

Wasps in the shadow: Looking at the pre-hibernating clusters of *Polistes dominulus*

Leonardo Dapporto & Elisabetta Palagi

Centro Interdipartimentale Museo di Storia Naturale e del Territorio, Università di Pisa, Via Roma 79, I-56011 Calci, Pisa, Italy (e-mails: leondap@gmail.com, betta.palagi@museo.unipi.it)

Received 1 Nov 2005, revised version received 30 Nov. 2006, accepted 15 July 2006

Dapporto, L. & Palagi, E. 2006: Wasps in the shadow: Looking at the pre-hibernating clusters of *Polistes dominulus*. — *Ann. Zool. Fennici* 43: 583–594.

In some *Polistes* species, hibernation begins with the formation of clusters. Pre-hibernating aggregations may be evolutionarily favoured because they provide a dilution effect, better active defence from predators, and insulation from cold and/or dryness. Many authors have suggested that the pre-hibernating phase represents a socially inactive period for wasps. This paradigm strongly influenced the direction of research; in fact, most studies on *Polistes* behaviour focus on the nesting phase. It has been demonstrated, however, that many social interactions occur in aggregations, and that a division of labour is also present in these aggregations. Here, we evaluate the influence of cluster formation and social networks on the main aspects of wasp social behaviour, such as the consequences on kin-assortment (philopatry and tolerance level), variation in chemical recognition, division of labour, and helping behaviour.

Introduction

The colony cycle differs across *Polistes* species, with the major features depending on local ecological conditions. For example, *Polistes* species living in zones with seasonality, alternate a nesting - with a non-nesting phase. The latter phase allows the animals to cope with extreme climatic conditions (Pardi 1942, Gibo 1972, Reeve 1991). Such a phase is often characterized by a dispersion of reproductive individuals from their maternal nest and by the formation of pre-hibernation clusters, which consist of a variable number of individuals (from few to hundreds). The advantages of these aggregations are difficult to evaluate in quantitative terms, but it is plausible that clusters may favour a dilution effect (i.e., a form of ‘safety in numbers’), better

active defence from predators, and insulation from cold and/or dryness (Hunt *et al.* 1999, Dapporto *et al.* 2005a). Moreover, by waiting for better environmental conditions to start the nesting phase, wasps decrease activity which minimizes their metabolic costs, thus reducing the need of food and, consequently, the exposure to predators (Reeve 1991, Hunt *et al.* 1999, Gobbi *et al.* 2006).

Some tropical species initiate nests at the start of the rainy season and leave them at the onset of the dry season. For example, at the beginning of the dry season, *P. major* has been seen to leave maternal nests to aggregate in crevices (Hunt *et al.* 1999). *Polistes instabilis* and *P. pacificus* migrate to elevated forests where they aggregate in very large numbers; this seasonal movement may allow wasps enter into a cold,

wet storage, and to pass the season when food for brood is lacking in the lowlands (Hunt *et al.* 1999, 2001). This behaviour has been also reported in *Mischocyttarus angolatus*, and in the swarm founding species *Apoica pallens*, *Protopolybia acutiscutis*, *Agelaia panamensis*, and *Ropalidia Montana* (Jeanne & Hunt 1992, Hunt *et al.* 1995, 2001).

At the end of summer in temperate zones, *Polistes* gynes mate then aggregate in sheltered areas (Rau [1930a, 1931] for *P. rubiginosus*, *P. pallipes*, *P. annularis*; Fernald [1940] for *P. exclamans*; Pardi [1942], Dapporto *et al.* [2004a, 2005a] for *P. dominulus*; Yoshikawa [1963] for *P. yokahamae*, *P. fadwigae*, *P. snellenii*, *P. antennalis*; West-Eberhard [1969] for *P. fuscatus*; Gonzalez *et al.* [2002]; and Gobbi *et al.* [2006] for *P. versicolor*, *P. ferreri*).

Cluster formation is the starting point of hibernation in many *Polistes* species. Hibernation is generally divided into three stages: pre-hibernating, diapause, and post-hibernating (Yoshikawa 1963). During the pre-hibernating phase, foundresses aggregate in temporary shelters where the animals are not yet completely idle (Rau 1930a, 1931, Yoshikawa 1963, Gonzalez *et al.* 2002, Dapporto *et al.* 2005a). At the onset of winter, when the temperature drops, *Polistes* wasps move in deeper and safer quarters, called hibernacula, where they spend the diapause phase (Rau 1930a, 1931, Pardi 1942, Yoshikawa 1963). As the temperature rises in early spring, the wasps become active and the post-hibernating stage begins. This final stage of hibernation ends with the initiation of the nests (Yoshikawa 1963).

However, over-wintering remains a very critical period for gynes; in fact, cluster formation, activity reduction, and high tolerance to low temperatures (Gibo 1972) are not sufficient to guarantee survival. It is well known that many gynes die before spring (Rau 1930b, Pratte 1982, Starks 2001, Gamboa *et al.* 2004), and we have found groups of 30–40 dead wasps in January. Identifying appropriate winter quarters is likely to be essential for survival, and wasps often over-winter in the same shelters year after year (Rau 1930, Turillazzi *et al.* 2006b, L. Dapporto pers. obs.). Recently, Turillazzi *et al.* (2006) strongly suggested that antibiotic cuticular peptides are

cues involved in the identification of previously used hibernacula (Turillazzi *et al.* 2006a, 2006b). In addition, nourishment and resource storage during the pre-hibernating stage seem to play an important role in the survival of gynes during the winter (Strassmann 1979, Hunt *et al.* 2003, Gonzalez *et al.* 2002, Dapporto *et al.* 2005a).

Cluster composition and its possible effects on kin-assortment

During the nesting phase, *Polistes* wasps are strongly xenophobic and non-nestmates are attacked when encountered on the nest (reviewed in Gamboa [1996, 2004]). As suggested by Pardi (1942), in the final phase of the nesting period, just before pre-hibernation aggregations are formed, wasp behaviour changes. As nest fidelity and tolerance levels depend on defendable resources, it is not surprising that aggressive interactions between wasps decreases during this period. In an experiment on semi-free ranging colonies, Dapporto *et al.* (2004b) observed that *P. dominulus* wasps switched between nests more frequently at the very end of summer (15 August–15 September) when compared to the previous period (15 July–14 August).

