

Nest Hydrocarbons as Cues for Philopatry in a Paper Wasp

A. Sumana*, Aviva E. Liebert*, Anne S. Berry†, Ghislaine T. Switz*, Colin M. Orians* & Philip T. Starks*

**Department of Biology, Tufts University, Medford, MA; †Oberlin College, Oberlin, OH, USA*

Abstract

Philopatric behavior has been demonstrated in a wide taxonomic spread of animals. In temperate environments, overwintered *Polistes* wasp foundresses often return to their natal nest prior to initiating colony construction. Previous research has shown that these spring foundresses can identify the natal nest in the absence of landmark and gross morphological cues. Hydrocarbons are essential recognition cues for *Polistes* nest and nestmate discrimination, but cuticular hydrocarbon profiles can become homogenized when foundresses overwinter in mixed colony groups. We examined the hydrocarbon profiles of *Polistes dominulus* foundresses and nests before and after an overwintering period, and found that the hydrocarbon profiles of nests remain unique over time and that this uniqueness is influenced by the original foundresses. Our data raise the possibility that in returning to the natal nest, foundresses reacquire their colony-specific signature, which may play a role in the formation of cooperative associations.

Correspondence: Philip T. Starks, Department of Biology, Tufts University, Medford, MA 02155, USA. E-mail: philip.starks@tufts.edu

Introduction

Philopatry is a phenomenon observed in many invertebrate and vertebrate animal species. Derived from the Greek for 'home loving', philopatry describes the tendency of animals to remain at certain locations or to return to them (Wilson 1975; Greenwood 1980). There are two forms of philopatry: one in which the animal spends its whole life at the natal site, and another in which the animal spends part of its life away from the natal site and then returns. Both types of philopatry can influence spatial characteristics of populations such as location and density, as well as the formation of social groups such as kin associations (Greenwood 1980; Wolff 1999).

The first type of philopatry, lifetime habitation in the natal territory, is a behavior that can be exhibited by one sex (male or female) or by both sexes. The

sex that is not philopatric disperses soon after birth or upon reaching reproductive maturity (Greenwood 1980). For example, female philopatry occurs in prairie dogs where males typically leave, and females remain at the natal site, whereas both male and female prairie voles are known to be philopatric (reviewed in Solomon 2003). The second type of philopatry – involving return to the natal site after a period away – occurs in animals such as salmon which return to spawning pools from the ocean (Hasler 1966), monarch butterflies which fly up to 1500 km to settle in the same tree each year (Urquhart 1960), and foundress wasps which return to natal nests after hibernation.

The philopatry observed in temperate species of *Polistes* wasps occurs in the spring, when foundresses emerging from winter diapause often return to their natal sites before initiating nest construction (reviewed in Reeve 1991). Although they return to the natal nest, spring foundresses very rarely reuse these nests. Instead, these females appear to use old nests as a perching site prior to leaving to initiate new nest construction. While the longevity of any old nest is dependent on local conditions, many nests are constructed in protected areas such as building eaves and other cavities. In such areas, nests may last years before decomposing (P.T. Starks, pers. obs.).

During the nest construction period, several different nesting tactics are available to foundresses; they can initiate nests solitarily, join cooperative nesting associations, usurp the dominant position on active colonies, or wait to adopt abandoned colonies later in the colony cycle (Reeve 1991; Nonacs & Reeve 1993; Starks 1998, 2001). Foundresses that nest cooperatively form a linear dominance hierarchy in which the dominant wasp becomes the primary egg-layer, while subordinates may receive little or no direct reproduction (West-Eberhard 1969; Queller et al. 2000; Reeve et al. 2000). Consequently, subordinates would benefit by preferentially joining relatives and gaining indirect benefits via kin selection (Hamilton 1964a,b). Indeed, many cooperative nesting associations do consist of close relatives (reviewed in Reeve 1991), and it has been suggested that philopatry acts as a mechanism to enhance the chances that foundresses will cooperate with relatives (Klahn 1979; Wenzel 1989, 1996).

