoretical predictions about social evolution. The behaviors typically associated with dominance in *Polistes* are similar to those observed in many vertebrate societies. Here, we review recent ethological, mechanistic, and evolutionary studies on how social dominance hierarchies are established and maintained in *Polistes* spp. From the ultimate perspective, we address individual and group benefits of hierarchy formation, as well as issues such as reproductive skew, queen-worker conflict, and costs of challenging the dominant. From the proximate perspective, we review social, physical, and physiological factors influencing hierarchy formation, including co-foundress interactions, age structure, body size, endocrine system, and chemical and visual signals. We also discuss the extensive inter- and intra-specific variation of *Polistes* in the formation and maintenance of hierarchies, as well as levels of within-colony aggression. We conclude the review by highlighting the utility of this variation for comparative studies and the immense potential of the genus *Polistes* to address fundamental and unanswered questions about the evolution and maintenance of dominance behavior in animals.

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Introduction

Stable animal social groups are characterized by both cooperation and competition among individuals (Ratnieks and Reeve, 1992; Heinze, 2004). In many groups in which individuals repeatedly contact each other, animals with superior competitive ability will assert their dominance over inferior individuals. Social dominance hierarchies are a "pecking order" of individuals with specific ranks, and may be established in animal groups because of the following two advantages: (1) a chance for individuals to achieve the benefits of high rank, and (2) stable, recognized ranks over the long term can reduce the costs of within-group conflict (Hemelrijk, 2000). There are many similarities across social taxa that maintain linear hierarchies. Typically, the most dominant individual has access to the best location and/or resources in the group (closest to mates, farthest from predators), whereas the subordinates are more likely to bring resources to the dominant, groom him/her, or remain on the periphery of the group (Hamilton, 1971; Hemelrijk, 2000). The dominant is also more likely to perform antagonistic or aggressive acts towards subordinates, whereas subordinates will only attempt to perform these behaviors toward higher-ranking individuals if they attempt to challenge them for rank. At these points, aggression escalates, one individual is the clear victor, the hierarchy is re-established, and overt aggression is again rare.

In the 1940s, Leo Pardi surprised the animal behavior community by first documenting the presence of linear dominance hierarchies in an insect, *Polistes dominula* (nee *dominulus*, *gallicus*) (Pardi, 1942, 1946; reviewed in Pardi, 1948). This complex social behavior was previously thought to be limited to large-brained, social vertebrates (Pardi, 1996). Since this remarkable discovery, dominance behavior has been documented in numerous other vespid wasps and other insect species (Bell and Gorton, 1978; van Doorn and Heringa, 1986; Monnin and Peeters, 1999), but wasps in the genus *Polistes* remain the premier insect model, and one of the best overall animal models, for studying the mechanistic and evolutionary factors that lead to the formation of dominance hierarchies (West, 1967; Reeve, 1991).

Dominance behavior in *Polistes* has been intensively studied and manipulated since the early 1940s. *Polistes* wasps generally build small, open-faced (no envelope), 1-tiered nests that can contain 1–75+ adults (depending on the species and stage of colony development). The small colony size allows researchers to individually mark and follow the behaviors of all colony members. The lack of nest envelope allows for in situ observations, and entire nests can also be easily captured and relocated to the laboratory for controlled studies. In 1969, West-Eberhard reviewed dominance behavior in the introduction of *The Social Biology of Polistine Wasps*. Much has been learned about dominance behavior in *Polistes* in the past 40 years, but subsequent reviews on *Polistes* biology (Strambi, 1990; Reeve, 1991; Turillazzi and West-Eberhard, 1996; Hunt, 2007) have not presented a comprehensive review of all of the ethological, mechanistic, and evolutionary studies on social dominance hierarchies. Thus, the time is right to provide an updated review of this topic, in particular to point out the similarities and differences across species, as well as to highlight recent work that explores mechanisms.

Here, we review ultimate explanations and proximate mechanisms that allow dominance hierarchies to form and be maintained in *Polistes*. *Polistes* are an ideal system to study ultimate and proximate questions of dominance, and to test theoretical predictions about social evolution (Reeve, 1991; Bonabeau et al., 1999). Furthermore, dominants can be behaviorally, physiologically, and/or genomically distinguished from subordinates. *Polistes* species also vary widely in how they form and maintain hierarchies, and the level of within-colony aggression. We conclude the review by highlighting the utility of this variation for comparative studies and the immense potential of the genus *Polistes* to address fundamental and unanswered questions about the evolution and maintenance of dominance behavior in animals.

Description of dominance behavior in *Polistes*

Dominance behavior can occur at several different stages of the *Polistes* colony cycle. The first is early in the colony cycle in the "founding phase," among females that initiate a nest together, called *foundresses* (mated females that have dispersed from their natal colonies to establish new colonies). Foundresses use multiple strategies to establish a colony: (1) initiate nest building alone, (2) cooperate with other foundresses throughout the founding stage, (3) 'sit-and-wait' until another foundress abandons her nest and adopt it (Starks, 1998; Starks, 2001; Liebert et al., 2005) or 4) challenge the sitting foundress in an attempt to usurp the nest (Nonacs and Reeve, 1995). Foundresses rear a first generation of female offspring, which typically become *workers* (unmated females with limited reproductive capacity that perform numerous colony maintenance behaviors), at which time the colony enters the "worker phase". The dominant foundress stays on the nest and assumes the role of *queen* (behaviorally dominant, egg-laying female), and there is a linear dominance hierarchy among workers, all subordinate to the queen (that is, alpha outranks all; beta outranks all but the alpha, etc.). Dominant workers have the potential to mate and become replacement queens if the resident queen dies or is removed. The workers assist in rearing males (which show no dominance behavior) and a second generation of females, called *gynes*, which will become future reproductive females. While on their natal nest, gynes do not engage in dominance behavior. However, in temperate species, gynes form aggregations prior to hibernation in the fall, and engage in dominance interactions that predict dominance rank in the spring (Dapporto et al., 2006). Thus, in nearly all stages of their lives, dominance behavior is an integral part of *Polistes* biology.

