SHORT COMMUNICATION

The energetic costs of stereotyped behavior in the paper wasp, *Polistes dominulus*

Susan A. Weiner · William A. Woods Jr. ·
Philip T. Starks

Abstract *Polistes* wasps engage in many behavioral inter-
actions. Although there has been debate over the meaning of
these interactions, these stereotypical behaviors can be used
to determine a colony's linear dominance hierarchy. Due to
the implicit relationship between behavioral and reproductive
dominance, behavioral interactions are commonly used to
distinguish the reproductively dominant alpha foundress
from the beta foundress. It has been suggested that in order
to maintain reproductive control, the alpha foundress is
forced to remain at a physiologically constrained activity
limit. This, in turn, may allow aggressive interactions to be
used as determinants influencing reproductive partitioning
between cooperating individuals. Energetic costs can place
important limitations on behavior, but the energetic cost of
the interactions has not previously been measured. To
address this, we measured the CO_2 production of 19 non-
nestmate pairs displaying interactive and noninteractive
behavior. The rate of energy used during interaction behavior
was positively associated with published rankings of
aggression. However, our results indicate that interactions
are not very energetically costly in *Polistes*, particularly
when compared to the likely cost of foraging. These data
suggest that maintaining reproductive dominance is not very
energetically expensive for the dominant and that the
dominant foundress expends energy at a lower rate than the
subordinate foundress.

S. A. Weiner (✉) · W. A. Woods Jr. · P. T. Starks
Department of Biology, Tufts University,
163 Packard Ave,
Medford, MA 02155, USA
e-mail: susan.weiner@tufts.edu

Introduction

Dominance hierarchies are central to social systems in
many animals, including humans (e.g., De Bruyn and Van
Den Boom 2005, de Waal 1986). Dominance hierarchies
can mediate distribution of food (e.g., Appleby 1980),
opportunities for reproduction (e.g., Blatrix and Herbers
2004), and delegation of communal tasks (e.g., Tentschert
et al. 2001). Dominance hierarchies are often set and
maintained by displays of aggression (reviewed in Forkman
and Haskell 2004). In eusocial insects, dominance hierar-
chies are particularly important since most or all of the eggs
in the colony are usually laid by the dominant individual
(Keller and Perrin 1995).

Dominance hierarchies are central to the social biology
of *Polistes* wasps (Pardi 1948). *Polistes* wasps are
considered primitively eusocial because the castes are
totipotent (Wilson 1971; Hunt 2006), meaning that workers
can mate and lay diploid eggs, and foundresses can adopt
subordinate roles that are similar to worker roles (Reeve
1991). In temperate species, including *Polistes dominulus*,
foundresses produce workers early in the season that
remain on the nest, and later in the season produce
reproductive gynes that mate and overwinter to found
colonies the following year (reviewed in Reeve 1991).

Some *Polistes* gynes found colonies in multiple foundress
associations (Pardi 1948). In colonies founded by multiple
reproductive females, a linear dominance hierarchy forms
between foundresses, and this hierarchy determines distribu-
tion of tasks and reproduction (West-Eberhard 1969). Due, in
part, to this colony-founding behavior, *Polistes* wasps are

considered models for insights into the origins of eusociality (reviewed in Reeve 1991; Turilazzi and West-Eberhard 1996, Starks and Turillazzi 2006).

In multiple foundress *Polistes* nests, the dominant individual reproduces more than subordinates, while the subordinates perform the riskier tasks, such as foraging (reviewed in Reeve 1991). The dominant foundress does not leave the nest as often, thus avoiding exposing herself to predators and other hazards. This likely explains why a dominant female has a better chance of surviving than do subordinates or lone foundresses (reviewed in Nonacs et al. 2006). This leads to increased rates of survival for nests founded by multiple females by improving the chances that at least one foundress will survive to worker emergence (Reeve 1991).