Research investigating philopatry in *Polistes* wasps shows that natal nest recognition is possible even in the absence of spatial and gross morphological cues. Starks (2003) found that *Polistes dominulus* females exposed to a novel environment located and preferentially perched on fragments of their natal nest. As all landmark and gross morphological cues were removed, surface hydrocarbons on the nest paper were likely to be the cues used to recognize the natal nest fragment. Numerous studies implicate these hydrocarbons in nest recognition by foundress and worker *Polistes* wasps. When surface hydrocarbons are removed from nest paper, wasps are unable to distinguish their nest from a neighboring colony's nest (Espelie et al. 1990; Singer & Espelie 1996; Lorenzi & Caprio 2000). However, recognition ability is returned once colony-specific chemical cues are reapplied (Singer & Espelie 1996, 1997). Although it has been suggested that nest hydrocarbons may play a role in philopatry (Starks 2003; Dapporto et al. 2004a), this has not yet been tested directly. By collecting samples of hydrocarbons from

foundresses and nests in spring of 2003 and comparing these samples to those found on the same nests in spring of 2004, we tested whether the hydrocarbon cues have sufficient longevity for use in philopatry.

Methods

Colonies Studied

We collected 17 single foundress nests of *P. dominulus* from different localities in eastern Massachusetts, USA, in May–Jun. 2003 and transferred them into a 2.4×2.7 m field enclosure at the Tufts University ISIRF (International Social Insect Research Facility) in Medford, MA, USA. The field enclosure contained a central feeding site with planted vegetation to simulate the natural habitat, and wooden eaves surrounding the perimeter to provide nesting substrate. After extraction of hydrocarbons from the cuticle of foundresses (F) and from the surface paper of nests (N1), wasps were provided with honey water, building material and diced crickets ad libitum for the remainder of the colony cycle. In Aug.–Sep. 2003 all adults were collected and nests were allowed to remain undisturbed in the enclosures. Hydrocarbons were extracted from these nests again in Jun. 2004 (N2), and these samples were compared with hydrocarbons collected in the previous year.

Cuticular Hydrocarbon Extraction

Cuticular hydrocarbons (CHC) were extracted from foundresses according to the protocol described in Turillazzi et al. (1998). A similar protocol was used to extract hydrocarbons from the nest material. In brief, while the nest was being held by the pedicel, hexane-washed cotton swabs were gently rubbed on the surface of the nest and in most cells and the back of the nest for 1.5 min. The hydrocarbon-bearing cotton was placed in a 2- μ l glass gas chromatograph vial, which was stored at 4°C until analysis was initiated. The extraction of chemicals from the cotton swab was carried out as in Turillazzi et al. (1998), and a 2- μ l aliquot of the sample was injected into a Hewlett Packard 6890 Gas Chromatograph (Barnum Hall, Tufts University, Medford, MA, USA) with a column consisting of 5% phenyl methyl siloxane and measuring $30 \text{ m} \times 320 \mu\text{m} \times 0.50 \mu\text{m}$. The following temperature protocol was used for the runs: 70–150°C at a rate of 30°C/min (held for 5 min), and 150–320°C at 5°C/min (held for 13 min). The resulting retention times and integrated areas under the hydrocarbon peaks allowed us to compare different CHC signatures according to the methods used in Sledge et al. (2001) and Dapporto et al. (2004b).

Statistical Analysis

We compared the absolute number of hydrocarbons as well as the relative quantities of the most common hydrocarbons present in the N1 and N2 samples

using Wilcoxon matched-pairs tests. The most common hydrocarbons were defined as those constituting 75% of the total peak area in the chromatograph. A chi-square test was used to compare the number of hydrocarbons present in both N1 and N2 samples. To compare the change in the chemical nature of the hydrocarbons from N1 to N2, we calculated the Chromatographic Barycenter – an imaginary point corresponding to the equilibrium point of each nest's chromatogram – for each sample (see Dapporto et al. 2004b). These values were subsequently compared using a Wilcoxon matched-pairs test.