The behaviors typically associated with dominance in *Polistes* are similar to those observed in other animal taxa. When establishing a hierarchy, individuals may bite at (Fig. 1a) or aggressively posture towards (Fig. 1b) the other individual. An escalated conflict may lead to grappling or a 'falling fight', where both individuals fall to the ground from the nest (West-Eberhard, 1969). After a hierarchy has been established, a dominant wasp may communicate her rank through less aggressive, ritualized behaviors. For example, mounting behavior is observed when a subordinate crouches and lowers her antennae while the dominant stands erect and positions herself above the subordinate, typically antennating her as well (Fig. 1c–d). In some species, subordinate co-foundresses will die (Hughes and Strassmann, 1988b) or be aggressively forced off the nest when worker offspring begin to emerge (Gamboa et al., 1978; Reeve, 1991). However, if the dominant foundress is removed from the nest before worker emergence, and the hierarchy among subordinate foundresses has not been determined, aggressive interactions will ensue re-establishing the hierarchy among the remaining co-foundresses [*P. canadensis* (West-Eberhard, 1969); *P. exclamans* (Strassmann and Meyer, 1983); *P. chinensis antennalis*

Fig. 1 Ritualized dominance behavior in *Polistes.* Foundress behavior when establishing dominance hierarchy: **a** biting; **b** aggressive posturing; **c**–**d** mounting; **c** a dominant female crawls over the subordinate; **d** a dominant female stands in an erect posture, while subordinate maintains a flatter posture and exposes the underside of her thorax—a signal of submission across animal taxa. All photos are of *Polistes fuscatus*; photos by J.M. Jandt

(Miyano, 1986)]. Furthermore, if queens are removed from the nest, workers will engage in dominance interactions with one another for an opportunity to be the primary layer of male-producing (unfertilized) eggs. If successful, some workers may even mate and become *replacement queens*. After a stable hierarchy has been formed, the dominant maintains her social status by eating the eggs of subordinates, possible chemical signaling of status, and/or repeated ritualized aggressive behavioral interactions.

How dominance is established in the short-term can differ from what is observed in a long-term stable hierarchy. In the short term, a *behavioral hierarchy* may be established within just a few minutes of intense interactions as one female continues to win behavioral contests over another. In the long-term, a physiological or *reproductive hierarchy* becomes established as individuals undergo physiological changes (including enhanced ovarian development in the dominant) that result in a single individual taking over as the main egg-layer on the nest (Reeve, 1991). While the behaviorally dominant individual is usually reproductively dominant [*P. dominula*: (Pratte, 1993)], there are exceptions [e.g., *P. japonicus* (Ishikawa et al., 2011); *P. jokahamae* (nee *jadwigae*) (Tsuchida and Ito, 1991)]. In *P. snelleni*, where foundresses are typically solitary, co-foundresses will share in foraging and egg-laying efforts and no discernible hierarchy is formed (Sayama, 2006).

Ultimate factors: fitness considerations associated with dominance hierarchy formation

Individual fitness benefits

In paper wasps, dominant foundresses are the primary reproductives, but in many cases, subordinates have at least some direct reproduction. What determines the relative reproductive shares, or reproductive skew, of dominants and subordinates? *Reproductive skew theory*, broadly defined, uses differences in ultimate and proximate factors such as relatedness and competitive ability between individuals to understand observed division of reproduction within animal groups. There are two main classes of models. The *transactional models* consider ultimate factors: that reproductive shares are the result of reproductive payments, that vary based on factors such as the subordinate's contribution to group productivity, the potential for solitary reproduction, and relatedness of group members (Reeve and Ratnieks, 1993; Reeve, 2000; Tibbetts and Reeve, 2000; Reeve and Jeanne, 2003; Nonacs and Hager, 2011). In contrast, *compromise* or *tug of war models* focus on proximate mechanisms: that relative competitive abilities influence reproductive sharing (Reeve and Keller, 2001; Nonacs and Hager, 2011). *Synthetic models* have attempted to combine both transactional and compromise models (Reeve, 2000; Reeve and Shen, 2006;

Buston and Zink, 2009), although predictions from these synthetic models rarely match what is observed in cooperative breeding groups (Nonacs and Hager, 2011).

Over the past decade, models and empirical work have proliferated and the field has become quite contentious. Much of the empirical work has supported transactional models of reproductive sharing in *Polistes* [e.g., *P. fuscatus* (Reeve, 2000); *P. dominula* (Tibbetts and Reeve, 2000; 2008)]. However, other work in *Polistes* found no evidence to support transactional [e.g., *P. dominula* (Liebert and Starks, 2006)] or compromise models [e.g., *P. fuscatus* (Nonacs et al., 2004)]. In *P. bellicosus*, neither relatedness (transactional model) nor fighting ability (compromise model) predicted reproductive skew (Field et al., 1998). One problem with testing skew theory may be the assumption that aggression relates to skew (Nonacs et al., 2004). In some *Polistes* species, as described above, aggression (behavioral dominance) does not always equal skew (reproductive dominance) (Tsuchida and Ito, 1991; Ishikawa et al., 2011). Additionally, it is difficult to rigorously test skew models, as the models are complex and many of the factors predicted to influence skew are hard to measure.

Co-foundress relationships

When choosing to join a nest, some co-foundresses join full sisters (Klahn, 1979; Ross and Gamboa, 1981; Strassmann, 1981b; Reeve, 1991; Field et al., 1998; Seppä et al., 2002), whereas others may nest with non-relatives (Reeve, 1991; Queller, 2000; Zanette and Field, 2008). Ideally, a foundress' contribution to the colony (in terms of direct or indirect fitness) will be preserved even if she leaves the nest [The *Assured Fitness Returns Hypothesis* (Shreeves et al., 2003)], though this is not always the case (Nonacs et al., 2006). While original foundresses rarely leave their nests, nest-switching among co-foundresses is common in some species (West-Eberhard, 1969; Field et al., 1998). Subordinate foundresses may switch nests and increase the indirect benefits of cooperating by joining sister foundresses [e.g., *P. carolina* (Seppä et al., 2012)], but the decision to switch nests does not always lead to sister associations [e.g., *P. dominula* (Zanette and Field, 2011)]. The *Social Heterosis Hypothesis* suggests that interactions among unrelated co-foundresses could ultimately lead to higher group productivity (Nonacs and Kapheim, 2007). Still, the main way in which an unrelated co-foundress directly benefits by being the subordinate in a cooperative nesting group is if she outlives the foundress and takes over the egg-laying role (Queller et al., 2000; Zanette and Field, 2011).

Co-foundresses that choose to join a nest might wait in a queue for an opportunity to achieve dominant status and become the primary egg-layer. However, unrelated subordinates are no more likely than a dominant's sisters to inherit the nest (Leadbeater et al., 2010). Therefore, unrelated subordinates do not gain indirect fitness from rearing the dominant's offspring, nor do they have a better chance at inheriting the nest and gaining high direct fitness. Still, a subordinate can, in some cases, lay more eggs than she might as a lone foundress (Leadbeater et al., 2011). In most species of *Polistes*, the queen will *police* (destroy or consume) eggs laid by subordinates (Strambi, 1990), but in *P. metricus* and *P. fuscatus*, the dominant may allow related subordinates to lay a small percentage of eggs as a staying incentive (Metcalf and Whitt, 1977a; Reeve et al., 2000). In other species, subordinates can achieve direct fitness benefits by sneaking eggs into a neighboring nest while the dominant is away [e.g., *P. carolina* (Seppä et al., 2012); *P. bellicosus* (Field et al., 1998)]. Generally, higher-ranked subordinates spend less time performing energy-expensive tasks compared to the lower-ranked subordinates on the nest (Reeve and Gamboa, 1987), and may be in better physical condition to attempt to usurp a nest far from the original nesting site and to obtain direct fitness opportunities (Gamboa et al., 1978; Klahn, 1988; Gamboa et al., 1999).