Cooperative foundresses have a dominance hierarchy, and this hierarchy can be determined by calculating one of two factors. One factor is behavior; the dominant animal initiates the majority of interactions (e.g., Sumana and Starks 2004). The other factor is reproduction; the dominant foundress lays the majority of the eggs (e.g., Reeve et al. 2000). With genetic techniques, the reproductive dominance hierarchy can be determined fairly easily (e.g., Liebert and Starks 2006). However, researchers often use behavioral interactions to determine the reproductive hierarchy due to the strong correlation between the two and due to the ease with which behavioral interactions can be observed (Reeve 1991; Reeve and Ratnieks 1993; but see Röseler and Röseler 1989). Perhaps due to this relationship, it has been assumed that interactions are used by foundresses to set and maintain reproductive dominance hierarchies (Reeve and Nonacs 1992; but see Nonacs et al. 2004).

Tibbetts and Reeve (2000) tested a model that suggested that if the relative distribution of reproduction is mediated by aggressive behavior, subordinates should "fight back" to maximize their own reproductive opportunities. One might assume that since the subordinate does most of the foraging (reviewed in Reeve 1991), the dominant may not need to expend much energy to maintain control. Tibbetts and Reeve (2000), however, suggested that the dominant is forced to remain near her physiologically constrained activity limit when maintaining reproductive dominance. Since wasps are poikilothermic, the authors reasoned, the physiological limit should increase with the surrounding temperature. Because an increase in aggression by the dominant in higher temperatures was observed, Tibbetts and Reeve (2000) suggested that the dominant was at or near her physiological maximum. If this is true, aggression would be an honest signal of quality, constrained by an inability to maintain a higher level of aggression.

While there are many limitations on behavior, one important limitation is energy. When supplemented with honey, *Polistes metricus* colonies produced first offspring earlier and produced offspring with a higher percentage of body fat, which suggests that colonies are energy limited (Rossi and Hunt 1988). We tested the possibility of an energetic limit on aggression by comparing the metabolic costs of interactive behaviors (including those involved in aggression) and noninteractive behaviors involved in foraging and other tasks. If a dominant foundress is energy limited, she must be expending at least as much energy as a subordinate. One way to test this hypothesis is to compare the energy use rate of interaction behaviors (which are mostly performed by the dominant) with foraging behaviors (which are mostly performed by the subordinate; reviewed in Reeve 1991).

Interactions are keys to understanding social behavior, but we do not yet know how energetically costly these behaviors are to wasps. *Polistes* has often been used as a model genus for the development of models of helping behavior and hierarchy maintenance (Tibbetts and Reeve 2000; reviewed in Reeve and Keller 2001). In order to better understand social behavior in this model genus, we examined the rates of energy use, as measured by CO_2 production, of various interactions between *P. dominulus* gynes. We compared the ranking of these behaviors by energy use to the published rankings of these behaviors by level of aggression. We also compared the rates of energy use during interactions to the rates of energy use during other behavior.

Methods

Animals

All *P. dominulus* colonies were collected in summer 2005 from the Tufts Cummings School of Veterinary Medicine in Grafton, MA, USA and maintained in cages ($60 \times 22 \times 24$ cm) on the Tufts campus in Medford, MA, USA. The colonies were fed wax-worms and honey-water *ad libitum*, and the lighting schedule was matched to local sunrise and sunset. All test animals were females that emerged after colonies had begun producing an approximately equal ratio of males and females and, thus, were assumed to be gynes. Individuals were taken from 19 colonies, and no individual was included in more than one test.

Behavioral observations

For each test, two *P. dominulus* gynes from different colonies were placed in a respirometry chamber, which consisted of a 250-cm³ clear plastic culture flask sealed with a rubber stopper. All trials were videotaped, and all interactions were recorded by an observer as were periods of walking, buzz-walking (defined below), and resting. The interactions we recorded were antennation (antenna-to-

antenna or antenna-to-body contact; Electronic supplementary data S1), darts (quick movements towards and away from the other wasp; Electronic supplementary data S2), lunges (darts with contact), uncontested mounts (one animal climbs onto the other animal, the bottom animal assumes a submissive posture), contested mounts (an attempted mount where the bottom animal attempted to prevent the other from mounting), bites (mandible-to-body contact; Electronic supplementary data S3), and grapples (wrestling; Electronic supplementary data S4; e.g., Starks et al. 1998).