We used discriminant analysis (DA) to determine whether the pairs of nest samples (N1 and N2) and associated foundresses (F) from one colony could be distinguished from other colonies according to their CHC profiles. First, we calculated the relative area under each peak. Then, using the procedures described in Liebig et al. (2000) and Sledge et al. (2001), we transformed the relative peak areas and performed principal components analysis (PCA) to reduce the number of variables into smaller number of uncorrelated principal components. We extracted 10 of the resulting factors with eigenvalues greater than 1, which together explained 76.3% of the total variance. In addition to these 10 factors, all variables with communalities < 0.8 in the PCA were included as independent variables for the DA, resulting in a total of 24 variables used in the analysis. Euclidian distances were used to estimate the chemical distances between N1 and the foundresses and N2 and foundresses (Z-scores were used for the matrices to standardize the percentages). The differences in chemical distance were then analyzed with a Wilcoxon matched-pairs test. Discriminant analysis, PCA and calculation of Euclidian distances were all performed using SPSS 12.0 for Windows (SPSS Inc., Chicago, IL, USA), while all non-parametric tests were carried out using DataDesk 6.0 (Data Descriptions Inc., Ithaca, NY, USA).

Results

The number of hydrocarbons present on the nest did not differ across the year (Wilcoxon matched-pairs test; $n = 17$, $N1 = 20.76 \pm 21.62$, $N2 = 12.35 \pm 6.13$, $p = 0.69$). Similarly, the quantities of the most common hydrocarbons were not significantly different between N1 and N2 (Wilcoxon matched-pairs test, p range = 0.1–1). Finally, the nature of hydrocarbons on the nest did not change across the year, as measured by the Chromatographic Barycenter (Wilcoxon matched-pairs test, $n = 17$, $p = 0.44$). Combined, these data suggest that hydrocarbons are relatively stable over the time period relevant for natal nest discrimination.

N2 shared a significantly higher number of hydrocarbons with N1 than expected by chance ($\chi^2_{16} = 95.32$, $p < 0.01$). Independent DA correctly discriminated among the 17 colonies, with 100% of N1 and N2 classified correctly according to colony (Fig. 1). The first discriminant function explained 73.2% of the variance (canonical correlation = 1.0, Wilks' $\lambda = 0.0001$, $\chi^2 = 429.3$, $p = 0.0001$), and the second function explained 22% of the variance (canonical correlation = 0.94, Wilks' $\lambda = 0.0001$, $\chi^2 = 324.5$, $p = 0.0001$). When the