Queen-worker interests

Unlike most social Hymenopterans, *Polistes* workers retain the potential to mate and lay fertilized eggs. Inclusive fitness benefits provide an explanation as to why workers might remain at the nest and help rear sisters, rather than fly off to found their own colonies (Reeve and Keller, 1995). An interesting situation arises in the case of subordinate co-foundresses that remain on the nest after worker emergence. Such co-foundresses can acquire direct fitness through occasional egg-laying or queen replacement. According to kin selection theory, workers should tolerate a subordinate co-foundress succeeding the queen as the new reproductive if the subordinate is closely related to the queen mother; if the subordinate co-foundress is distantly related, workers should prefer an older worker to achieve this status (Queller et al., 1997). However, unrelated subordinate *P. annularis* co-foundresses are more likely to succeed in egg-laying after the queen dies than are workers (Hughes et al., 1987; Reeve, 1991; Queller et al., 1997). This suggests that some other mechanism may play a stronger role in determining dominance rank than collective relatedness preferences.

Kin selection also predicts that workers that are highly related to one another increase indirect fitness when they help to raise nephews (haploid male eggs laid by sisters) over brothers (queen-laid male eggs) (Reeve and Keller, 1995; Queller et al., 1997; Arevalo et al., 1998). However, in *P. bellicosus* and *P. dorsalis*, male eggs are laid by the queen—suggesting that either queens physically dominate offspring, or this behavior was selected because it minimizes within-colony conflict (Arevalo et al., 1998).

Queen-worker conflict may also occur when the queen has reduced fertility. For example, in single foundress *P. dominula* colonies, removal of brood leads to an increase in worker egg-laying/ovary development (Liebig et al., 2005; Monnin et al., 2009). Since the queen does not stop egg-laying (her rate of egg-laying actually increases), she will *police* (detect and eat) worker-laid eggs and replace them with her own (Liebig et al., 2005). Workers, too, are more likely to replace worker-laid eggs than queen-laid eggs. This suggests that workers have a 'hierarchy of cues' to assess queen fertility, and brood presence may affect this (Liebig et al., 2005).

Worker-worker interests

Like co-foundresses, workers may drift between colonies—but are more likely to drift among related colonies than unrelated ones (Sumner et al., 2007). These drifters do not receive direct benefits (they do not show increase in ovarian development), so they may instead increase indirect fitness by helping to raise offspring in related colonies. Alternatively, drifting may be non-adaptive, reflecting errors in navigation and recognition.

When the queen and all other co-foundresses are removed from the nest (or have perished), worker offspring can become replacement queens (Metcalf and Whitt, 1977a; Miyano, 1991). Like co-foundresses, once the queen has been removed, workers engage in aggressive interactions and establish a dominance hierarchy, the dominant worker becoming the primary egg-layer (Miyano, 1991; Reeve, 1991; Tibbetts and Huang, 2010).

Cost of challenging the dominant

After dominance is established, subordinates do not challenge the dominant for reproductive supremacy. However, challenges by unfamiliar rivals are common throughout the founding stage (Nonacs and Reeve, 1995). Attempts to usurp or challenge the dominant for status of primary reproductive can incur costs to one or both of the individuals. Grappling, biting, and/or falling fights can lead to mutilation or death (Gamboa, 1978; Reeve, 1991; Pratte and Gervet, 1995). Often, a successful usurper will destroy most of the immature brood in the nest, a direct fitness cost for the previous dominant (Cervo and Lorenzi, 1996). In the cases where the dominant loses (but remains alive), she can choose to remain on the nest as a subordinate, or attempt to join or usurp another already established nest (Gamboa, 1978).

Colony (group) benefits

The formation of groups structured by dominance hierarchies provides some shared benefits to all group members. Studies to date have highlighted a major increase in the productivity and survival of colonies with multiple compared to single foundresses. In addition, the coexistence of dominant and subordinate females with different behavioral repertoires on the nest may also lead to a more efficient colony-wide division of labor.

Nest survival, competitiveness

Multiple foundresses on a nest increase the odds that the nest will survive throughout the founding phase (see Table 7.2 in Hunt, 2007; de Oliveira et al., 2010; Zanette and Field, 2011). This may be because individual foundresses are more likely to survive on multi-foundress nests [The *Survival Insurance Hypothesis*: (Reeve, 1991; Nonacs and Reeve, 1995; Tibbetts and Reeve, 2003)], and/or because multiple foundresses can better defend a nest from usurpation than single foundresses (Gamboa, 1978; Reeve, 1991). Colonies with multiple foundresses rarely leave their nests unattended (Gamboa et al., 1978), so are less likely to be usurped (Reeve, 1991; Gamboa et al., 1992). Multi-foundress colonies may also outcompete single foundresses for resources, as subordinates can readily leave the nest to forage while the dominant remains at the nest to protect and tend to the brood (see 'Division of Labor' below). Furthermore, workers tend to emerge earlier in multiple foundress colonies than in colonies with single foundresses [*P. metricus* (Metcalf and Whitt, 1977b; Gamboa, 1980)], and nests tend to be larger [in terms of cell number when workers begin to emerge; *P. fuscatus* and *P. dominula* (West-Eberhard, 1969; Tibbetts and Reeve, 2003)]. This early advantage could continue to allow multi-foundress colonies to find and exploit resources in the environment faster and more efficiently than a slower-growing colony. However, there is little evidence that multiply founded nests are more likely to evade attack from predators, such as birds, or parasites than single foundress nests (Strassmann, 1981a; Reeve, 1991), although they are more likely to reestablish a nest after a predation event (Gibo, 1978).

There are species where solitary nesting is adaptive, or multiple foundress colonies are rare (see Table 7.2 in Hunt, 2007). In *P. aurifer*, solitary nests have the same reproductive success as cooperative nests, and there is no evidence that a potential subordinate would have less success independently founding a nest than a solitary dominant (Liebert et al., 2005). In this species, late starting nests have a good chance of producing offspring, so there is little selective pressure to protect an initial nest when rebuilding the nest later in the season will still lead to the same outcome.

Division of labor

Dominance hierarchy formation may structure the division of labor among colony members. Division of labor itself is a huge benefit, and is well-recognized to increase group efficiency. Once a hierarchy is established, the dominant and subordinate foundresses divide colony tasks. The dominant generally spends more time laying eggs, tending larvae (though all adults will feed larvae), initiating new nest cells in which to lay eggs, or remaining inactive (Heldmann, 1936; Pardi, 1948; West-Eberhard, 1969; Gamboa et al., 1978; Strassmann, 1981b; Reeve and Gamboa, 1983; Pratte, 1989; Strambi, 1990; O'Donnell, 1995; Cant and Field, 2001). In *P. fuscatus*, dominants are more likely to engage in nest defense than subordinates (Judd, 2000), and in *P. instabilis* dominants tend to receive materials from returning foragers (O'Donnell, 1995).

