

Nests built on the dorsum of conspecifics in *Polistes*: the value of anomalous behaviour

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Nests are central to the colonial life of social insects, but they are less well studied than issues of dominance and reproductive caste (Ross & Matthews 1991). Unusual events sometimes reflect a greater interaction between construction and caste than most researchers appreciate. For example, intense study of *Polistes* wasps has produced repeated and provocative observations of the initiation of nests upon the dorsum of conspecific wasps in captivity. To some, this may appear to be an act of extreme domination, a view we believe is incorrect. In this paper we explain that the motions of early nest construction are similar to the motions of domination, and that the conspecific-borne nests are due to some wasps subordinating themselves to the builder because they misinterpret her actions. Thus, the nests are the result of simultaneous fulfilment of different parts of the behavioural programme by the respective wasps.

Ishay & Perna (1979) observed, apparently more than once, construction on the back of the subordinate individual of *P. gallicus* (*P. foederatus* of authors; see Day 1979, page 63, for current nomenclature). They suggested that construction of their conspecific-borne nests followed domination behaviour. They stated that 'Invariably before the α female starts to build on the thorax of the other female, the subordinate or β female, she first dominates her. This she does by beating with her antennae on the β female, while the latter assumes the subordinate position' (page 266). This interpretation does not explain why, after normal domination, the queen then proceeds to build a nest on the subordinate. Ishay & Perna proposed

that their observations suggested a 'building initiation pheromone' that determines the site of the nest and triggers building behaviour on the site. They believed that this hypothetical compound was accidentally applied to the subordinate during transport from the field to the laboratory. The existence of such a pheromone has not been supported by later work (see review by Downing 1991), and recent evidence indicates that chemical signals relevant to nest construction relate only to nestmate and nest recognition rather than to the release of specific behaviour patterns (Cervo & Turillazzi 1989; Espelie et al. 1990).

In the course of other laboratory experiments on *P. dominulus*, one of us (I.K.) observed several nests like those that Ishay & Perna (1979) built on the dorsum of conspecifics. These nests appeared in two of 15 plastic cages, two of four glass cages, but in none of 33 natural sites. Both captive and natural females were overwintered gynes that had not established dominance or a nest. The day after one to three wasps were introduced into each cage, one individual chose a specific place where she spent most of her time resting and walking locally. The wasps distinguished this locality by licking and defecating on the substrate. Normally the wasps build their nests on this 'hot spot', glueing the pulp to this specific region of the substrate (Karsai & Theraulaz 1995). Twice in plastic cages and twice in glass cages, a female added pulp to the back or wing of another wasp, but we never observed this in nature.

In cages, females that were used as substrates by other wasps often moved away from the hot spot, and if they moved as far as 15 cm the builder returned to the vicinity of the hot spot and focused her activities there. Sometimes the substrate wasp did not move from the initiation location for a long time, allowing the builder to complete the application of a load of pulp. When a cell cup (without a narrow, stalk-like pedicel)

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was complete, it became more attractive to the builder than the original hot spot, and the builder did not return to the hot spot any more. One such wasp built on the backs of both wasps with whom it shared the cage, one nest of two cells and one of a single cell. On subsequent days, the builder continued construction of the bi-cellular nest, as did the third wasp who herself supported the discontinued nest of a single cell. On the fourth day, the active nest consisted of five well-developed cells from 18 separate applications of pulp, and harboured four eggs. Although the builder spent considerable time on this nest, the substrate wasp became active and was followed around the cage by the other two animals. The substrate wasp fanned her wings frequently and dislodged the nest on the fifth day.

Two subroutines in the behavioural programme overlap in time: nest initiation and dominance. We propose that the ambiguity of the actions involved in both nest initiation and dominance are the cause of the conspecific-borne nests. In one subroutine, the incipient queen must initiate a nest on a suitable substrate. Nest initiation is generally accompanied by site preparation involving biting motions (repeated, slow mandibular openings and closings) on the chosen site, frequently involving application of minor amounts of pulp and oral secretion (Downing & Jeanne 1988, 1990; Karsai & Theraulaz 1995). Computer simulations revealed that simple behavioural rules based on local cues suffice to generate life-like nests (Karsai & Péntzes 1993; Péntzes & Karsai 1993). Early steps of nest construction are strictly controlled by the interaction between body posture and cues and constraints coming from the structure of the nest itself (Downing & Jeanne 1990; Karsai & Theraulaz 1995).