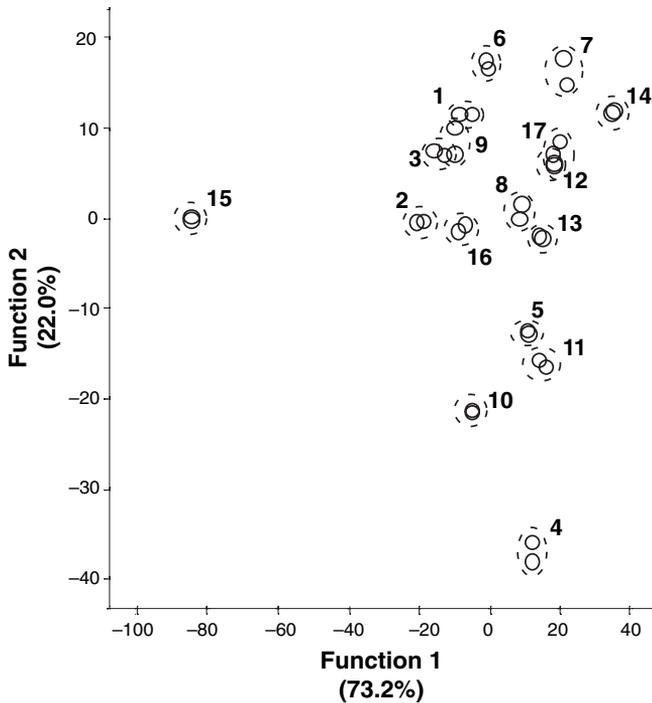


Fig. 1: Canonical discriminant functions showing the relative positions of N1 and N2 samples from 17 colonies. Percentages given on each axis indicate the amount of variance explained by each function. Small circles indicate the location of the separate N1 and N2 data for each colony, with dashed circles surrounding the N1/N2 pairs and numbers indicating the different colonies. See Results section for statistical details

foundresses were included along with the two nest measurements, DA correctly classified 98% of F, N1 and N2 to their respective colonies, with the first two discriminant functions explaining 24.5 and 19% of the total variance respectively (function 1: canonical correlation = 0.95, Wilks' $\lambda = 0.0001$, $\chi^2 = 441$, $p = 0.0001$; function 2: canonical correlation = 0.94, Wilks' $\lambda = 0.0001$, $\chi^2 = 372$, $p = 0.15$).

Discriminant analysis was also performed separately with the foundress and N1, and the foundress and N2. F and N1 were correctly classified in 100% of the cases, with the first discriminant function explaining 90.6% of the variance (canonical correlation = 1.0, Wilks' $\lambda = 0.0001$, $\chi^2 = 417$, $p = 0.0001$), and the second function explaining 7.9% of the variance (canonical correlation = 0.99, Wilks' $\lambda = 0.0001$, $\chi^2 = 291.9$, $p = 0.01$). F and N2 were also correctly classified in 100% of the cases, with the first two discriminant functions explaining 72.6 and 12.8% of the variance respectively (function 1: canonical correlation = 0.99, Wilks' $\lambda = 0.0001$, $\chi^2 = 314$, $p = 0.008$; function 2: canonical correlation = 0.98, $\chi^2 = 233$, Wilks' $\lambda = 0.0001$, $p = 0.3$). To directly measure the similarity of

the foundresses to her nest in N1 and N2, we used Euclidian distances. The distances between the F-N1 and F-N2 were not significantly different (Wilcoxon matched-pairs test, $F-N1 = 24.9 \pm 19.06$, $F-N2 = 25.2 \pm 19.49$; $p = 0.83$). Combined, these data suggest that (1) hydrocarbon profiles are unique to nests, (2) hydrocarbon profiles are maintained through the overwintering period, (3) at least part of this difference is due to profiles of individual foundresses, and (4) the similarity to the original foundresses is also maintained through the overwintering period.

Discussion

To leave a site and return after a period of time, an individual must be able to recognize the natal territory. This process likely requires that individuals form a template of the natal site, retain a memory of this template, and discriminate in favor of the natal site upon return. However, it is theoretically possible that no memory is used in this process. For example, an animal may use itself as a template in a self-referencing process (sensu Hauber & Sherman 2001) or use a template that is innate and fixed (sensu Liebert & Starks 2004). In both cases, correct discrimination is dependent on static environmental cues or, in the case of the former, any cues associated with self and site that must change in predictable and similar ways. While some environmental cues may be static (e.g. magnetic cues), most environmental cues (e.g. visual and olfactory cues) used in recognition are likely to change over time.