In aggregations, the absence of the natal nest probably decreases aggression, as predicted by Starks *et al.* (1998) and Gamboa *et al.* (1991). In fact, despite the experiments of Allen *et al.* (1982) which suggested that *P. exclamans* gynes form clusters of former nestmates, most species aggregate in multi-colony clusters. Indeed Rau (1930a) for *P. annularis*, Pardi (1942) for *P. dominulus*, and Hunt *et al.* (1999) for *P. exclamans* argued that clusters of aggregating wasps are too numerous to complain wasps belonging to only one nest. In 2003, Starks demonstrated that *P. dominulus* clusters are composed of wasps from multiple nests. Moreover, it has even been shown that clusters may be composed of different species (Rau [1930a, 1931] for *P. annularis*, *P. pallipes* and *P. rubiginosus*; Yoshikawa [1963] for *P. fadwigae*, *P. yokahamae* and *P. antennalis*; Pardi [1942], L. Dapporto [pers. obs.] for *P. dominulus*, *P. gallicus* and *P. nympha*).

Within European species, *P. dominulus* shows the highest aggregation tendency, forming large

clusters which may contain individuals of multiple species (Pardi 1942, L. Dapporto pers. obs.). Indeed, the presence of co-hibernating animals from different genera (*Polistes dominulus*, *Vespa germanica*, and *Vespa crabro*; L. Dapporto pers. obs.) is an indicator of the high levels of tolerance of *P. dominulus* during this phase.

While tolerance during winter may increase wasp survival, tolerance may result in disadvantages during nest initiation in spring. A “tolerant foundress” that becomes subordinate to an unrelated dominant female cannot obtain indirect fitness payoffs. Therefore, for such a female to obtain some reproductive success, she must either inherit the colony or be provided some direct reproductive opportunities. Alternatively, a “selective foundress” increases the probability of founding a new nest with a related former nestmate, thus increasing its probability of obtaining indirect fitness. Indeed, within many *Polistes* species, spring associations are mainly composed of full sister foundresses (Field *et al.* [1998] for *P. bellicosus*; Seppa *et al.* [2002] for *P. carolina*; Reeve *et al.* [2000] for *P. fuscatus*). This is in line with kin selection theory, which predicts that in order to obtain indirect fitness unselfish individuals must be related to the individuals they help (Hamilton 1964a, 1964b).

Philopatry is a behavioural mechanism that facilitates related individuals gathering at the end of hibernation. In spring, foundresses of various *Polistes* species return to their natal nests where they often found a new nest. Philopatry facilitates the formation of kin groups after dispersal for hibernation (Pardi 1942, West-Eberhard 1969, Klahn 1979, Post & Jeanne 1982, Strassmann 1983, Cervo & Turillazzi 1985, Starks 2003, Sumana *et al.* 2005). As expected, the nest hydrocarbon profiles (the cues for chemical kin recognition in *Polistes*; Lorenzi *et al.* 1996) maintain colony specific signatures after the overwintering period (Sumana *et al.* 2005). Moreover, within a laboratory enclosure, *P. dominulus* were able to recognise and preferentially perch on their original nest (and even pieces of nest paper) after hibernation (Starks 2003).

But philopatry is not the only mechanism involved in the formation of kin groups. Post and Jeanne (1982), in an elegant laboratory experiment on *P. fuscatus*, found that foundresses

preferentially associate with former nestmates, and not with unrelated females with which they hibernated in clusters. This finding indicates that in this species cluster hibernation does not inhibit kin recognition in spring. This finding also demonstrates that these animals can identify kin in the absence of their natal nest. This evidence suggests that some colony specific cues are maintained after overwintering. The nature of these cues may be chemical (e.g. cuticular hydrocarbons; Lorenzi *et al.* 1996) and/or visual (Tibbetts 2002).

Within *Polistes* species, *P. dominulus* appears to be an exception to the full sister association rule. It has been demonstrated that nearly 35% of *P. dominulus* multiple foundress associations are composed of unrelated females (Queller *et al.* 2000). In addition, laboratory tests (similar to the experiments by Post and Jeanne [1982]) indicated that foundresses of this species do not associate preferentially with former nestmates (Pratte 1982, Röseler 1985). However, Dapporto *et al.* (2004a) demonstrated that some mechanisms to avoid association with unrelated individuals are present in *P. dominulus*. In the laboratory, foundresses prefer to form associative nest foundations with individuals from the same locality. Even though this is not an example of direct kin recognition, at the moment it is the only direct evidence of discrimination among *P. dominulus* females before nest foundation.

Dapporto *et al.* (2004a) also showed that hibernation clustering in *P. dominulus* may induce associations between unrelated foundresses. Gynes from two different localities were induced to hibernate in a single cluster. In the following spring, these foundresses did not show any preference to associate with individuals coming from the same original locality. Importantly, the cuticular chemical profiles of individuals from the mixed hibernation clusters were similar and significantly different from those of individuals who hibernated with other foundresses from the same locality. Finally, our recent observations revealed that colony-specific cuticular profiles are lost during hibernation (L. Dapporto *et al.* unpubl. data).

In conclusion, even though *P. dominulus* can lose its colony signature during the overwintering period, the nest retains its basic hydrocarbon

signature (Sumana *et al.* 2005), and wasps are able to recognize it in spring (Starks 2003). This evidence allows us to hypothesize that returning to the natal nest may allow individuals to re-acquire their colony specific hydrocarbon signature, which may facilitate nestmate recognition. The acquisition of the colony specific odour after a short period on the comb is well known in young *Polistes* wasps and in *Polistes* social parasites (Gamboa 1996, 2004, Sledge *et al.* 2001). The occurrence of the high rate of unrelated pairs found by Queller *et al.* (2000) in a population where many combs are lost during winter (Strassmann *et al.* 2004), further supports this hypothesis.

This research represents a good platform from which more focussed efforts should be completed. Particularly, genetic studies on populations where nests are sheltered may provide clarifying data. Indeed, we are not far from demonstrating what Rau hypothesized in 1930a (p. 464): “*It seems not at all impossible that queen wasps which spend the last weeks of autumn on the nests should remember and return to these nests after winter’s absence, and there again become gregarious, lick or caress one another, or perhaps renew acquaintances, or revive the old feeling of family oneness – however you may wish to express it – and possibly strengthen the bond by the mutual aid of giving to each other some refreshment, however slight it may be, at this serious time of need.*”

Behaviour in pre-hibernating clusters

Yoshikawa (1963) stated that the death of the last workers indicates the end of the social stage in wasps, because provisioning and food exchanging among gynes does not occur. Accordingly, the lack of foraging by workers implies a functional disintegration of the social phase. Many authors emphasized that the pre-hibernating phase represents a socially inactive period for wasps (Rau 1930a, Pardi 1942, Yoshikawa 1963, Hunt *et al.* 1999, Gonzalez *et al.* 2002). This paradigm has probably biased the direction of behavioural research. In fact, most studies on

Polistes behaviour focuses on the nesting phase. As a consequence, social interactions in aggregations have remained a “neglected behaviour”. In his paper *The behaviour of hibernating Polistes wasps*, Rau (1930a) described migration sites, cluster hibernation behaviour, and timing for three *Polistes* species. However, Rau did not mention any social behaviour among the aggregating wasps. Gonzalez *et al.* (2002) observed the behaviour of tropical *P. versicolor* in winter aggregations, and found that wasps forage for food but do not show social interactions such as trophallaxis. In *P. dominulus*, neither Pardi ([1942], in pre-hibernating clusters) nor Hughes *et al.* (2004, in clusters of wasps parasitized by the Strepsiptera *Xenos vesparum*) reported data on interactions between females.

