ISSN 0013-8738, Entomological Review, 2011, Vol. 91, No. 7, pp. 820–827. © Pleiades Publishing, Inc., 2011.
Original Russian Text © L.Yu. Rusina, L.A. Firman, I.Yu. Rusin, Ch.K. Starr, 2011, published in Entomologicheskoe Obozrenie, 2011, Vol. 90, No. 3, pp. 514–523.

Pulp Partitioning and Worker Specialization in Polistine Wasps (Hymenoptera, Vespidae, Polistinae)

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Received May 22, 2011

Abstract—The character of pulp partitioning was studied in three Palaearctic polistine wasps (*Polistes dominula* and *P. gallicus* in the Black Sea Biosphere Reserve, and *Polistes nimpha* in the Lugansk Nature Reserve, Ukraine) and in five Neotropical species (*P. lanio*, *P. versicolor*, *Mischocyttarus injucundus*, *M. alfkeni*, *Metapolybia cingulata*, and *Protopolybia exigua* in Trinidad). In independent-founding *Polistes* and *Mischocyttarus* species, all cases of pulp partitioning were connected with aggression on the part of the foundresses. An experimental increase of nesting density of *P. dominula* led to changes in the relative abundance of workers in the polyethic task groups. Some workers practically stopped hunting and switched over to pulp delivery; some of these workers possessed well-developed ovaries and were able to lay eggs. The experimentally removed part of the nest envelope in the swarm-founding wasp *Metapolybia cingulata* was restored only in colonies that included young workers. The specific features of nest building activity in independent-founding and swarm-founding polistine wasps are discussed.

DOI: 10.1134/S0013873811070025

The nest-building behavior of polistine wasps is related to some specific traits of colony organization and functioning, described by Jeanne (1991) in terms of independent-founding and swarm-founding, and by Zakharov (1991) in terms of resociality and nomosociality.

The independent-founding species are characterized by small open nests and colonies with an annual life cycle. A special role in the organization of their colonies belongs to postimaginal caste determination leading to incomplete separation of two functional spheres: reproductive and supplying. The age-related polyethism and individual specialization of workers are weakly developed in independent-founding polistine wasps and strongly developed in swarm-founding species, including those with relatively small colonies (Jeanne, 1991a, 1991b).

The workers of independent-founding species start foraging at the age of several days and combine foraging with in-nest activities during their entire lifespan. The foragers bring food (nectar and prey) and building materials (wood pulp and water) into the nest. The water is also used for cooling the nest. The division of labor among the workers manifests itself both in preference for a particular kind of foraging (polyethism) and in the manner of processing the load (task partitioning): the forager either performs all the subsequent actions itself, or passes its load partly or completely to other members of the colony. In some independent-founding species the loads are more frequently passed to other workers as the colony grows (Post et al., 1988; Rusina, 2006). In addition, the foragers of these wasps more readily pass food than building materials.

Specialization of workers with respect to the ways of handling prey and preferences for building activity was described in *Polistes fuscatus* (F.) (Post et al., 1988), in which three functional groups could be distinguished: (1) workers that prefer hunting to building and tend to pass proteinaceous food to other individuals; (2) workers that deliver building materials and do not pass prey to other workers; and (3) non-foraging workers occupied exclusively by in-nest activities. A similar pattern of specialization was observed in *P. dominula* (Christ), *P. nimpha* (Christ), and *P. gallicus* (L.); however, in the last two species the active builders were involved in the establishment and maintenance of the workers' dominance structure (Rusina, 1999, 2006). The dominant workers of *Mischocyttarus mastigophorus* Richards more frequently collect building materials and obtain proteinaceous food from the prey foragers than the subordinate individuals do (O'Donnell, 1998a).

It was shown that the colonies of *P. dominula* nesting on plants more often included specialized prey foragers, as compared to those nesting in shelters (Rusina, 2006). These differences may be accounted

for by the influence of food availability or nesting density on the foraging activity. The results of an experimental assessment of one of these factors, namely the nesting density, are reported in this communication.