The cues used in recognition by *Polistes* wasps have been shown to be chemical in nature (reviewed in Gamboa 2004). Here we provide the first demonstration that hydrocarbon profiles of *P. dominulus* nests remain unique over the overwintering period, and that this uniqueness is influenced by cues associated with the original foundresses. Specifically, the number of hydrocarbons, the relative quantities of the most common of these hydrocarbons, and the chemical nature of these hydrocarbons do not differ between the time wasps leave their natal nest and when they return the following spring. Combined with previous reports (e.g. Starks 2003; Dapporto et al. 2004a), these results suggest that hydrocarbons are important in philopatry for *P. dominulus*. However, the profiles of overwintering wasps do not remain static (see Dapporto et al. 2004a), which suggests that philopatric wasps do not use a self-referencing process when discriminating in favor of their natal nest (see also Gamboa 1996, 2004). Given that nests retain their basic hydrocarbon signature (Fig. 1), and that foundress signatures can change greatly during the overwintering period (see Dapporto et al. 2004a), it is likely that philopatric females retain a memory of their natal nest.

Polistes wasps are ideal for studying recognition behavior (Gamboa 1996, 2004). Research has shown that *Polistes* wasps are capable of discriminating nestmates from non-nestmates (e.g. Gamboa et al. 1991; Fishwild & Gamboa 1992; Singer et al. 1992; Venkataraman & Gadagkar 1992; Singer & Espelie 1996, 1997; Starks et al. 1998; Pickett et al. 2000), male from female nestmates (Starks & Poe 1997), related from unrelated non-nestmates (e.g. Gamboa et al. 1987;

Gamboa 1988; Bura & Gamboa 1994), related from unrelated larvae (Panek & Gamboa 2000), and their own from foreign nests (Ferguson et al. 1987; Espelie et al. 1990; Pfennig 1990; Starks et al. 1998; Lorenzi & Caprio 2000; Starks 2003). In spite of this, *P. dominulus* spring foundresses sometimes initiate nests with non-nestmates (Queller et al. 2000).

From an evolutionary perspective, cooperating in nest founding with a non-relative may be an extreme recognition error for *P. dominulus* if one of these cooperating females is likely to forego reproduction (see Queller et al. 2000). One possible mechanism bringing about this recognition error was suggested by Dapporto et al. (2004a), where they found that hydrocarbon cues become homogenized when wasps hibernated in mixed groups. From previous studies we know that wasps indeed hibernate in groups comprising individuals from different colonies (Starks 2003; Dapporto et al. 2004a).

As suggested by Klahn (1979) and Starks (2003), natal philopatry may be a means to meet nestmates after overwintering and thus reduce the chance of forming associations with unrelated individuals. For this to work as suggested, however, spring foundresses must associate on the natal nest prior to founding a colony. Data presented here allow us to speculate that philopatry may decrease recognition errors even if eventual co-foundresses do not meet on the natal nest. Returning to the natal nest may allow individuals to reacquire their colony-specific hydrocarbon signature, which has been maintained by the nest (Fig. 1).

While it remains unclear how and if the information on the natal nest is used in recognition, our data show that unique hydrocarbon cue profiles are retained by the natal nest after the overwintering period. Given that nesting sites can be exceptionally dense (Gamboa 1978; Wenzel 1989), and given that natal nest recognition occurs in the absence of landmark and gross morphological indicators (Starks 2003), it is likely that these hydrocarbon profiles are used to discriminate the natal nest from other nests after hibernation.

Acknowledgements

We thank C. Blackie, D. Steele, and T. Zaman for help with the colony collection. S. Sakaluk and two anonymous referees provided helpful comments on an early version of this paper. Support for A. Berry was provided by an NSF REU site award (DBI-0243668).

Literature Cited

- Bura, E. A. & Gamboa, G. J. 1994: Kin recognition by social wasps: asymmetric tolerance between aunts and nieces. *Anim. Behav.* **47**, 977–979.
- 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., Theodora, P., Spacchini, C., Pieraccini, G. & Turillazzi, S. 2004b: Rank and epicuticular hydrocarbons in different populations of the paper wasp *Polistes dominulus* (Christ) (Hymenoptera, Vespidae). *Insect Soc.* **51**, 279–286.
- Espelie, K. E., Wenzel, J. W. & Chang, G. 1990: Surface lipids of social wasp *Polistes metricus* Say and its nest and nest pedicel and their relation to nestmate recognition. *J. Chem. Ecol.* **16**, 2229–2240.