However, social interactions are reported for *P. dominulus* and *P. rubiginosus* in the post-hibernating period before nest initiation. Rau (1930a: p. 466) stated that females “*would crowd close together and lick one another, and when a P. rubiginosus returned from the field (if not from a longer journey) they would fight for the opportunity of touching its mouth with their own*”. Pardi (1942) described these post-hibernating encounters in a more detailed manner. In particular, he reported that wasps sometimes fight by straightening up, grappling with forelegs, and attempting to bite each other. In some cases, these fights are unresolved with “no winners or losers” (Pardi 1942: p. 19) in other cases, after a brief period of such agonistic interactions, one of the two foundresses adopts a subordinate posture and, sometimes, offers regurgitated fluid.

Some years ago, observing a pre-hibernating cluster of *P. dominulus*, we realized that some behaviour reported by Rau (1930a) and Pardi (1942) for post-hibernating wasps were present in September. The most evident behaviour occurred when individuals went back to the aggregation. At this time, the other wasps immediately inspected and tried to dominate the returning female, often soliciting food and, sometimes, obtaining it. A similar behaviour was observed in clusters of *P. fuscatus* kept in the lab (M. J. West-Eberhard pers. comm.). We quantified this peculiar behaviour by systematically collecting data on aggregations. We individually

marked the animals on the wings and caged them in containers with water and sugar. We placed the containers in an open gallery, which ensured the maintenance of similar environmental conditions as those from where the aggregations were collected (Dapporto *et al.* 2005a).

We recorded social activity, which included some behavioural patterns such as attacks and fights, dominance interactions, food requests, and trophallaxis (Dapporto *et al.* 2005a). Particularly, in all pre-hibernating clusters, a few wasps helped others by performing external tasks and providing food. During daily activity, these helpers spent most of their time on the sugar but also returned to the aggregation. Here, several wasps competed for the opportunity to obtain food from the “helpers” by persistently soliciting them. Alternatively, when non-helpers returned to the aggregation they were usually ignored. This discrimination led us to hypothesize a recognition process mediated by food volatiles (Day & Jeanne 2001).

We also found that all helpers were mated and died within early December before the rigours of winter (Dapporto *et al.* 2005a). In six studied clusters, we identified 22 helpers out of a total of 303 wasps (7.3% of the individuals). This percentage was relatively constant over the six aggregations studied during three different years. This finding led us to assume that helping in aggregations is not an episodic behaviour. The importance of helpers may be inferred by the incidence of their effort. We found that from 27% to 50% of foraging bouts recorded were completed by helpers. These data suggest that helpers provide significant quantities of food, which suggests that other aggregating wasps do not incur the full costs related to foraging (predation risk and energy loss).

In sum, helpers are fertilized individuals that behave and die in winter as workers do. So, it is unclear whether helpers should be identified as gynes or workers.

Workers or gynes?

Reproductive division of labour is one of the key defining characteristics of insect societies,

and is found in a vast range of forms (Wilson 1971). Social insect colonies typically contain two castes: queens, who lay most of the eggs, and workers, who have reduced fertility and perform most of the colony maintenance tasks. Some groups of social insects (many species of bees, termites, and most ants) are characterised by differences between queens and workers established at the larval stage (termed pre-imaginal), often as a result of differential feeding by workers (Wilson 1971, Holldobler & Wilson 1990, Hunt & Amdam 2005). In other more “simple” societies (allodapine and halictine bees, hover wasps and ponerine ants), morphological differences between reproductives and workers are few or absent, and all individuals retain the ability to reproduce or perform helper roles (Turillazzi 1991). Within the social wasps, the full range of social organisation can be found, from solitary to highly eusocial species (Jeanne 1980, Turillazzi 1991, O’Donnell 1998).

The polistine wasps are a heterogeneous group and contain swarm founding species with evident pre-imaginal caste differentiation (found in the Ropalidiini and Epiponini) (Jeanne 1991, Hunt *et al.* 2001). In other genera (e.g. *Polistes*, and *Mischocyttarus*), the presence of true caste determination has not been positively confirmed. Size differences between queens and workers occur in some *Polistes* species (Haggard & Gamboa [1980] for *P. metricus*; Dani [1994] for *P. gallicus*), while in others differences disappear as the season progresses and as the number of workers increases (West-Eberhard [1969] for *P. fuscatus*; Pardi [1946], Turillazzi [1980] for *P. dominulus*; Miyano [1983, 1990] for *P. antennalis*). O’Donnell (1998) stated that pre-imaginal cast determination is not necessarily expressed in external morphology and the author proposed that the critical issue to delimiting castes is whether adult females can mate and lay diploid eggs. Accordingly, helpers in aggregations should be considered future queens. However, it has been shown that in several *Polistes* species the first emerged females (and thus virtually workers) can mate and lay fertilised eggs (Strassmann 1981, Kasuya 1983, Suzuki 1985).

A further difference between queen and worker castes is evident in temperate species

where some individuals are able to overwinter while others are not (Delaurance 1952, Strassmann 1985). Nevertheless, even in this case there are some exceptions in *Polistes* wasps; in *P. exclamans*, in the absence of larvae on the nest, adult workers are able to modify their own characteristics (e.g. increasing the resistance to cold) to match those of foundresses (Solís & Strassmann 1990). It was demonstrated in *P. fuscatus* (Reeve *et al.* 1998) and *P. dominulus* (Starks 2001) that several of the first workers may pursue alternative reproductive tactics, where, instead of remaining on the nest to aid their mother, they abandon the nest to overwinter and attempt to become foundresses the following spring. Finally, as mentioned above, many future foundresses die in winter before spring and, from this perspective, they should be considered as “workers”.