Subordinate foundresses are the primary prey foragers in most *Polistes* species (West-Eberhard, 1969; Gamboa et al., 1978; Reeve and Gamboa, 1983; West-Eberhard, 1986; Pratte, 1989). There is variation in helping effort within subordinates based on relatedness to the dominant, relative indirect fitness gains, and potential for future, direct reproduction (Field and Cant, 2006). For example, in *P. dominula*, higher-ranked subordinates are more likely to build the nest whereas lower-ranked subordinates are more likely to perform dangerous off-nest tasks like foraging (Pratte, 1989). When the dominant wasp does forage, she will collect vegetable fiber, whereas subordinates will perform riskier foraging tasks such as nectar collection and prey hunting [*P. metricus* (Gamboa et al., 1978); *P. ferreri* (De Souza et al., 2008)].

Workers may also divide tasks based on their hierarchical rank, with lower-ranked workers performing riskier tasks (Reeve, 1991; Theraulaz et al., 1992). Either queens or workers may act as 'pacemakers' of the colony by regulating worker activity. In *P. fuscatus*, the presence of the queen and her interactions with workers can lead to an increase in activity (Reeve and Gamboa, 1983; 1987; Sumana and Starks, 2004). However, in *P. instabilis* and *P. dominula*, dominance interactions and the activity of returning workers may be just as, if not more, important than the presence of the queen in determining worker activity rates (O'Donnell, 1998; Jha et al., 2006; Molina and O'Donnell, 2009).

Proximate factors: the influences of social environment and individual traits on dominance

Social environment

Dominance rank depends heavily on social interactions. These interactions may occur in *Polistes* at various stages: among gynes prior to nest initiation in pre-hibernation aggregations; among co-foundresses on a nest in the spring; and among workers after the primary reproductive is gone from the nest.

Social interactions in hibernation clusters

Before gynes of temperate species of *Polistes* undergo winter diapause, they aggregate in hibernation clusters. These clusters may provide additional protection from predators and insulation from cold in the winter. In *P. annularis*, gynes are more likely to aggregate with sisters, and if they emerge from hibernacula on warm days throughout the winter, they will retreat to their original hibernacula in the evenings (Strassmann, 1981b).

Prior to hibernation, dominance interactions within these clusters are associated with spring co-foundress relationships (Dapporto and Palagi, 2006). In *P. dominula*, the more dominant individuals in the fall have greater ovarian development and are more likely to dominate co-foundresses in the spring (Dapporto et al., 2006).

Post-hibernation, *P. dominula* foundresses are more likely to join a foundress from the same hibernation cluster than a sibling (Zanette and Field, 2011), whereas in *P. annularis*, both hibernation clusters and co-foundress associations are more likely composed of sisters than unrelated individuals (Strassmann, 1981b).

Co-foundress interactions

After emerging from diapause in the spring, foundresses that decide to join a nest engage in aggressive interactions to establish hierarchical rank. The intensity and duration of contests can vary among species (Reeve, 1991) and initiators can vary throughout a colony life cycle [e.g., dominant individuals are more likely to retreat from subordinates early in the colony life cycle, but their aggressiveness increases as the colony cycle progresses (Gamboa and Dropkin, 1979)]. However, the order in which foundresses join the nest can also be an early determinant of hierarchical status (Reeve, 1991; Seppä et al., 2002; Zanette and Field, 2009), even if forced to nest together (Pratte and Gervet, 1992). Nest ownership, therefore, is more likely achieved by those foundresses that terminate diapause earlier, a factor that may be mediated by individual differences in temperature sensitivity. If early emergence is a measure of foundress strength, then the variation among foundresses in terms of temperature to emerge (Tibbetts et al., 2011b) may be a mechanistic explanation why early arrival at a nesting site is associated with dominance.

Often, subordinates are subjected to aggressive acts from the dominant wasp [e.g., *P. annularis* (Strassmann, 1981b)]. To avoid overt, aggressive conflict, dominants and subordinates may remain on opposite ends of the nest [e.g., *P. fuscatus* (West-Eberhard, 1969)], or retreat from one another [e.g., *P. metricus* (Gamboa and Dropkin, 1979)]. Policing behavior, where dominants eat eggs laid by subordinates (West-Eberhard, 1969), may also be a way to control subordinate reproduction without direct aggressive interaction.

As the season progresses, aggressive behavior among co-foundresses tends to increase (Gamboa and Dropkin, 1979; Gamboa and Stump, 1996; Tibbetts and Reeve, 2000; Cant et al., 2006b). In *P. versicolor*, more dominance interactions are performed by females of higher rank post-worker emergence (de Oliveira et al., 2006). In *P. fuscatus*, the dominant wasp may communicate dominance or stimulate inactive subordinates through rapid movements toward conspecifics known as darts (Gamboa et al., 1990; Sumana and Starks, 2004).

Foundresses may also modulate their aggression levels according to ecological constraints on independent reproductive opportunities (e.g., by decreasing aggression towards high-ranking subordinates when abandoned nests with pupae are nearby). Subordinate productivity may also affect aggression: if low ranking subordinates are removed, dominant wasps will increase aggression towards higher-ranking subordinates until they perform more brood care (Tibbetts and Reeve 2008). The dominant's level of aggression in *P. dominula* is dependent upon the resources controlled by the subordinate (Tibbetts and Reeve, 2000). On the other hand, when conflict is experimentally induced among *P. dominula* co-foundresses, subordinates with lower ovarian development (i.e., less to lose) are more likely to escalate conflict than subordinates with high ovarian development (Cant et al., 2006a).

Hypotheses that antennal drumming, abdominal wagging, or lateral vibrations are involved with dominance assessment may be incorrect (Brennan, 2007), particularly since solitary foundresses perform these behaviors (Gamboa et al., 1978; Reeve, 1991; Brennan, 2007). In *P. fuscatus*, solitary foundresses perform these behaviors more often than dominant foundresses in a multi-foundress association (Downing and Jeanne, 1985). These behaviors were thought to be involved in dominance assessment across *Polistes* spp., because they were often performed by dominants following encounters with subordinates (West-Eberhard, 1969; Gamboa et al., 1978; West-Eberhard, 1986; reviewed in Jeanne, 2009). Further, in the less aggressive *P. japonicus*, abdominal wagging was proposed to communicate the 'vigor' of the dominant to subordinates (Ishikawa et al., 2011). However, in *P. fuscatus*, although foundresses of higher rank perform more lateral vibrations, this behavior is not associated with (e.g., preceded or followed by) aggressive behavior (Savoyard et al., 1998). More recent hypotheses posit that nest vibrations may be signals to larvae, perhaps mechanisms used by the queen to control caste development of offspring (Brillet et al., 1999; Jeanne, 2009; Jeanne and Suryanarayanan, 2011; Suryanarayanan et al., 2011; Hunt and Richard, 2013). The substrate-borne vibration signals may trigger caste-specific genes to turn on or off, resulting in a chain of physiological and behavioral responses, mediated by biogenic amines, in the developing larvae (Jeanne, 2009).