In the swarm-founding wasp species with a high level of social organization, the specialization of workers results from age-related polyethism; in addition, such species are characterized by individual specialization of foragers. The handling of the delivered loads (building materials, water, prey, and nectar) in these wasps is completely subdivided into 2 subtasks: collection and utilization. The foragers of two functional groups bring food (prey and nectar) and building materials (wood pulp and water) into the nest and pass them to other workers. An individual forager may deliver either one specific kind or both kinds of loads during its entire active period. If a forager switches to a different kind of load, it more frequently belongs to the same functional group (food or nest materials). The preference for a particular kind of loads was found to be more stable in larger colonies of *Polybia occidentalis* (Olivier) and *Metapolybia* spp. (Jeanne, 1986b; Karsai and Wenzel, 1998, 2000). There are data indicating that the workers of *Polybia aequatorialis* (Zavattari) with the same foraging specialization are genetically close (O'Donnell, 1996a, 1998b).

Since the specific traits of building activity and its organization have been described only in a few species of polistine wasps, we decided to study these aspects in 3 Palaearctic and 6 Neotropical species.

MATERIALS AND METHODS

The foraging behavior of 271 workers from 14 colonies of *Polistes gallicus* and 325 workers from 17 colonies of *P. dominula* was analyzed in the Black Sea Biosphere Reserve (BSR) (Ukraine, Kherson Prov.; Ivano-Rybalchanskii and Solenoozernyi plots, 46°25′ and 46°27′N, 32°07′ and 31°59′E, respectively) in June–August 2003–2009. Similar studies of 232 workers from 17 colonies of *P. nimpha* were made in the Lugansk Nature Reserve (LNR) (Ukraine, Lugansk Prov.; Provalskaya steppe, 48°8′N, 39°49′E) in July 2009. From October 25, 2004 to January 16, 2005 a similar analysis was carried out for 12 foragers from 3 colonies of *Mischocyttarus alfkeni* (Ducke), 27 foragers from 1 colony of *M. injucundus* (Saussure), 4 foragers from 2 colonies of *P. lanio* (F.), 16 foragers from 4 colonies of *P. versicolor* (Olivier), 328 foragers from 5 colonies of *Metapolybia cingulata* (F.), and 147 foragers from 2 colonies of *Protopolybia exigua* (Saussure) nesting in Caura settlement, 18 km from St. Augustine, Trinidad Island (10°41′N, 61°22′W).

The demography of the colonies was described using the nest mapping method (description of the brood composition in the cells) and individual marking of adult wasps (foundresses, workers, and males) (Rusina, 2006).

The daily activity of *Metapolybia cingulata* and *Protopolybia exigua* was observed during 4 days, from 6 a.m. to 7 p.m. local time. The specific traits of foraging activity of different wasp species were studied daily from 8.30 to 4 p.m. local time. The recorded parameters included the kind of the delivered load and the different variants of its handling in the nest: (1) the forager processed its load itself, (2) it passed part of the material to another individual (foundress and/or worker), or (3) it passed the entire load to another individual. In variants 2 and 3, other colony members were involved in communication.

The relation between the way of handling building materials and the colony size in *Polistes nimpha* (each colony observed for 2 h), *P. gallicus*, and *P. dominula* (2 or 3 colonies observed for 6 h every year) was analyzed using the Spearman correlation test.

The influence of nesting density on the preference for collecting building materials or hunting in *P. dominula* foragers was studied in a field experiment performed in BSR in June 2005. The colonies discovered in May–June were transferred to cages and left at their original nesting sites. Two wasp settlements were selected in which the nests were positioned more than 15 m apart. During the night, 2 nests were installed close to one original (resident) nest in such a way that 3 nests appeared within an area of 1 m^2. The preferences for particular kinds of foraging and ways of load handling were analyzed in the resident colonies before and after the density was artificially increased. The following polyethic groups were distinguished: (1) builders: the workers that preferred to collect paper pulp and did not pass proteinaceous food to other colony members after hunting; (2) prey foragers: the foragers that delivered proteinaceous food more often than paper pulp; (3) generalized foragers that combined hunting and delivery of building materials in an approximately equal proportion; (4) nectar foragers; (5) water foragers; and (6) in-nest workers (Rusina, 2006). The occurrence of workers from different polyethic groups was compared by χ^2 criterion.

The specialization of workers in the swarm-founding species *Metapolybia cingulata* and *Protopolybia exigua* was studied by removing (1) a part of the nest envelope and (2) the most active foragers from the recently swarmed colonies (3 colonies of *M. cingulata* and 1 of *P. exigua*) and mature ones (3 of *M. cingulata* and 1 of *P. exigua*).