In summary, *Polistes* wasps seem to be characterized by caste plasticity, in which the roles are highly sensitive to environmental circumstances (Solís & Strassmann 1990, Mead & Gabouriaut 1993, Mead *et al.* 1995, Reeve *et al.* 1998). However, some differences in reproductive potential may be determined during preimaginal stages by larval nourishment (Hunt 1991, Karsai & Hunt 2002). In the initial part of the colony cycle, due to low worker number, the first larvae are often under fed and become smaller workers (West-Eberhard 1969, Turillazzi 1980, Hunt & Amdam 2005). Some authors have suggested that queens manipulate the size of the first workers to ensure that they are smaller at emergence (e.g. by shortening their development time; Strassmann & Orgren 1983, Miyano 1983, 1990). This would ensure the earlier presence of workers and would reduce the risk that workers would abandon their mother to establish nests on their own (Miyano 1983, 1990, Strassmann & Orgren 1983, Reeve *et al.* 1998).

Hunt *et al.* (2003) showed in *P. fuscatus* that females emerging in August (and thus presumably foundresses) possess a storage protein of the hexamerine family that is not present in females emerging earlier in the colony cycle (workers). Hunt and Amdam (2005) proposed an explanatory framework based on the assumption that the solitary ancestor of Polistines may have been bivoltine. The authors renovated the hypothesis

that a true caste differentiation may occur in *Polistes* genus. They hypothesized that *Polistes* workers correspond to the first generation (G1) but instead of directly producing the second generation offspring (G2), they take care of it in the natal nest. Future queens correspond to the second generation (G2). Hunt and Amdam (2005) proposed that a nutrient-dependent switch mechanism during larval growth may explain caste differentiation in *Polistes*. Variation in nutrient inflow may result in a temporal overlapping of the two generations that cause the emergence of early gynes (Strassmann 1981, Reeve *et al.* 1998) and late workers. Hunt and Amdam (2005) hypothesized that these late workers may become helpers in aggregations.

What are the helpers' benefits?

Kin selection theory provides a unique framework from which the evolution of cooperation can be explained (Hamilton 1964a, 1964b). A gene promoting altruism can increase in frequency when there is a chance that the beneficiary also carries a copy, which may happen if the individuals are related. According to kin selection, to obtain some indirect fitness, a helper must direct its efforts towards relatives (Hamilton 1964a, 1964b). If wasps are able to recognize former nestmate in aggregations (as suggested for *P. fuscatus* gynes, Allen *et al.* [1982]), helpers should preferentially direct their efforts towards full sisters, even in aggregations where wasps from different colonies are present (Starks 2003). In this case, helping in aggregations may be as beneficial as helping on the nest. At present, however, evidence suggests that recognition among *P. dominulus* gynes in aggregations is not likely (Pratte 1982, Queller *et al.* 2000, Dapporto *et al.* 2004a). It is possible, however, that in viscous populations such as those of *Polistes* wasps, a significant background relatedness is shared not only among nestmates but also among individuals from neighbouring colonies (Ross & Carpenter 1991). Indeed, in viscous populations, individuals have a limited dispersal potential (philopatry) because offspring tend to remain close to their natal nest. As such, a wasp is likely to have relatives in its neighbourhood. A

helper may therefore convey the benefit (at least partly) to its relatives via random helping effort (Hamilton 1964a, 1964b, van Baalen & Rand 1998, Mitteldorf & Wilson 2000).

Relatedness, however, may not be the main factor determining helping effort. Variation among group members in the cost of helping might determine the differences in altruistic traits (Cant & Field 2001, 2005). We do not know if the high mortality among helpers is due to the cost of tasks (as it may be inferred by the findings of O'Donnell & Jeanne [1995]), or to some intrinsic characteristics of helpers (as suggested by Hunt & Amdam [2005]). In the former case, the cost of helping is high. In contrast, if helpers are weak gynes, or workers with reduced possibilities to survive winter, they should suffer low costs by helping individuals with higher reproductive potential (West-Eberhard 1975, 2003, Cant & Field 2001, Hunt *et al.* 2003). Cant and Field (2001: p. 1959) suggested that “*helpers will face a trade-off between current investment in help and their own future reproductive success*”. Indeed, social wasps adopt alternative tactics to obtain some certain and immediate benefits. For example, in *P. exclamans* early males and workers found satellite nest. The early emergence of reproductive individuals may have originated as an adaptation in response to the large number of queens that die before autumn when reproductive offspring are usually produced (Strassmann 1981).

Nevertheless, Sober and Wilson (1998) and Taylor (1992) predicted that altruistic behaviour, blindly dispersed to individuals of a given population, is not likely to evolve even in the presence of an increased relatedness (viscosity) and low costs for helpers (Cant & Field 2001, 2005). Indeed, in order for an altruistic trait to be selected, the benefits must fall disproportionately on other individuals carrying the same altruistic gene.

Currently, in the absence of empirical studies demonstrating (i) the occurrence of kin recognition in aggregations, (ii) the relatedness level among aggregating wasps, and (iii) the costs linked to helping behaviour and the benefit gained by non helpers, all the assumptions discussed above remain speculative.

Do autumn interactions reflect (and possibly improve) dominance potential of *Polistes dominulus* foundresses?

Within the first days of cooperative colony foundation, a dominance hierarchy is established among foundresses through aggressive interactions (Pardi 1942, 1946). The intensity of these interactions decreases with time, from severe fights during the first encounters, to ritualized dominance interactions after several days. Behavioral and physiological differences between dominant and subordinate foundresses are determined and maintained by a feedback loop involving dominance, task performance, nutrition, and reproductive physiology (Markiewicz & O'Donnell 2001). In fact, by winning the first fights and reaching the dominant position, the alpha female avoids external tasks and acquires food from subordinates. Thanks to food provisioning, the dominant foundress may develop ovaries and, consequently, improve its endocrine activity thus enhancing the capability to dominate (Bonabeau *et al.* 1999, Markiewicz & O'Donnell 2001). This feed-back loop hypothesis suggests that winner loser effects may be present in *Polistes* wasps.

In this view, it could be advantageous for *Polistes* foundresses to exit the overwintering period with characteristics typical of dominant individuals, in order to increase the probability of winning the first agonistic interactions. Indeed, physiological differences among foundresses seem to be present before nest foundation (Strambi *et al.* 1982, Röseler *et al.* 1984, 1985). Strambi *et al.* (1982) demonstrated that *P. dominulus* females differed during overwintering in their haemolymph protein concentration. In particular, females affected by the strepsipteran parasite *Xenos vesparum* exhibited low protein level in haemolymph. The same low levels were found in several females that were not affected by the parasite. Such differentiation in protein levels was not determined at a pre-imaginal stage, as these differences became evident 10 days after emergence (Strambi *et al.* 1982).

According to Hunt *et al.* (2003) and Hunt and Amdam (2005), the protein content in the wasp tissues plays a role in caste determination.