Group age structure

Among workers that become replacement queens, the oldest tend to assume reproductive dominance [*P. exclamans* (Strassmann and Meyer, 1983); *P. chinensis antennalis* (Miyano, 1986); *P. instabilis* (Hughes and Strassmann, 1988a); *P. annularis* (Queller et al., 1997); *P. dominula* (Theraulaz et al., 1990); also reviewed in (Reeve, 1991)]. However, in tropical species, the younger workers are more likely to replace the queen [*P. canadensis* (West-Eberhard, 1969); but see *P. instabilis* (Hughes and Strassmann, 1988a)]. This difference between temperate and tropical species can be explained by the remaining lifespan of the colony. In tropical species with long colony lifespans, a young worker (whose remaining lifespan exceeds that of the queen) may be more likely to challenge for dominance status (Tsuji and Tsuji, 2005). On the other hand, in temperate species where colony perpetuation by queen replacement is rare (i.e., remaining colony lifespan is shorter) (West-Eberhard, 1969), older workers are more likely to be replacement queens [*P. instabilis* (Hughes and Strassmann, 1988a)]. It is not yet known how such an age-based system of queen replacement is orchestrated, but cuticular hydrocarbons may mediate this process, because they are used for recognition and can change with age [*P. fuscatus* (Panek et al., 2001)].

Probability of queen replacement may be constrained, not just by worker age, but also by the time in the season (or colony cycle) that workers emerge. *P. dominula* workers that emerge earlier in the season tend to have shorter lifespans, and are unlikely to survive hibernation (Mead and Gabouriaut, 1993). However, there is evidence in *P. fuscatus* and *P. dominula* that a few early eclosing workers leave their nests, enter early diapause, and emerge the following year as foundresses (Reeve et al., 1998; Tibbetts, 2007). Early-emerging females can also found their own nest within the same breeding season if their natal nest and queen are removed, suggesting the constraint is on lifespan, and not ability to found a nest (Mead et al., 1995). Similarly, the first emerging females of *P. exclamans* may leave the nest to found satellite nests (Strassmann, 1981a). Age as a predictor of dominance can also shift throughout the season. Among first brood workers in *P. japonicus*, older individuals are more highly ranked, but as the season progresses, younger wasps tend to rank more highly (Ishikawa et al., 2010).

Individual physical and physiological traits

In some animal societies, physical attributes such as size are correlated with competitive ability and may be used by others to assess dominance status. In addition, some animals possess conspicuous visual attributes, such as bright coloration, that can serve as honest signals of their competitive ability. Dominant social status is often associated with profound differences in reproductive physiology, hormone levels, and brain function. All of these general attributes of animal social dominance systems have also been documented in *Polistes*, and are described below.

Adult body size

Adult body size is a direct consequence of larval nutrition. Queens are generally larger than their worker offspring (West-Eberhard, 1969; Strambi, 1990), and are often larger than subordinate co-foundresses [*P. metricus* (Dropkin and Gamboa, 1981; Tibbetts and Sheehan, 2012); *P. dominula*: (Cervo et al., 2008; Tibbetts and Izzo, 2009; Tibbetts et al., 2011c)], but this is not always the case [*P. annularis* (Sullivan and Strassmann, 1984), *P. bellicosus* (Field et al., 1998)]. In *P. instabilis* and *P. carolina*, foundress size does not correlate with rank; instead hierarchical order correlates with the order in which foundresses arrive at the nest (Hughes and Strassmann, 1988a; Seppä et al., 2002). This strategy may allow later-emerging large foundresses to avoid costly aggressive interactions when joining a nest (Seppä et al., 2002).

The lack of a consistent correlation across species between size and dominance does not mean that size has no influence on reproductive capacity. For example, larger or fattier *P. annularis* wasps tend to have more reproductively viable oocytes (Sullivan and Strassmann, 1984), a common measurement of reproductive dominance.

Facial differences

Multiple *Polistes* species have visual signals that reduce conflict over dominance rank. Although detailed research on visual signaling has only been performed in a handful of *Polistes* species, the type of facial pattern variation associated with visual signaling has evolved multiple times in *Polistes* species that form cooperative foundress associations (Tibbetts, 2004) as well as two species of stenogastrine wasps (Baracchi et al., 2013).

At least three *Polistes* species have visual signals of fighting ability [*P. dominula* (Tibbetts and Dale, 2004); *P. satan* (Tannure-Nascimento et al., 2008); *P. exclamans* (Tibbetts and Sheehan, 2011)]. In *P. dominula*, individuals with more broken black facial patterns are dominant over those with less broken facial patterns and are preferentially avoided by rivals (Tibbetts and Lindsay, 2008; Tibbetts et al., 2011a). Facial pattern brokenness is also linked to numerous traits associated with dominance, including JH titer (Tibbetts et al., 2011a), timing of diapause termination (Tibbetts et al., 2011b), and nutrition during early development (Tibbetts and Curtis, 2007; Tibbetts, 2010).

Agonistic signals are typically used during competition with unfamiliar rivals and are often ignored during interactions with familiar conspecifics (Maynard-Smith and Harper, 2003). In paper wasps, facial patterns minimize the costs of conflict during periods when wasps interact with numerous unfamiliar rivals (i.e., early in the nest-founding period and during nest usurpation contests: (Tibbetts and Shorter, 2009; Tibbetts et al., 2011a). However, wasps likely use chemical signals to mediate dominance interactions on stable nests (Monnin, 2006), so facial patterns may not be important during worker interactions.

In *P. dominula*, the paper wasp where agonistic signals have been studied most extensively, there is geographic variation in facial patterns associated with temperature. Wasps that develop in cooler locations have more broken facial patterns than wasps that develop in warmer locations (Tibbetts et al., 2011d; Green et al., 2012). The geographic variation in facial patterns may be associated with variation in signal function (Cervo et al., 2008; Tibbetts et al., 2011d). For example, Spanish populations of *P. dominula* have fewer black spots on their faces than North American populations (Zanette and Field, 2009). Still, even though facial patterns are correlated with dominance rank in Spain (Zanette and Field, 2009), experiments suggest that wasps may not pay attention to each other's facial patterns (Green and Field, 2011).

There is at least one other type of visual signal in *Polistes*. *Polistes fuscatus* have variable facial patterns that signal individual identity. During competition, wasps learn each other's unique facial patterns, then recall these facial patterns during subsequent interactions (Tibbetts, 2002; Sheehan and Tibbetts, 2008). Individual recognition often stabilizes dominance hierarchies. In wasps, individual recognition has likely evolved to minimize aggressive conflict among cooperating co-foundresses (Sheehan and Tibbetts, 2009). Workers are capable of individually recognizing nestmates (Injaian and Tibbetts, in press), though it is unlikely that individual recognition has evolved to facilitate interactions among workers. Instead, worker individual recognition may be a byproduct of selection for individual recognition among foundresses.

Brain

Among the insects, Hymenoptera have large brains for their body size and well-developed mushroom bodies, the insect brain region related to learning and sensory integration (Farris and Schulmeister, 2011). It is appealing to speculate that sociality, and in particular, the cognitive demands of dominance interactions including individual recognition, could result in the evolution of large brain size and well-developed mushroom bodies (Farris, 2005). There does not appear to be any general correlation between large brain size and sociality in insects (Lihoreau et al., 2012). In a comparison of mushroom bodies across Hymenoptera, there is no evidence for a general association between mushroom body volume and sociality; in fact, on average, solitary parasitoid Hymenoptera possess as large and well-developed mushroom bodies as social Hymenoptera (Farris and Schulmeister, 2011).