- Ferguson, I. D., Gamboa, G. J. & Jones, J. K. 1987: Discrimination between natal and non-natal nests by the social wasps *Dolichovespula maculata* and *Polistes fuscatus* (Hymenoptera: Vespidae). *J. Kansas Entomol. Soc.* **60**, 65–69.
- Fishwild, T. G. & Gamboa, G. J. 1992: Colony defence against conspecifics: caste-specific differences in kin recognition by paper wasps, *Polistes fuscatus*. *Anim. Behav.* **43**, 95–102.
- Gamboa, G. J. 1978: Intraspecific defense: advantage of social cooperation among paper wasp foundresses. *Science* **199**, 1463–1465.
- Gamboa, G. J. 1988: Sister, aunt-niece, and cousin recognition by social wasps. *Behav. Genet.* **18**, 409–423.
- Gamboa, G. J. 1996: Kin recognition in social wasps. In: *Natural History and Evolution of Paper-Wasps* (Turillazzi, S. & West-Eberhard, M. J., eds). Oxford Univ. Press, Oxford, pp. 161–177.
- Gamboa, G. J. 2004: Kin recognition in eusocial wasps. *Ann. Zool. Fenn.* **41**, 789–808.
- Gamboa, G. J., Klahn, J. E., Parman, A. O. & Ryan, R. E. 1987: Discrimination between nestmate and non-nestmate kin by social wasps (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* **21**, 125–128.
- Gamboa, G. J., Foster, R. L., Scope, J. A. & Bitterman, A. M. 1991: Effects of stage of colony cycle, context and intercolony distance on conspecific tolerance by paper wasps, *Polistes fuscatus*. *Behav. Ecol. Sociobiol.* **29**, 87–94.
- Greenwood, P. J. 1980: Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
- 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.
- Hasler, A. D. 1966: *Underwater Guideposts: Homing of Salmon*. Univ. of Wisconsin Press, Madison, WI.
- Hauber, M. E. & Sherman, P. W. 2001: Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends Neurosci.* **24**, 609–616.
- Klahn, J. E. 1979: Philopatric and nonphilopatric foundress associations in the social wasp *Polistes fuscatus*. *Behav. Ecol. Sociobiol.* **5**, 417–424.
- Liebert, A. E. & Starks, P. T. 2004: The action component of recognition systems: a focus on the response. *Ann. Zool. Fenn.* **41**, 747–764.
- Liebig, J., Peeters, C., Oldham, N. J., Markstädter, C. & Hölldobler, B. 2000: Are variations in cuticular hydrocarbons of queens and workers a reliable signal of fertility in the ant *Harpegnathos saltator*? *Proc. Natl. Acad. Sci. U.S.A.* **97**, 4124–4131.
- Lorenzi, M. C. & Caprio, P. 2000: Nest recognition in neighboring colonies: a comparison of two European species of *Polistes* wasps (*P. dominulus* and *P. nimphus*, Hymenoptera: Vespidae). *J. Ethol.* **18**, 65–68.
- Nonacs, P. & Reeve, H. K. 1993: Opportunistic adoption of orphaned nests in paper wasps as an alternative reproductive strategy. *Behav. Process* **30**, 47–60.
- Panek, L. M. & Gamboa, G. J. 2000: Queens of the paper wasp *Polistes fuscatus* (Hymenoptera: Vespidae) discriminate among larvae on the basis of relatedness. *Ethology* **106**, 159–170.
- Pfennig, D. W. 1990: Nestmate and nest discrimination among workers from neighboring colonies of social wasps *Polistes exclamans*. *Can. J. Zool.* **68**, 268–271.
- Pickett, K. M., McHenry, A. & Wenzel, J. W. 2000: Nestmate recognition in the absence of a pheromone. *Insect Soc.* **47**, 212–219.
- 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.
- Reeve, H. K. 1991: *Polistes*. In: *The Social Biology of Wasps* (Ross, K. G. & Matthews, R. H., eds). Cornell Univ. Press, Ithaca, NY, pp. 99–148.
- 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.
- Singer, T. L. & Espelie, K. E. 1996: Nest surface hydrocarbons facilitate nestmate recognition for the social wasp, *Polistes metricus* Say (Hymenoptera: Vespidae). *J. Insect. Behav.* **9**, 857–870.
- Singer, T. L. & Espelie, K. E. 1997: Exposure to nest paper hydrocarbons is important for nest recognition by a social wasp, *Polistes metricus* Say (Hymenoptera, Vespidae). *Insect Soc.* **44**, 245–254.