Moreover, evidence suggests that *Polistes* future foundresses start to develop ovaries during the aggregation phase well before nest foundation (Turillazzi 1980, Dapporto *et al.* 2006, Gobbi *et al.* 2006). Röseler *et al.* (1984, 1985) showed that in the hours immediately after hibernation, foundresses were already physiologically differentiated: some foundresses showed the physiological characteristics of dominant females (larger ovaries and corpora allata), and these animals dominated more subordinate-like foundresses. Indeed, differences in endocrine activity, ovarian development and, therefore, the ability to exhibit dominant behaviour, exist before the first encounter after hibernation. These characteristics are independent of body size, even among individuals from the same hibernation site (Röseler *et al.* 1984, 1985). This early differentiation may result from a number of possible factors that play different roles from egg deposition to the end of hibernation: genotype effects, nourishment at imaginal (Strassmann 1979, Dapporto *et al.* 2005a) and/or larval stage (Hunt 1991, Karsai & Hunt, 2002, Hunt *et al.* 2003, Hunt & Amdam 2005), or social context (Solis & Strassmann 1990, Dapporto *et al.* 2005a, 2006).

The main question is whether factors operating at the pre-imaginal (West-Eberhard 1975, Hunt 1991, Hunt *et al.* 2003, Tibbetts & Dale 2004, Hunt & Amdam 2005) or adult stages (Solis & Strassmann 1990, Reeve *et al.* 1998, Dapporto *et al.* 2005a, 2005b, 2006) affect winter survival and hierarchical relationships of foundresses in spring associations. Generally, factors affecting the establishment of the dominance hierarchy are divided into intrinsic and extrinsic factors (Landau 1951a, 1951b). Intrinsic factors refer to traits that correlate with fighting ability in terms of physical skill such as size and strength; in wasps, these factors are likely determined at pre-imaginal stage. Wasp size is obviously established before emergence, as insect adults do not grow. Larger wasps have higher probabilities of being dominant on the nest (Turillazzi & Pardi 1977). The subfertility hypothesis proposed by West-Eberhard (1975), suggests that some individuals emerge with a reduced reproductive potential and, therefore, are more likely to become subordinates. However, there is presently little empirical support to this hypothesis as isolated subordinate foundresses

usually show the same reproductive potential of their former dominant females (Röseler 1985, Reeve 1991, Field & Foster 1999).

Conversely to intrinsic factors, extrinsic factors are related to social experience and, obviously, operate at the adult stage. Two well-known extrinsic mechanisms that affect hierarchy establishment are winner and loser effects, which predict that the outcome of prior fights influences an individual's probability of winning or losing a future contest. Winner and loser effects may be appropriate in social wasps. As mentioned above, Markiewicz and O'Donnell (2001) hypothesized a feedback loop, triggered by dominance interactions, that determines differences in behavioural and physiological characteristics between dominant and subordinate foundresses.

As demonstrated for several animal species (Landau 1951a, 1951b, Chase *et al.* 1994, Chase *et al.* 2002, Beacham 2003, Dugatkin & Druen 2004), a combination of intrinsic and extrinsic factors most likely determines hierarchical rank in *Polistes* wasps (Turillazzi & Pardi 1977, Dapporto *et al.* 2006). We have observed an aggregation of wasps from the onset of the pre-hibernating period until the beginning of winter, and then we measured head size (intrinsic factor) and ovarian development. Ovarian development did not correlate with head width, suggesting that ovarian status is linked to environmental factors rather than to intrinsic ones (as also suggested by Röseler 1985, Field & Foster 1999, Markiewicz & O'Donnell 2001). We also demonstrated that both head width and ovarian development affected the tendency to dominate in aggregation (Dapporto *et al.* 2006). In fact, only wasps having both larger heads and ovaries were dominant. Moreover we showed that, in the 85% of the cases, dominance relationships of a given pair of females in autumn were maintained after the nest foundation in spring (Dapporto *et al.* 2006); this suggests that autumnal social interactions may be accurate indicators of the dominance potential of wasps.

Since ovarian development after nest foundation seems to be determined by the social context (Röseler 1991), we suggest that ovarian status may be affected by social interactions in aggregations. According to findings by Röseler *et al.* (1984, 1985), and to the model proposed by Markiewicz O'Donnell (2001), foundresses exiting hiberna-

tion with larger ovaries and corpora allata, have greater chances to obtain the dominant position after nest foundation. Thus we suggest that social encounters in pre-hibernation clusters may serve to assess early — and possibly improve — one's own dominance potential well before the nest foundation stage (Dapporto *et al.* 2006).

Conclusions

Polistes wasps are considered as a model for studies of behavioural plasticity, caste determination, cooperation and competition according to kinship, and related phenomena such as nesting choice, kin recognition, and alternative reproductive strategies. Most studies, however, focus on the nesting phase, and consider winter aggregations little more than groups of “sleeping wasps”. In contrast, we have shown that aggregating wasps are not only active, but they perform the main social interactions occurring on the nest (Dapporto *et al.* 2005a, 2006). The aggregation may represent a “no man's land” that provides the opportunity to study wasp social behaviour in a diverse environment, where reproductive competition is lacking. In this sense, all social interactions in clusters seem to lose their primary functional meaning, that is, maintaining the colony's reproductive dominance. In fact, the absence of the nest, together with the advantages of grouping during autumn, reduces competition and, consequently, aggression levels in aggregating wasps. As such, the gynes, engage in dominance interactions that may result in immediate (receiving food from helpers; Dapporto *et al.* 2005a) and delayed benefits (improving and assessing own reproductive potential; Dapporto *et al.* 2006) in a relatively “relaxed field”.

In this view, studying social networks in clusters may help to shed light of the ontogeny of behaviour and on the mechanisms which are at the basis of division of labour and caste determination in this genus.

Acknowledgments

We wish to thank Phil Starks and Stefano Turillazzi for the opportunity to attend the Talloires Symposium. Thanks are

also due to Alessandro Cini, Chiara Cotoneschi, Cristina Pansolli, Tommaso Paoli, and Giorgia Tacconi for helping in collecting data and for enlightening discussions.