Nonetheless, within the social vespid wasps, a number of differences in brain structure have been linked to social traits, including dominance (Molina et al., 2009). Species living in open nests, such as *P. instabilis*, have better developed mushroom body collars (part of the calyx receiving visual input) than wasp species living in closed nests, and this region is also larger in dominant queens compared to workers (Molina et al., 2009). The volume of the mushroom body calyces was associated with worker dominance status after the removal of dominant workers in *P. instabilis* (Molina and O'Donnell, 2007), a result that was mirrored in another primitively eusocial polistine, *Mischocyttarus mastigophorus* (O'Donnell et al., 2007; Molina and O'Donnell, 2008). Members of multiple foundress associations in *P. dominula* were found to have larger antennal lobes, and dominant foundresses had larger mushroom body collars than subordinates (Ehmer et al., 2001). Thus, there is ample evidence to suggest that dominance interactions can be associated with increases in the volume of certain brain subregions across several species of social wasps. These differences are likely unrelated to visual signaling, as comparative analysis of four species indicates that there are only minor differences in neuroanatomy between species with and without visual communication (Gronenberg et al., 2008).

Endocrine system

Most research on the endocrine factors associated with dominance has focused on juvenile hormone (JH). Röseler originally showed that JH plays a key role in both dominance and fertility of *P. dominula* foundresses (Röseler et al., 1984; Röseler, 1991). Röseler's original research was performed at a time when it was not possible to measure JH titers directly, but subsequent research has confirmed his early results. JH titers are correlated with dominance rank and fertility of foundresses (Tibbetts et al., 2011a). Further, experimentally increasing JH increases foundress fertility and dominance [*P. dominula* (Tibbetts and Izzo, 2009); *P. metricus* (Tibbetts and Sheehan, 2012)].

The effect of JH on workers is more complex. In *Polistes*, as in more advanced eusocial insects, higher JH is associated with earlier age at first foraging in workers (Giray et al., 2005; Shorter and Tibbetts, 2009). However, JH is also involved in dominance and fertility of workers. For example, JH titers increase in workers following experimental queen removal. The worker that takes over as the new queen has significantly higher JH than other workers (Tibbetts and Huang, 2010). Foraging and dominance are often thought to be on opposite ends of the behavioral spectrum, so how can the same hormone mediate such different behaviors? One hypothesis is that the effects of JH vary with individual condition. Specifically, individuals in good physical condition (i.e., queens) respond to JH by increasing their fertility and dominance, while those in poor physical condition (i.e., workers) forage in response to JH (Turillazzi and West-Eberhard, 1996). There is some evidence that response to JH is condition-dependent, as JH has an effect on the fertility and dominance of larger, fatter workers, but less effect on smaller workers (Tibbetts and Izzo, 2009; Tibbetts et al., 2011c).

Less research has focused on ecdysteroids, the other main class of insect hormones. Across social and non-social insects, ecdysteroids are commonly linked with fertility (Nijhout, 1994; Geva et al., 2005). In *Polistes* foundresses, ecdysteroids are more closely linked with fertility than dominance. Ovariectomy dramatically reduces foundress ecdysteroid titer, but ovariectomized foundresses are still able to achieve behavioral dominance despite a low ecdysteroid titer (Röseler et al., 1985). Additional research on ecdysteroids in foundresses and workers will help to better illuminate the role of these hormones in *Polistes* dominance.

Biogenic amines are also likely to be important in paper wasp dominance and fertility. In *P. chinensis* workers, dopamine and serotonin are positively correlated with ovarian development (Sasaki et al., 2009). Octopamine is also commonly associated with agonistic behavior in insects (e.g., Stevenson et al., 2005), though its role has not been specifically tested in paper wasps. Biogenic amines have been hypothesized to mediate larval caste development (Jeanne, 2009), and it is possible that they may play a key role in physiologically reinforcing an individual's hierarchical rank as it affects dominance behavior and fertility.

The clear next step in this area of research is to integrate information on hormones and biogenic amines with the molecular mechanisms underlying dominance behavior. A recent microarray study (Toth et al., in revision) examined *P. metricus* dominant and subordinate members of both the reproductive and worker caste. The results confirmed linkages to the expression of a small number of genes related to juvenile hormone and biogenic amine synthesis. This study also suggests that some of the molecular pathways associated with dominance in *P. metricus* are associated with aggressive behaviors in honey bees, fruit flies, and even rats. Further studies will be necessary to establish whether there are causative associations between these genes and dominance in *Polistes.* In addition, recent studies have documented important epigenetic effects on behavioral variation in honey bees (Herb et al., 2012). Early evidence from *Polistes* (Kronforst et al., 2008; Weiner et al., 2013) also suggests the potential for epigenetic effects on behavioral castes in *Polistes dominula*, leaving the door open for epigenetic studies on dominance behavior.

Chemical cues

Cuticular hydrocarbon (CHC) profiles may provide a mechanism to assess dominance rank, as CHC profile is associated with fertility across all major groups of social insects (Liebig, 2010). Co-foundresses commonly use CHCs to assess dominance status [*P. dominula*: (Sledge et al., 2004); *P. satan* (Tannure-Nascimento et al., 2008)]. The CHC profiles of queens can also differ from workers [*P. dominula* (Bonavita-Cougourdan et al., 1991); but see *P. fuscatus* (Espelie et al., 1994)]. Furthermore, profiles can change after a subordinate co-foundress (Sledge et al., 2001) or worker (Dapporto et al., 2005) assumes dominant rank. Although hydrocarbons may be used in the establishment of hierarchies, there is no consistent dominant or subordinate profile across colonies or populations (Dapporto et al., 2004; Monnin, 2006).

Chemical cues used for dominance recognition may originate in the Dufour's gland (Downing, 1991b, 1991a; Dani et al., 1996; Jeanne, 1996), ectal mandibular glands, or sternal glands (Downing and Jeanne, 1985; Downing, 1991a; Jeanne, 1996). The mixture of chemicals produced from these exocrine glands, along with those that accumulate on the nest substrate, likely affects the composition of the cuticular hydrocarbon (CHC) profile of an individual (Bonavita-Cougourdan et al., 1991; Espelie et al., 1994; Dani et al., 1996; Sledge et al., 2001; Monnin, 2006; Richard and Hunt, 2013).

Evidence suggests that juvenile hormone provides a link between CHC profiles, behavioral, and reproductive dominance throughout the nesting season. For example, early in the season, the behavioral hierarchy indicates intrinsic fighting ability (Dapporto et al., 2010a) and JH (a hormone correlated with CHC profile, egg production, and dominance rank) may be a mechanism that links CHCs to dominance and fertility in over-wintered foundresses (Izzo et al., 2010). As the dominant wasp reinforces her rank in the behavioral hierarchy, the size of her corpora allata (producer of JH) increases (Röseler et al., 1980; Röseler et al., 1985; Sledge et al., 2004), and CHC profiles of dominant and subordinate wasps continue to diverge (Sledge et al., 2004; Dapporto et al., 2007; Dapporto et al., 2010a).