Only one lunge was recorded; thus, lunges were not included in the analysis. Although sustained free flight was not possible in the confinement of the chamber, there were periods during which individuals would fan their wings in repeated brief bouts with locomotion that was a combination of rapid walking and very brief airborne intervals; it is these behaviors that we collectively term "buzz-walking" (Electronic supplementary data S5). Buzz-walking is expected to be less costly than true flight, offering a very conservative comparison between interactions and foraging behavior. Video images of each test were used to confirm the observed behaviors. Each dyad remained in the respirometry chamber for 60 min and was observed continuously during that time.

Respirometry

Metabolic rate measurements were made at $27 \pm 0.5°C$. CO_2 production was measured continuously by differential open-flow respirometry using a Li-Cor 6262 CO_2/H_2O analyzer (Li-Cor, Lincoln NE, USA) calibrated with a gravimetric mixture (Scott Specialty Gases, Plumsteadville PA, USA) and re-zeroed between measurements (Woods et al 2005). A flow rate of 500 cm^3 min^{-1} of medical grade compressed air was maintained by Sierra Side-Trak mass flow meters (Sierra Instruments, Monterey NV, USA) and a Sable Systems flow controller (Sable Systems, Henderson NV, USA). Excurrent CO_2 concentration was sampled every 6 s; each recorded value represented the mean excurrent CO_2 concentration for the previous 6 s as calculated by the Li-Cor unit (see Woods et al 2005).

Respirometry data were collected and analyzed in Datacan V (Sable Systems). Behavioral observations were synchronized with respirometry data taking into account time lag and washout properties of the respirometry system as determined by bolus injection. Washout is simply the temporal sluggishness of the data arising from the "cushioning" of the raw signal in a chamber necessarily much larger than the subjects and the subsequent exponential decay of the signal as the chamber "washes out." We used the standard Z-transform implemented in Datacan V, which enhances temporal resolution by largely correcting for this effect (Bartholemew and Casey 1978).

In our primary dataset, all measurements were of pairs of animals. CO_2 production rate during each behavior was normalized to the resting rate, which was established separately for each trial during periods when both individuals were motionless. If only one animal was engaged in a particular behavior, the mean rate of energy use associated
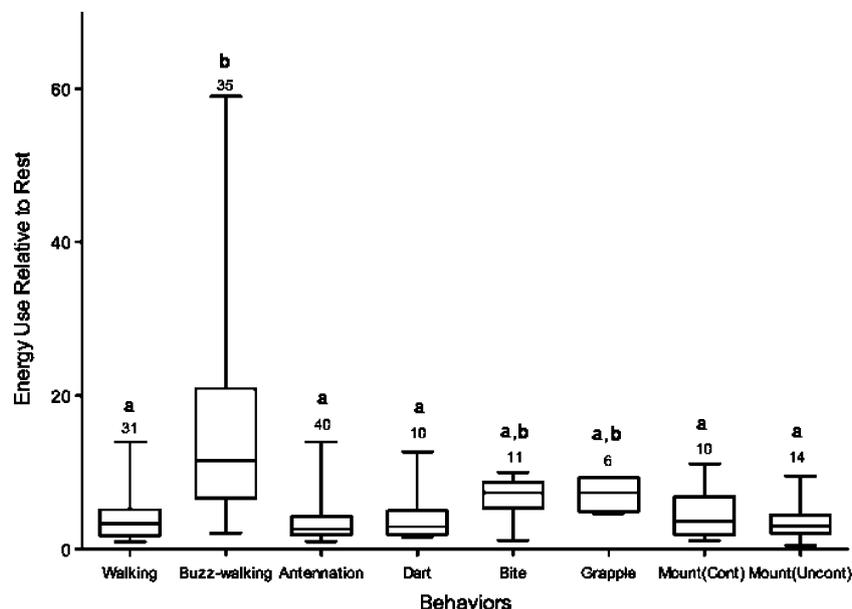