References

- Allen, J. L., Schulze-Kellman, K. & Gamboa, G. J. 1982: Clumping pattern during overwintering in the paper wasp, *Polistes exclamans*: effects on relatedness. — *J. Kansas Entomol. Soc.* 55: 97–100.
- Beacham, J. L. 2003: Models of dominance hierarchy formation: effect of prior experience and intrinsic traits. — *Behaviour* 140: 1275–1303.
- Bonabeau, E., Theraulaz, G. & Deneubourg, J. L. 1999: Dominance orders in animal societies: the self-organization hypothesis revisited. — *Bull. Math. Biol.* 61: 727–757.
- Cant, M. A. & Field, J. 2001: Helping effort and future fitness in cooperative animal societies. — *Proc. R. Soc. Lond. B* 268: 1959–1964.
- Cant, M. A. & Field, J. 2005: Helping effort in a dominance hierarchy. — *Behav. Ecol.* 16: 708–715.
- Cervo, R. & Turillazzi, S. 1985: Associative foundation and nesting sites in *Polistes nympa*. — *Naturwissenschaften* 72: 48–49.
- Chase, I. D., Craig, T., Sprangler-Martin, D. & Manfredonia, M. 2002: Individual differences versus social dynamics in the formation of animal dominance hierarchies. — *Proc. Natl. Acad. Sci. USA* 99: 5744–5749.
- Dani, F. R. 1994: Caste differences in *Polistes gallicus* (L.) (Hymenoptera Vespidae). — *Ethol. Ecol. Evol.* Special Issue 3: 67–73.
- Dapporto, L., Pansolli, C. & Turillazzi, S. 2004a: Hibernation clustering and its consequences for associative nest foundation in *Polistes dominulus* (Hymenoptera Vespidae). — *Behav. Ecol. Sociobiol.* 56: 315–321.
- Dapporto, L., Palagi, E., Cini, A., Cotoneschi, C., Paoli, T., Turillazzi, S. 2004b: Do nest fidelity and intolerance decrease at the end of the colony cycle in *Polistes dominulus* (Christ.) (Hymenoptera Vespidae)? — *Redia* 87: 227–229.
- Dapporto, L., Palagi, E. & Turillazzi, S. 2005a: Sociality outside the nest: helpers in pre-hibernating clusters of *Polistes dominulus*. — *Ann. Zool. Fennici* 42: 135–139.
- Dapporto, L., Sledge, M. F. & Turillazzi, S. 2005b: Dynamics of cuticular chemical profiles of *Polistes dominulus* workers in orphaned nests. — *J. Ins. Physiol.* 51: 969–973.
- Dapporto, L., Palagi, E., Cini, A. & Turillazzi, S. 2006: Pre-hibernating aggregations of *Polistes dominulus*: an occasion to study early dominance assessment in social insects. — *Naturwissenschaften* 93: 321–324.
- Day, S. E. & Jeanne, R. L. 2001: Food volatiles as attractants for yellowjackets (Hymenoptera: Vespidae). — *Environ. Entomol.* 30: 157–165.
- Delaurance, É.-P. 1952: Le polymorphisme social et son déterminisme chez les guêpes. — *Struct. Physiol. Soc. Anim. Cooq. Cent. Natl. Rech. Sci.* 34: 141–155.

- Dugatkin, L. A. & Druen, M. 2004: The social implications of winner and loser effects. — *Proc. R. Soc. Lond. B* (suppl.) 271: S488–S489.
- Fernald, H. T. 1940: A probable prenuptial gathering of *Polistes*. — *Ann. Entomol. Soc. Am.* 33: 33–34.
- Field, J. & Foster, W. 1999: Helping behaviour in facultatively eusocial hover wasps: an experimental test of the subfertility hypothesis. — *Anim. Behav.* 57: 633–636.
- Field, J., Solís, C. R., Queller, D. C. & Strassmann, J. E. 1998: Social and genetic structure of paper wasp cofoundress associations: test of reproductive skew models. — *Am. Nat.* 151: 545–563.
- Gamboa, G. J. 1996: Kin recognition in social wasps. — In: Turillazzi, S. & West-Eberhard, M. J. (eds.), *Natural history and evolution of paper-wasps*: 161–177. Oxford University press, Oxford.
- Gamboa, G. J. 2004: Kin recognition in eusocial wasps. — *Ann. Zool. Fennici* 41: 789–808.
- Gamboa, G. J., Foster, R. L., Scope, J. A. & Bitterman, A. M. 1991: Effects of colony cycle, context, and intercolony distance on conspecific tolerance by paper wasp (*Polistes fuscatus*). — *Behav. Ecol. Sociobiol.* 29: 87–94.
- Gamboa, G. J., Noble, M. A., Thom, M. C., Togal, J. L., Srinivasan, R. & Murphy B. D. 2004: The comparative biology of two sympatric paper wasps in Michigan, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). — *Insectes Soc.* 51: 153–157.
- Gibo, D. L. 1972: Hibernation sites and temperature tolerance of two species of *Vespula* and one species of *Polistes* (Hymenoptera: Vespidae). — *New York Entomological Society* 2: 105–108.
- Gobbi, N., Noll, F. B. & Penna, M. A. H. 2006: “Winter” aggregations, colony cycle, and seasonal phenotypic change in the paper wasp *Polistes versicolor* in subtropical Brazil. — *Naturwissenschaften* 93: 487–494.
- Gonzalez, J. A., Nascimento, F. S. & Gayubo, S. F. 2002: Observations on the winter aggregates of two polistine paper wasps (Hymenoptera vespidae polistinae). — *Trop. Zool.* 15: 1–4.
- Haggard, C. M. & Gamboa, G. J. 1980: Seasonal variation in body size and reproductive condition of a paper wasp, *Polistes metricus* (Hymenoptera, Vespidae). — *J. Kansas Entomol. Soc.* 112: 239–248.
- Hamilton, W. D. 1964a: The genetical evolution of social behaviour. I. — *J. Theor. Biol.* 7: 1–16.
- Hamilton, W. D. 1964b: The genetical evolution of social behaviour. II. — *J. Theor. Biol.* 7: 17–52.
- Hölldobler, B. & Wilson, E. O. 1990: *The ants*. — Springer, Berlin Heidelberg New York.
- Hughes, D. P., Kathirithamby, J., Turillazzi, S. & Beani, L. 2004: Social wasps desert the colony and aggregate outside if parasitized: parasite manipulation? — *Behav. Ecol.* 15: 1037–1043.
- Hunt, J. H. 1991: Nourishment and the evolution of the social Vespidae. — Ross, K. G. & Matthews, R. W. (eds.), *The social biology of wasps*: 426–450. Comstock, Ithaca.
- Hunt, J. H. & Amdam, G. V. 2005: Bivoltinism as an antecedent to eusociality in the paper-wasp genus *Polistes*. — *Science* 308: 264–267.
- Hunt, J. H., Buck, N. A. & Wheeler, D. E. 2003: Storage proteins in vespid wasps: characterization, developmental pattern, and occurrence in adults. — *J. Ins. Phys.* 49: 785–794.
- Hunt, J. H., Jeanne, R. L. & Keeping, M. G. 1995: Observations on *Apoica pallens*, a nocturnal Neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). — *Insectes Soc.* 42: 223–236.
- Hunt, J. H., O'Donnell, S., Chernoff, N. & Brownie, C. 2001: Observations on two neotropical swarm-founding wasps, *Agelaia yepocapa* and *A. panamensis* (Hymenoptera: Vespidae). — *Ann. Entomol. Soc. Am.* 94: 555–562.
- Hunt, J. H., Brodie, R. J., Carithers, T. P., Goldstein, P. Z. & Janzen, D. H. 1999: Dry season migration by Costa Rican lowland paper wasps to high elevation cold dormancy sites. — *Biotropica* 31: 192–196.
- Jeanne, R. L. 1980: Evolution of social behaviour in the Vespidae. — *Annu. Rev. Entomol.* 25: 371–396.
- Jeanne, R. L. 1991: The swarm founding Polistinae. — In: Ross, K. G. & Matthews, R. W. (eds.), *The social biology of wasps*: 191–231. Comstock, Ithaca.
- Jeanne, R. L. & Hunt, J. H. 1992: Observations on the social wasp *Ropalidia montana* from peninsular India. — *J. Biosci.* 17: 1–14.
- Karsai, I. & Hunt, J. H. 2002: Food quantity affects traits of offsprings in the paper wasp *Polistes metricus*. — *Environ. Entomol.* 31: 99–106.
- Kasuya, E. 1983: Social behaviour of early emerging males of a Japanese paper wasp, *Polistes chinensis antennalis* (Hymenoptera, Vespidae). — *Res. Popul. Ecol.* 25: 143–149.
- Klahn, J. E. 1979: Philopatric and nonphilopatric foundress associations in the social wasp *Polistes fuscatus*. — *Behav. Ecol. Sociobiol.* 5: 417–424.
- Landau, H. G. 1951a: On dominance relations and the structure of animal societies. I. Effects of inherent characteristics. — *Bull. Math. Biophysics* 13: 1–19.
- Landau, H. G. 1951b: On dominance relations and the structure of animal societies. II. Some effects of possible social causes. — *Bull. Math. Biophysics* 13: 245–262.
- Lorenzi, M. C., Bagnères, A. G. & Clément, J. L. 1996: The role of cuticular hydrocarbons in social insects: is the same in paper wasps? — In: Turillazzi, S. & West-Eberhard, M. J. (eds.), *Natural history and evolution of paper-wasps*: 178–189. Oxford University Press, Oxford.
- Markiewicz, D. A. & O'Donnell, S. 2001: Social dominance, task performance and nutrition: implications for reproduction in eusocial wasps. — *J. Comp. Physiol. A* 187: 327–333.
- Mead, F. & Gabouriaux, D. 1993: Posteclosion sensitivity to social context in *Polistes dominulus* Christ females (Hymenoptera, Vespidae). — *Insectes Soc.* 40: 11–20.
- Mead, F., Gabouriaux, D. & Habersetzer, C. 1995: Nest-founding behavior induced in the first descendants of *Polistes dominulus* Christ (Hymenoptera: Vespidae) colonies. — *Insectes Soc.* 42: 385–96.
- Miyano, S. 1983: Number of offspring and seasonal changes of their body weight in a paperwasp, *Polistes chinensis antennalis* Pérez (Hymenoptera, Vespidae). — *Res.*