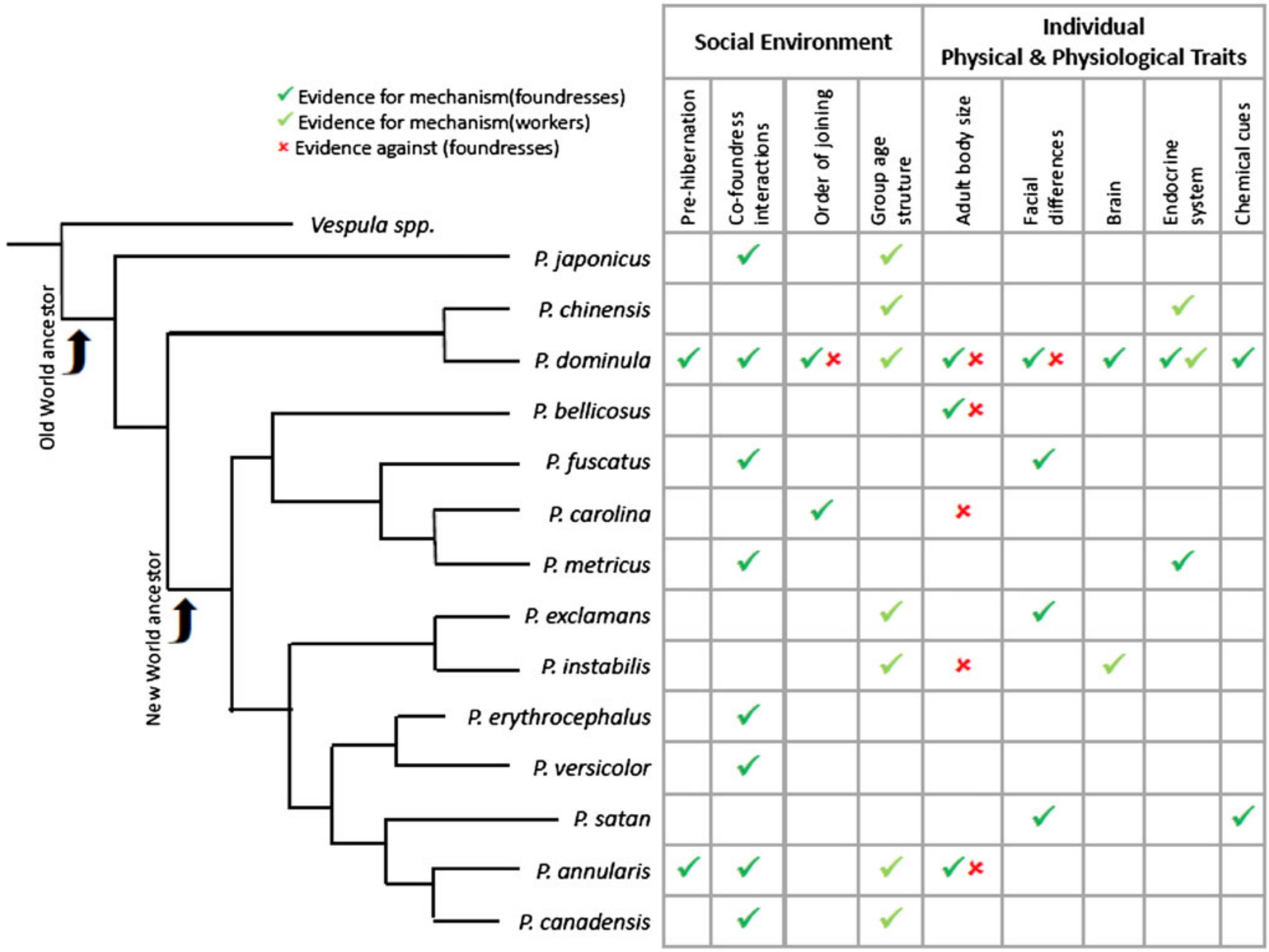
Cuticular hydrocarbons may also be useful when workers police eggs laid by a wasp other than the queen. If an egg-layer coats her eggs with CHCs or a chemical secreted directly from the Dufour's gland, nestmates can discriminate dominant- from subordinate-laid eggs (Downing, 1991b; Jeanne, 1996; Jackson, 2007; Dapporto et al., 2010b). In cases where the dominant cedes some reproductive opportunity to a subordinate (perhaps as an incentive to remain at the nest), not all subordinate eggs are eaten (Dapporto et al., 2010b).

Inter- and intra-specific variation in *Polistes*

Above, we reviewed the available literature on dominance hierarchies in *Polistes*, encompassing 15 species, spread across the *Polistes* phylogeny (Fig. 2). Figure 3 summarizes the different factors influencing dominance across the genus *Polistes*. In this diagram, we attempt to draw general conclusions about how multiple mechanisms may interact, but it is important to note that *Polistes* is a diverse and cosmopolitan social insect genus that has successfully adapted to both tropical and temperate habitats. As such, there is substantial variation within the genus in terms of founding strategy (solitary vs. cooperative), colony size, extent of dominance interactions, and the various mechanisms employed to establish and maintain dominance hierarchies. Although the end result is generally consistent across species (one or two individuals are primarily responsible for egg-laying, the remaining individuals perform colony tasks), the factors that are the primary drivers of dominance can vary. Figure 2 delineates differences among species in terms of mechanisms that affect dominance. We suggest that this inter- and intra-specific variation in dominance systems can provide a useful comparative framework for better understanding open questions related to dominance behavior.

Interspecific variation: *Polistes* genus

Not all *Polistes* species benefit from multi-foundress relationships and, in many species, nests are typically founded by a single foundress. Even within species that nest cooperatively, there is striking variation in the degree to which size, age, or facial recognition are associated with hierarchical status (Fig. 2). Only a few studies have taken advantage of a comparative approach within *Polistes* to understand the evolutionary gain and loss of these features. Reeve (1991) reviews how the frequency of aggression and a clear division of labor correlate with the degree to which a species has evolved a well-developed hierarchy. Tibbetts (2004) mapped the presence/absence of facial recognition ability onto the *Polistes* phylogeny to infer that there have been at least three independent gains of facial recognition in the genus, all in species with cooperative foundress associations. A similar approach applied to other traits of dominance hierarchies, and further expanding such a



	Social Environment				Individual Physical & Physiological Traits				
	Pre-hibernation	Co-foundress interactions	Order of joining	Group age struture	Adult body size	Facial differences	Brain	Endocrine system	Chemical cues
P. japonicus		✔		✓					
P. chinensis				✓				✓	
P. dominula	✔	✔	✔×	✓	✔×	✔×	✔	✔✓	✔
P. bellicosus					✔×				
P. fuscatus		✔				✔			
P. carolina			✔		×				
P. metricus		✔						✔	
P. exclamans				✓		✔			
P. instabilis				✓	×		✓		
P. erythrocephalus		✔							
P. versicolor		✔							
P. satan						✔			✔
P. annularis	✔	✔		✓	✔×				
P. canadensis		✔		✓					