Fig. 1 Median observed average rate of energy use for each behavior as a multiple of resting rate. *Bars* show first and third quartiles and lines show the extremes. *Numbers* refer to the number of times each behavior was observed. *Different letters* indicate significant differences
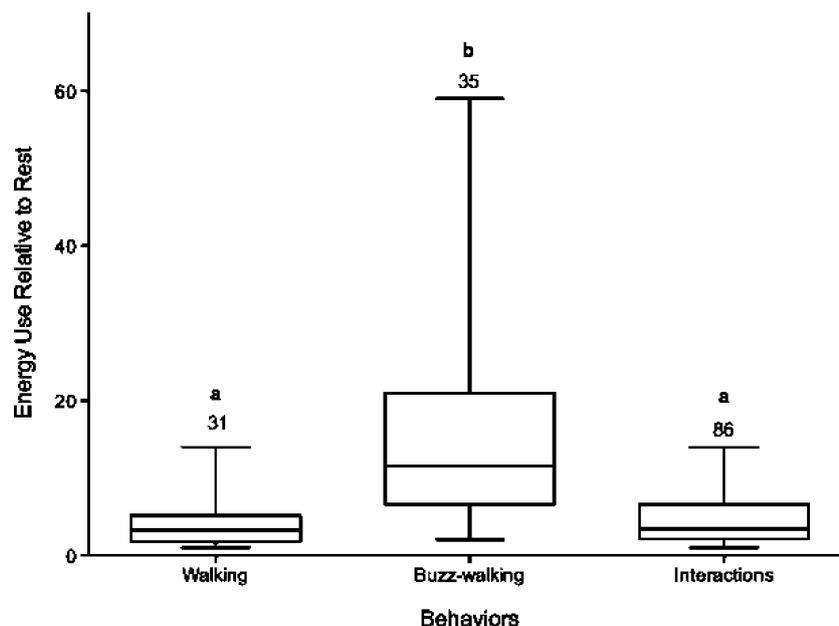
Fig. 2 Median observed average rate of energy use for each behavior as a multiple of resting rate. The category of interactive behaviors includes bites, grapples, darts, antennations, and mounts. *Bars* show first and third quartiles, and *lines* show the extremes. *Numbers* refer to the number of times each behavior was observed. *Different letters* indicate significant differences ($p < 0.001$)

with the behavior of the other animal was subtracted from the rate recorded. Our transformation reduced the energy use by half, so the remaining value was multiplied by 2. If both animals were engaged in the same behavior, the recorded rate was not transformed. Data were not used for bouts of behaviors that occurred less than 30 s apart. Each data point is the mean value over the duration of a bout of a particular behavior. The data were not normally distributed and so were analyzed for significance using a Kruskal–Wallis test followed by Dunn's Multiple Comparison test.

To enable comparison of resting CO_2 production with that of other animals, we measured a separate sample of 47 *P. dominulus* representing all castes. Methods were similar except that animals were placed individually in a 70-cm^3 chamber with a flow-rate of 250 cm^3 min^{-1}. The average of these data was then taken.

Results

The rates of energy use of all non-resting behaviors were at least double the resting rate, with buzz-walking having the highest rate (Fig. 1). In order to compare the energy use rates of behaviors, we categorized the behavior as interactive or noninteractive. No interaction behavior differed significantly from any other interaction behavior (Kruskal–Wallis one-way analysis of variance (ANOVA) $H=53.44$, $df=8$, $P<0.0001$; Dunn's multiple comparison $P<0.05$ for all pairings, Fig. 1). Buzz-walking had a significantly higher rate of energy use than darts, antennation, and both

contested and uncontested mounts (Kruskal–Wallis one-way ANOVA $H=53.44$, $df=8$, $P<0.0001$; Dunn's multiple comparison: Darts: $P<0.05$, Antennation: $P<0.001$, Uncontested Mounts: $P<0.01$, Contested Mounts: $P<0.05$, Fig. 1) but did not have a significantly higher rate of energy use than bites or grapples (Kruskal–Wallis one-way ANOVA $H=53.44$, $df=8$, $P<0.0001$; Dunn's multiple comparison $P>0.05$ for both, Fig. 1).
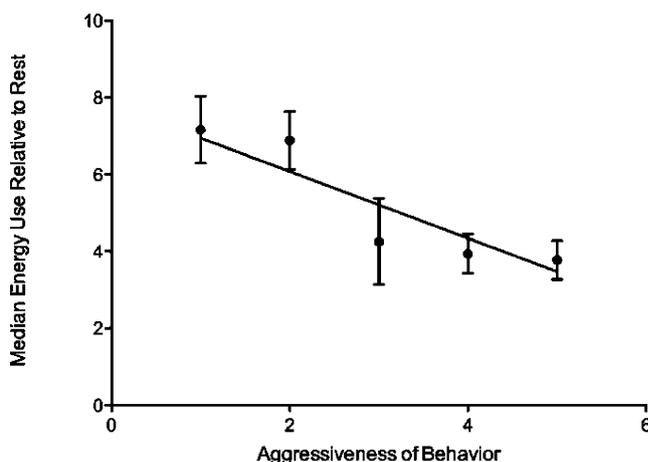