- Popul. Ecol.* 25: 198–209.
- Miyano, S. 1990: Number, larval durations and body weights of queen-reared workers of a Japanese paper wasp, *Polistes chinensis antennalis* (Hymenoptera, Vespidae). — *Nat. Hist. Res.* 1: 93–97.
- O'Donnell, S. 1998: Reproductive caste determination in eusocial wasps (Hymenoptera: Vespidae). — *Annu. Rev. Entomol.* 43: 323–346.
- O'Donnell, S. & Jeanne, R. L. 1995: Worker lipid stores decrease with outside-nest task performance in wasps: implications for the evolution of age polyethism. — *Experientia* 51: 749–752.
- Pardi, L. 1942: Ricerche sui Polistini. V. La poliginia iniziale di *Polistes gallicus* (L.). — *Boll. Ist. Entomol. Univ. Bologna* 14: 1–106.
- Pardi, L. 1946: Ricerche sui Polistini. VII. La 'dominazione' e il ciclo ovario annuale in *Polistes gallicus* (L.). — *Boll. Ist. Entomol. Univ. Bologna* 15: 25–84.
- Post, D. C. & Jeanne, R. 1982: Recognition of former nestmates colony founding by the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). — *Behav. Ecol. Sociobiol.* 11: 283–285.
- Pratte, M. 1982: Relations antérieures et association de fondation chez *Polistes gallicus* L. — *Insectes Soc.* 29: 352–357.
- Queller, D. C., Zacchi, F., Cervo, R., Turillazzi, S., Henshaw, M. T., Santorelli, L. A. & Strassmann J. E. 2000: Unrelated helpers in a social insect. — *Nature* 405: 784–787.
- Rau, P. 1930a: The behavior of hibernating *Polistes* wasps. — *Ann. Entomol. Soc. Am.* 23: 461–466.
- Rau, P. 1930b: Mortality of *Polistes annularis* wasps during hibernation. — *Can. Ent.* 62: 81–83.
- Rau, P. 1931: An additional note on the behavior of hibernating *Polistes* wasps. — *Ann. Entomol. Soc. Am.* 24: 514–518.
- Reeve, H. K. 1991: *Polistes*. — In: Ross, K. G. & Matthews, R. W. (eds.), *The social biology of wasps*: 99–148. Comstock, Ithaca.
- Reeve, H. K., Peters, J. M., Nonacs, P. & Starks, P. T. 1998: Dispersal of first "workers" in social wasps: Causes and implications of an alternative reproductive strategy. — *Proc. Natl. Acad. Sci. USA* 95: 13737–13742.
- Reeve, H. K., Starks, P. T., Peters, J. M. & Nonacs, P. 2000: Genetic support for the evolutionary theory of reproductive transactions in social wasps. — *Proc. R. Soc. Lond. B* 267: 75–79.
- Röseler, P. F. 1985: Endocrine basis of dominance and reproduction in polistine paper wasps. — In: Holldobler, B. & Lindauer, M. (eds.), *Experimental behavioral ecology and sociobiology*: 259–272. Sinauer, Sunderland.
- Röseler, P. F., Röseler, I., Strambi, A. & Augier, R. 1984: Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp *Polistes gallicus*. — *Behav. Ecol. Sociobiol.* 15: 133–142.
- Röseler, P.-F., Röseler, I. & Strambi, A. 1985: Role of ovaries and ecdysteroids in dominance hierarchy establishment among foundresses of the primitively social wasp, *Polistes gallicus*. — *Behav. Ecol. Sociobiol.* 18: 9–13.
- Ross, K. G. & Carpenter, J. M. 1991: Population genetic structure, relatedness, and breeding systems. — In: Ross, K. G. & Matthews, R. W. (eds.), *The social biology of wasps*: 451–479. Comstock, Ithaca.
- Seppa, P., Queller, D. C. & Strassmann, J. E. 2002: Reproduction in foundress association of the social wasp, *Polistes carolina*: conventions, competition, and skew. — *Behav. Ecol.* 13: 531–542.
- Sledge, M. F., Dani, F. R., Cervo, R., Dapporto, L. & Turillazzi, S. 2001: Recognition of social parasites as nestmates: adoption of colony-specific host cuticular odours by the paper wasp parasite *Polistes sulcifer*. — *Proc. R. Soc. Lond. B* 268: 2253–2260.
- Sober, E. & Wilson, D. S. 1998: *Unto others*. — Harvard University Press, Cambridge.
- Solís, C. R. & Strassmann, J. E. 1990: Presence of brood affects caste differentiation in the social wasp, *Polistes exclamans* Viereck (Hymenoptera: Vespidae). — *Funct. Ecol.* 4: 531–541.
- Starks, P. T. 2001: Alternative reproductive tactics in the paper wasp, *Polistes dominulus* with specific focus on the sit-and-wait tactic. — *Ann. Zool. Fennici* 38: 198–199.
- Starks, P. T. 2003: Natal nest discrimination in the paper wasp, *Polistes dominulus*. — *Ann. Zool. Fennici* 40: 53–60.
- Starks, P. T., Fischer, D. J., Watson, R. E., Melikian, G. L. & Nath, S. D. 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.
- Strambi, C., Strambi, A. & Augier, A. 1982: Protein levels in the haemolymph of the wasp *Polistes gallicus* L. at the beginning of imaginal life and during overwintering. Action of the strepsipteran parasite *Xenos vesparum* Rossi. — *Experientia* 38: 1189–1191.
- Strassmann, J. E. 1979: Honey caches help female paper wasps (*Polistes annularis*) survive Texas winters. — *Science* 204: 207–209.
- Strassmann, J. E. 1981: Evolutionary implications of early male and satellite nest production in *Polistes exclamans* colony cycles. — *Behav. Ecol. Sociobiol.* 8: 55–64.
- Strassmann, J. E. 1983: Nest fidelity and group size among foundresses of *Polistes annularis* (Hymenoptera: Vespidae). — *J. Kansas Entomol. Soc.* 54: 621–634.
- Strassmann, J. E. 1985: Worker mortality and the evolution of castes in the social wasp *Polistes exclamans*. — *Insectes Soc.* 32: 275–285.
- Strassmann, J. E. & Orgren, M. C. 1983: Nest architecture and brood development times in the paper wasp, *Polistes exclamans* (Hymenoptera: Vespidae). — *Psyche* 90: 237–248.
- Strassmann, J. E., Queller, D. C., Emerson, J. J., Stagi, M., Cervo, R. & Turillazzi, S. 2004: Comparing the costs and benefits of grouping with non-relatives in the social amoeba *Dictyostelium discoideum* (amoebazoa) and the social wasp *Polistes dominulus* (hymenoptera vespidae). — *Redia* 87: 145–148.
- Sumana, A., Liebert, A. E., Berry, A. S., Switz, G. T., Orians, C. M. & Starks, P. T. 2005: Nest hydrocarbons as cues for philopatry in a paper wasp. — *Ethology* 111: 469–477.