In a different subroutine, 'mauling' behaviour is common when a dominant individual suppresses a subordinate (West Eberhard 1969). This behaviour pattern involves simple biting, which is usually directed on the dorsum of the subordinate animal because the latter tucks in her appendages and may remain motionless during the attack of the incipient queen. Thus, the movement of the wasp is similar in both building and mauling despite the fact that in the first case the behavioural programme dictates the female should proceed to build a nest, and in the second she should proceed to chase or ignore the subordinate animal. Because these animals use their mandibles in similar motions in both behaviour patterns, interpretation

of their actions might be confused, particularly if the construction behaviour is towards the dorsum of the other individual. The builder begins testing the substrates near the hot spot, including the dorsum of another wasp, perhaps because the odour of the conspecific may somewhat resemble the body secretions applied to the hot spot and the body surface is rougher (more attractive) than the plastic or glass. The other wasp mistakenly interprets this as mauling and adopts a subordinate posture. The foundress can retrieve pulp and fulfil the building behaviour, and the second wasp responds to apparent mauling behaviour by remaining still. Continued building is interpreted as continued mauling, and the second wasp subordinates herself during the misunderstanding.

The opportunity to initiate a nest on another individual would rarely arise in nature because a lone female usually initiates the nest, and other wasps arrive later either to dispute her ownership or to adopt a position subordinate to her. In the absence of a nest, the designation of 'queen' and 'worker' have no meaning in species where females found nests independently, and normal dominance behaviour is evident only after a nest is established.

The fact that one queen built on both of her subordinates is noteworthy in that simultaneous foundation of multiple nests by a single female is virtually unknown in *Polistes* (Wenzel, in press; cf. Ono 1989). This observation suggests that the female may have found one nest to be unacceptable and began a new one, repeating the same steps as before. Furthermore, in this case one of the subordinates also built on the dorsum of the third wasp, suggesting that the structure was recognized as a nest by an animal not involved in the behavioural interactions that led to that specific structure.

The nests reported here and the one photographed by Ishay & Perna (1979) lack the narrow, resinous pedicel that is typical of normal nests. This omission is noteworthy because pedicel construction is known to be highly conservative, ordinarily displaying little variation (Downing & Jeanne 1986, 1988). Other nests built in similar (unusual) sites may be otherwise typical. For example, Verstraeten (1976) reported a normal, pedicelate *Polistes* nest several days old built upon the back of a live tenebrionid beetle in nature. Therefore, the lack of a pedicel in conspecific-borne nests indicates confusion in the building

programme, such that several steps are skipped during initiation. One explanation of this behaviour might be that the pedicel is normally extended until it spans a distance about equal to the gap between the substrate and the builder's mouth when she stands with her middle legs extended (Karsai & Theraulaz 1995). This distance is only slightly larger than that from the substrate to the dorsum of a crouching wasp. Therefore, the posture of the builder, when initiating on the dorsum of a conspecific, is similar to the posture that marks the transition between pedicel construction and cell construction. Thus, the initial application of pulp may be executed as if it were part of cell construction. This interpretation would not explain the non-pedicelate nests built upon the substrate by other wasp species (Wenzel 1991).

The aberrant nest construction is not rare. Four of 19 captive starting groups produced nests built on conspecifics. The frequency of such anomalies may provide critical clues to understanding normal behavioural expression. Behavioural programmes may be most easily deciphered by examining uncommon situations in which they produce so-called aberrations. Yet, even if these products are considered 'incorrect', they represent the simultaneous fulfilment of several processes of the behavioural phenotype. This report demonstrates that the intersection of similar subroutines in two complex behaviour patterns can easily explain one class of repeatedly observed aberrations, building a nest on the body of another animal. Future investigations of simple, underlying principles of the organization of complex behaviour patterns should profit from repeated observations of anomalous behaviour patterns.

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