Fig. 3 The correlation of the energetic cost of behaviors with the Pfennig and colleagues (1983) ranking of tolerance. The behaviors are ranked from least tolerant to most tolerant as follows: *1* Grapple ($n=6$), *2* Bite ($n=11$), *3* Dart ($n=10$), *4* Avoid or detour (represented by walking; $n=31$), *5* Antennation ($n=40$). Buzz-walking, at 11.57 would be off this graph. The significant regression is shown ($P<0.001$, $R^2=0.1143$)

The rate of energy use of buzz-walking was significantly higher than the combined interaction behavior (Kruskal–Wallis one-way ANOVA $H=39.51$, $df=3$, $P<0.0001$; Dunn's multiple comparison $P<0.001$, Fig. 2) and significantly higher than walking (Kruskal-Wallis one-way ANOVA $H=39.51$, $df=3$, $P<0.0001$; Dunn's multiple comparison $P<0.001$, Fig. 2). Walking and interaction behavior were not significantly different (Kruskal–Wallis one-way ANOVA $H=39.51$, $df=3$, $P<0.0001$; Dunn's multiple comparison $P>0.05$, Fig. 2). In general, the rate of energy use of a behavior correlated positively with how aggressive it has been considered (Fig. 3).

For the separate sample of 47 *P. dominulus*, mean CO_2 production at rest was 0.557 ± 0.199 ml g^{-1} h^{-1}. This value is consistent with values for arthropods of similar (0.106 ± 0.021 g) body mass (Lighton and Fielden, 1995), especially those capable of flight (Reinhold, 1999).

Discussion

Our results indicate that the rates of energy use of interactions in *P. dominulus* may be much lower than had been expected. Aggressive interactions are important in many species for developing dominance hierarchies. These hierarchies influence many factors, including food access (Scott and Lockard 2006, Brown et al. 2005), territory control (Brown et al. 2005), mate access (Mennil et al. 2004), and may even directly determine the proportion of reproduction an individual receives (Dewsbury 1982, but see Nonacs et al 2004). However, the actual energetic costs of the behavior that appears to mediate these hierarchies are not known in many animals (but see *Acheta domesticus*: Hack 1997; *Pachycondyla obscuricornis*: Gobin et al. 2003; *Uca lactea perplexa*: Matsumasa and Murai 2005; *Oreochromis mossambicus*: Ros et al. 2006).

Our ranking by rate of energy use matched well with rankings of aggression that have been used by other researchers (Fig. 3; e.g., see Pfennig et al 1983 for *Polistes fuscatus*). This indicates that published assessments of the aggressiveness of interactive behaviors correlate with the energy use rate and, hence, the energetic cost to the animal of the behaviors. This suggests that energy use could be a cost of interaction, with escalating aggressiveness being accompanied by escalating energetic costs, although we did find the rate of energy use to be low relative to the expected cost of foraging.

Our data show that most interactions used less energy than buzz-walking (Fig. 1). These data indicate that foraging is likely to be one of the most energetically costly behaviors expressed, since true flight is expected to be more costly than buzz walking. The rate of energy use in buzz-walking averaged only 7.1 times that of rest. In other insects with

endothermic flight, such as sphingid and saturniid moths (Bartholemew and Casey 1978) and honeybees (Kammer and Heinrich 1978), rates of energy use during flight can be as high as 100 times resting rates. The lowest flight metabolic rate measured for an insect was 7.4 times rest in *Drosophila hydei* (Dickinson and Lighton 1995). Since *Polistes* wasps have elevated temperature during flight (unpublished data), their flight metabolic rate is expected to be closer to that of honeybees than that of *Drosophila*.