- Singer, T. L., Camann, M. A. & Espelie, K. E. 1992: Discriminant analysis of cuticular hydrocarbons of social wasp *Polistes exclamans* Viereck and nest surface hydrocarbons of its nest paper and pedicel. *J. Chem. Ecol.* **18**, 785–797.
- Sledge, M. F., Boscaro, F. & Turillazzi, S. 2001: Cuticular hydrocarbons and reproductive status in the social wasp *Polistes dominulus*. *Behav. Ecol. Sociobiol.* **49**, 401–409.
- Solomon, N. G. 2003: A reexamination of factors influencing philopatry in rodents. *J. Mammal.* **84**, 1182–1197.
- Starks, P. T. 1998: A novel 'sit and wait' reproductive strategy in social wasps. *Proc. R. Soc. Lond. B* **265**, 1407–1410.
- Starks, P. T. 2001: Alternative reproductive tactics in the paper wasp *Polistes dominulus* with specific focus on the sit-and-wait tactic. *Ann. Zool. Fenn.* **38**, 198–199.
- Starks, P. T. 2003: Natal nest discrimination in the paper wasp, *Polistes dominulus*. *Ann. Zool. Fenn.* **40**, 53–60.
- Starks, P. T. & Poe, E. S. 1997: 'Male-stuffing' in wasp societies. *Nature* **389**, 450.
- 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.
- Turillazzi, S., Sledge, M. F. & Moneti, G. 1998: Use of a simple method for sampling cuticular hydrocarbons from live social wasps. *Ethol. Ecol. Evol.* **10**, 293–297.
- Urquhart, F. A. 1960: *The Monarch Butterfly: International Traveler*. Univ. of Toronto Press, Toronto.
- Venkataraman, A. & Gadagkar, R. 1992: Kin recognition in a semi-natural context: behavior towards foreign conspecifics in the social wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *Insect Soc.* **39**, 285–299.
- Wenzel, J. W. 1989: Endogenous factors, external cues and eccentric construction in *Polistes annularis* (Hymenoptera: Vespidae). *J. Insect Behav.* **2**, 679–699.
- Wenzel, J. W. 1996: Learning, behaviour programs, and higher-level rules in nest construction of *Polistes*. In: *Natural History and Evolution of Paper-Wasps* (Turillazzi, S. & West-Eberhard, M. J., eds). Oxford Univ. Press, pp. 58–74.
- West-Eberhard, M. J. 1969: The social biology of polistine wasps. *Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1–101.
- Wilson, E. O. 1975: *Sociobiology: the New Synthesis*. The Belknap Press of Harvard Univ. Press, Cambridge, MA.
- Wolff, J. O. 1999: Behavioral model systems. In: *Landscape Ecology of Small Mammals* (Barrett, G. W. & Peles, J. D., eds). Springer-Verlag, New York, pp. 11–40.

Received: October 1, 2004

Initial acceptance: November 11, 2004

Final acceptance: November 19, 2004 (S. Sakaluk)