- Suzuki, T. 1985: Mating and laying of female-producing eggs by orphaned workers of a paper wasp, *Polistes snelleni* (Hymenoptera: Vespidae). — *Ann. Entomol. Soc. Am.* 78: 736–739.
- Taylor, P. D. 1992: Altruism in viscous populations—an inclusive fitness model. — *Evol. Ecol.* 6: 352–356.
- Tibbetts, E. A. 2002: Visual signals of individual identity in the wasp *Polistes fuscatus*. — *Proc. R. Soc. Lond. B* 269: 1423–1428.
- Tibbetts, E. A. & Dale, J. 2004: A socially enforced signal of quality in a paper wasp. — *Nature* 432: 218–222.
- Turillazzi, S. 1980: Seasonal variation in the size and anatomy of *Polistes gallicus* (L.) (Hymenoptera Vespidae). — *Monitore Zool. Ital. (n.s.)* 14: 63–75.
- Turillazzi, S. & Pardi, L. 1977: Body size and hierarchy in polygynic nests of *Polistes gallicus* (L.) (Hymenoptera Vespidae). — *Monitore Zool. Ital. (n.s.)* 11: 101–112.
- Turillazzi, S. 1991: The *Stenogastrinae*. — In: Ross, K. G. & Matthews, R. W. (eds.), *The social biology of wasps*: 74–98. Comstock, Ithaca.
- Turillazzi, S., Dapporto, L., Pansolli, C., Boulay, R., Dani, F. R., Moneti, G. & Pieraccini, G. 2006a: Habitually used hibernation sites of paper wasps are marked with venom and cuticular peptides. — *Current Biology* 16: R530–R531.
- Turillazzi, S., Mastrobuoni, G., Dani, F.R., Moneti, G., Pieraccini, G., La Marca, G., Bartolucci, G., Perito, B., Lambardi, D., Cavallini, V. & Dapporto L. 2006b: Dominulin A and B: two new antibacterial peptides identified on the cuticle and in the venom of the social paper wasp *Polistes dominulus* using MALDI-TOF, MALDI-TOF/TOF, and ESI-Ion Trap. — *J. Am. Soc. Mass Spectrom.* 17: 376–383.
- van Baalen, M. & Rand, D. A. 1998: The unit of selection in viscous populations and the evolution of altruism. — *J. Theor. Biol.* 193: 631–648.
- West-Eberhard, M. J. 1969: The social biology of polistine wasps. — *Misc. Publ. Mus. Zool. Univ. Michigan* 140: 1–101.
- West-Eberhard, M. J. 1975: The evolution of social behavior by kin selection. — *Quart. Rev. Biol.* 50: 1–33.
- West-Eberhard, M. J. 2003: *Developmental plasticity and evolution*. — Oxford University Press.
- Wilson, O. E. 1971: *The insects societies*. — Harvard University press, Cambridge.
- Yoshikawa, K. 1963: Introductory studies on the life economy of polistine wasps. V. Three stages relating to hibernation. — *J. Biol. Osaka. City Univ.* 14: 87–96.