Also, on spring nests, trophallaxis is much more frequent than aggression (Dapporto et al. 2006), suggesting that foraging occupies a much larger portion of time than aggressive interaction. The subordinate generally does more foraging than the dominant (Pratte 1989) and is, therefore, probably expending more energy than the dominant. While the dominant may be physiologically constrained in other ways, preworker colonies seem to be energetically limited (Rossi and Hunt 1988), and so, the energy use of foundresses is expected to be important to the colony's success. Increased energy expenditure will lead either to decreased brood production (Rossi and Hunt 1988) or increased foraging, which would increase the risk of foundress loss. The finding that the dominant likely uses less energy for nonreproductive actions than the subordinate is important for understanding the costs and benefits of the two tactics. In future research, this difference could be clarified by the creation of energy budgets for the different tactics (as in Carefoot et al 1998; Roberts and Harrison 1999; Woods et al 2007).

P. dominulus is used as a model species for studying dominance hierarchies in eusocial societies. By examining the costs of interactions in *P. dominulus*, this study brings a new understanding to these important and well-studied behaviors. Our data show that Pfennig and colleagues' (1983) ranking of aggressiveness correlates with energy use in *P. dominulus* and suggest that these behaviors have a lower rate of energy use than foraging. This study opens up the way for a more thorough understanding of these behaviors, and with this, the establishment and maintenance of dominance hierarchies in model species.

References

Appleby MC (1980) Social rank and food access in red deer stags. Behaviour 74:294–309

Bartholemew GA, Casey TM (1978) Oxygen consumption of moths during rest, pre-flight warm-up and flight in relation to body size and wing morphology. J Exp Biol 76:11–25

Blatrix R, Herbers JM (2004) Intracolonial conflict in the slave-making ant *Protomognathus americanus*: Dominance hierarchies and individual reproductive success. Insectes Soc 51:131–138

Brown KM, Keenan SF, Banks PD (2005) Dominance hierarchies in xanthid crabs: Roles in resource-holding potential and field distributions. Mar Ecol Prog Ser 291:189–196

Carefoot TH, Taylor BE, Brett K (1998) A day in the life of an isopod: Time and energy allocations in the semiterrestrial *Ligia pallasii*. Isr J Zoology 44:463–471

Dapporto L, Turillazzi S, Palagi E (2006) Dominance interactions in young adult foundresses of a paper wasp: a play-like behaviour? J Comp Psychol 120:394–400

De Bruyn EH, Van Den Boom DC (2005) Interpersonal behavior, peer popularity, and self-esteem in early adolescence. Soc Dev 14:555–573

de Waal FB (1986) The integration of dominance and social bonding in primates. Q Rev Biol 61:459–479

Dewsbury DA (1982) Dominance rank, copulatory behavior, and differential reproduction. Q Rev Biol 57:135–159

Dickinson MH, Lighton JRB (1995) Muscle efficiency and elastic storage in the flight motor of *Drosophila*. Science 268:87–90

Forkman B, Haskell MJ (2004) The maintenance of stable dominance hierarchies and the pattern of aggression: Support for the suppression hypothesis. Ethology 110:737–744

Gobin B, Heinze J, Strätz M, Roces F (2003) The energetic cost of reproductive conflicts in the ant *Pachycondyla obscuricornis*. J Insect Physiol 49:747–752

Hack MA (1997) The energetic costs of fighting in the house cricket, *Acheta domesticus* L. Behav Ecol 8:28–36

Hunt JH (2006) Evolution of castes in *Polistes*. Ann Zool Fennici 43:407–422

Kammer AE, Heinrich B (1978) Insect flight metabolism. Adv Insect Physiol 13:133–228

Keller L, Perrin N (1995) Quantifying the level of eusociality. Proc Royal Soc B 260:311–315

Liebert AE, Starks PT (2006) Taming of the skew: transactional models fail to predict reproductive partitioning in the paper wasp *Polistes dominulus*. Anim Behav 71:913–923

Lighton JRB, Fielden LJ (1995) Mass scaling of standard metabolism in ticks: a valid case of low metabolic rates in sit-and-wait strategists. Phys Zool 68:43–62

Matsumasa M, Murai M (2005) Changes in blood glucose and lactate levels of male fiddler crabs: Effects of aggression and claw waving. Anim Behav 69:569–577