Fig. 2 Mechanisms correlated with behavioral and/or reproductive hierarchy across *Polistes* species. Phylogeny adapted from Pickett et al. (2006). For *P. japonicus* and *P. canadensis*, co-foundress interactions imply abdominal wagging. Interactions for the other species are in reference to classical dominance behavior (lunges, darting, biting, mounting)

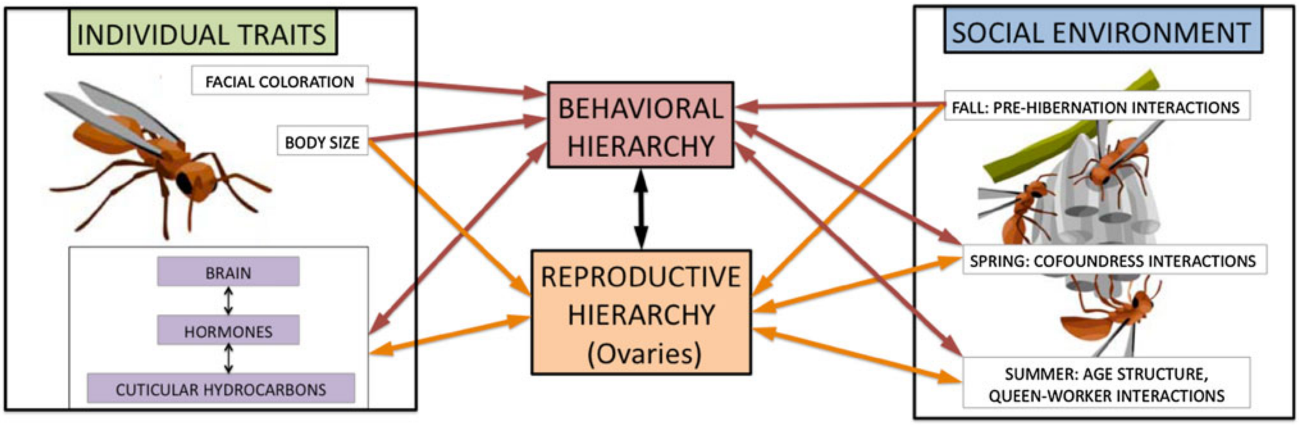


Fig. 3 Summary of how individual traits and social environment affect dominance hierarchy in *Polistes* spp. *Polistes* are considered 'primitively' eusocial because reproductive dominance is plastic among females on the nest. Females engage in behavioral displays and establish a behavioral hierarchy before they establish a reproductive hierarchy, i.e., an individual will be the primary egg-layer. As the hierarchy is being worked out, however, physiological changes are positively reinforcing the dominant's position in the hierarchy. Note—this is a generalization; for some species or colony stages, not all factors may be relevant (see Fig. 2). Wasp cartoons adapted from (Hunt et al., 2011)

phylogenetic perspective to include other social vespids, could provide a better understanding of which behavioral, physiological, and genetic mechanisms are ancestral, derived, or convergent within *Polistes*.

Intraspecific variation: *Polistes dominula*

There is also substantial variation in the factors associated with dominance across populations of a single *Polistes* species. One of the best-studied species of *Polistes* is *P. dominula*. *Polistes dominula* is native to Europe, but has invaded extensive regions of the United States, making it an economically important invasive species to investigate (Liebert et al., 2006). Populations of *P. dominula* have been studied in various regions of the world, and interestingly, the mechanisms used to establish and maintain dominance hierarchy can vary across populations and within populations across colony life cycle (Reeve, 1991). For example, when establishing co-foundress relationships, Italian populations of *P. dominula* are more likely to join sisters (Queller, 2000), whereas in Spanish populations, foundresses will join other foundresses that are less related to them (Zanette and Field, 2008). Rank correlates with body size in Italian populations (Cervo et al., 2008), but is better predicted by facial patterns than body size in Spanish populations (Zanette and Field, 2009). Comparisons of dominance hierarchy formation and maintenance are promising avenues for understanding the invasion biology of *Polistes* (Liebert et al., 2006).

Polistes variation in dominance behavior: a powerful tool for comparative analysis

There is great variation among *Polistes* species, so *Polistes* provide a useful model for studying the evolution of behavioral traits, the gains and losses of those traits throughout the phylogeny, and the relative importance of those traits has to the maintenance of hierarchy. Comparative analyses can provide a useful framework for addressing numerous key questions about dominance hierarchies, and we highlight a few below.

Ultimate factors

- *Why do foundresses cooperate even when some will take a subordinate role?* As reviewed above, results to date provide support for diverse group-level benefits associated with cooperation, including productivity, survival, inclusive fitness, and inheritance benefits.
- *Do the costs and benefits of cooperative strategies vary across individuals?* Although average benefits of cooperation have been studied extensively, we know less about whether costs and benefits vary based on individual traits such as quality or behavioral syndrome.
- *Why do some workers cooperate, while others pursue independent reproduction?*
- *What factors influence variation in cooperation within and between species?* Do historical contingency or the fitness benefits of cooperation account for variation in the probability of forming cooperative groups?

Proximate factors

- *Do the same mechanisms regulate dominance in both founding stage and worker stage of the colony life cycle?* If so, mechanisms underlying dominance in one context may have been co-opted for use in another social context, thus illuminating new evidence about the evolution of sociality.
- *Are differences in brain structure, hormone levels, and gene expression between dominants and subordinates a cause or consequence of their dominance status?*
- *What are the effects of physical dominance attacks on biogenic amine levels, hormone levels, and gene expression patterns in subordinates?* Do vibrational signals—lateral vibration, abdominal wagging, and others—also mediate these effects in adults, just as antennal drumming appears to modulate the development of larvae?
- *Are the molecular mechanisms regulating dominance behavior conserved across taxa, both within the genus* Polistes *and further afield in other vespids and in other animal taxa?* In cases where similar dominance behavior has evolved multiple times (e.g., facial recognition), are there common molecular pathways regulating this behavior?
- *What are the molecular mechanisms regulating dominance hierarchy formation?* Do genetic pathways regulating dominance relate to hormone signaling, stress (which is widely associated with dominance in animals), aggression, or other biological functions? Do the same molecular mechanisms regulate behavioral and reproductive dominance?
- *Are interactions within hibernating clusters correlative or causative factors that affect spring dominance relationships?* In *P. dominula*, dominance relationships established pre-hibernation can be used to predict hierarchical relationships in the spring (post-hibernation). Are these spring relationships a product of the fall interactions, or are they the result of other physiological factors that affect the probability of a foundress achieving dominant status?

Applied questions

- *Do differences in dominance behavior (e.g., cooperativeness) affect the invasion success of* Polistes dominula? Are there subpopulations of *P. dominula* throughout the native range that possess dominance-related pre-adaptations to becoming invasive?

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