Mennil DJ, Ramsay SM, Boag PT, Ratcliffe LM (2004) Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. Behav Ecol 15:757–765

Nonacs P, Liebert AE, Starks PT (2006) Transactional skew and assured fitness return models fail to predict patterns of cooperation in wasps. Am Nat 167:467–480

Nonacs P, Reeve HK, Starks PT (2004) Optimal reproductive-skew models fail to predict aggression in wasps. Proc Royal Soc B 271:811–817

Pardi L (1948) Dominance order in Polistes wasps. Phys Zool 21:1–13

Pfennig DW, Reeve HK, Shellman JS (1983) Learned component of nestmate discrimination in workers of a social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). Anim Behav 31:412–416

Pratte M (1989) Foundress association in the paper wasp *Polistes dominulus* Christ. (Hymen. Vesp.). Effects of dominance hierarchy on the division of labour. Behaviour 111:208–219

Reeve HK (1991) *Polistes*. In: Ross KG, Matthews RW (eds) The Social Biology of Wasps. Cornell University Press, Ithaca, pp 99–114

Reeve HK, Nonacs P (1992) Social contracts in wasp societies. Nature 359:823–825

Reeve HK, Keller L (2001) Tests of reproductive-skew models in social insects. Ann Rev Entomol 46:347–385

Reeve HK, Ratnieks FL (1993) Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. In: Keller L (ed) Queen Number and Sociality in Insects. University Press, Oxford, pp 45–85

Reeve HK, Starks PT, Peters JM, Nonacs P (2000) Genetic support for the evolutionary theory of reproductive transactions in social wasps. Proceedings of the Royal Society B 267:75–79

Reinhold K (1999) Energetically costly behaviour and the evolution of resting metabolic rate in insects. Funct Ecol 13:217–224

Roberts SP, Harrison JF (1999) Mechanisms of thermal stability during flight in the honeybee *Apis mellifera*. J Exp Biol 202:1523–1533

Ros AFH, Becker K, Oliveira RF (2006) Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*. Physiol Behav 89:164–170

Röseler P, Röseler I (1989) Dominance of ovariectomized foundresses of the paper wasp, polistes gallicus. Insectes Soc 36:219–234

Rossi AM, Hunt JH (1988) Honey supplementation and its developmental consequences: Evidence for food limitation in a paper wasp, *Polistes metricus*. Ecol Entomol 13:437–442

Scott J, Lockard J (2006) Captive female gorilla agonistic relationships with clumped defendable food resources. Primates; Journal of Primatology 47:199–209

Starks PT, Fischer DJ, Watson RE, Melikian GL, Nath SD (1998) Context-dependent nestmate discrimination in the paper wasp, *Polistes dominulus*: A critical test of the optimal acceptance threshold model. Anim Behav 56:449–458

Starks PT, Turillazzi S (2006) Special Issue, *Polistes* paper wasps: Emergence of a model genus. Ann Zool Fennici 43:385–624

Sumana A, Starks PT (2004) The function of dart behavior in the paper wasp, *Polistes fuscatus*. Naturwissenschaften 91:220–223

Tentschert J, Kolmer K, Hölldobler B, Bestmann HJ, Delabie JHC, Heinze J (2001) Chemical profiles, division of labor and social status in *Pachycondyla* queens (hymenoptera: Formicidae). Naturwissenschaften 88:175–178

Tibbetts EA, Reeve HK (2000) Aggression and resource sharing among foundresses in the social wasp *Polistes dominulus*: testing transactional theories of conflict. Behav Ecol Sociobiol 48:344–352

Turilazzi S, West-Eberhard MJ (1996) Natural history and evolution of paper-wasps. Oxford University Press, Oxford

West-Eberhard (1969) The social biology of polistine wasps. Miscellaneous Publications University of Michigan Museum of Zoology 140:1–101

Wilson EO (1971) The insect societies. Belknap Press of Harvard University Press, Cambridge, MA

Woods WA, Heinrich D, Steveson RD (2005) Honeybee flight metabolic rate: does it depend on air temperature. J Exp Biol 208:1161–1173

Woods WA Jr., Hendrickson H, Mason J, Lewis SM (2007) Energy and predation costs of firefly courtship signals. Am Nat 170:702–708