The total duration of observations was 402 h; in all, 1343 episodes of a forager arriving with a load of building material were recorded.

In case of a normal distribution of characters, the sample is characterized in the text by the mean M ± the mean square deviation SD, and in case of a non-normal distribution, by the median Me [25; 75] (where 25 and 75 are the 1st and the 3rd quartiles) (Glantz, 1999). The minimum and maximum values [min; max] are also provided. The results were processed using the Statistica v. 6.0 package (Statsoft, Inc. USA 1984–2001).

RESULTS

The Independent-founding Species of Polistine Wasps

The way of handling building material. The arrival of a forager with a load is followed by a series of behavioral elements that are similar in different species. Unlike the highly variable ways of handling prey and nectar, the process of nest building is largely the same in the species studied. It includes the following elements: delivery of paper pulp–chewing–seeking the construction place (when moving over the area, the foundress may perform wagging and/or tapping movements with its abdomen)–grasping of the complete batch of material or some part of it by the foundress–construction of the petiole, cell base, or cell wall. However, contrary to what is observed in *Polistes dominula*, the foundresses of *P. nimpha* and *P. gallicus* (and also workers of the latter species) wag their abdomens while keeping the batch of pulp in their mandibles and looking for a suitable place to apply it.

In all the species studied, only food was shared by the foragers whereas batches of building material or water were utilized by the same workers which had brought them. The foundress sometimes took the nest material (partly or completely) from the forager. Such behavior was observed in all the independent-founding wasp species except *P. lanio* and *Mischocyttarus injucundus*; however, the difference may be due to a small duration of observations and a small number of studied colonies of these species.

It should be noted that such behavior was more frequently recorded in foundresses with high fecundity. In particular, *P. nimpha* colonies in the territory of LNR were characterized by the following parameters during the study period: nest size 95 [62; 114] [49; 192] cells (here and below, the data are shown as the median, quartiles, and the minimum and maximum values Me [25; 75] [min; max]), number of workers 12 [8; 18] [4; 32], number of eggs 25 [11; 32] [5; 40], number of young instar larvae 6 [5; 10] [1; 14], number of old instar larvae 14 [10; 23] [4; 28], number of pupae 19 [9; 22] [6; 32]. The frequency of arrivals of workers with building material was on average 3 (maximum 7) per hour.

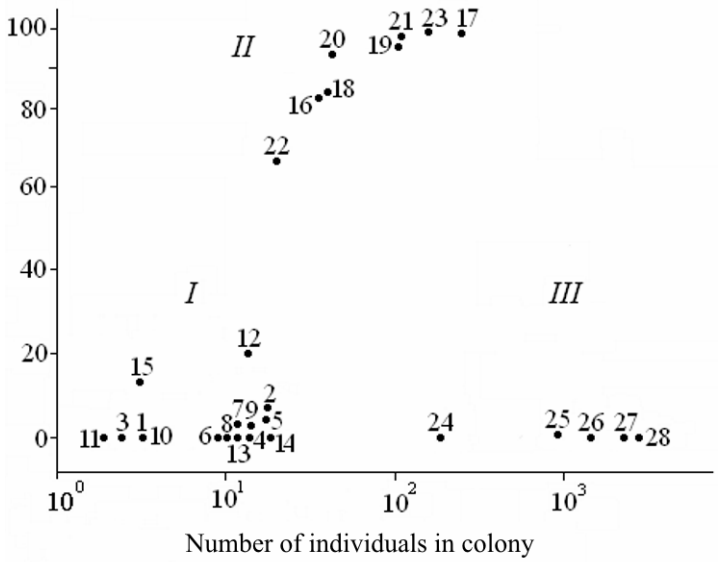
The number of eggs in the nest (characterizing the fecundity of the foundresses) was found to be positively correlated with the nest size and the number of pupae and workers (r_s = 0.76, 0.68, and 0.66; n = 17; $0.001 < p < 0.01$, respectively).

Besides, the foundresses in larger nests of *P. nimpha* (considering the number of cells, workers, eggs, and pupae) more frequently took building material from the foragers that brought it to the nest (r_s = 0.80, 0.85, 0.77, and 0.72; n = 17; $0.0001 < p < 0.05$, respectively).

During the periods of population growth in the territory of BSR (2003 and 2008), when the wasp colonies were almost twice as large as during the population peak and decline (2004–2007 and 2009), the cases of foundresses taking nest material away from the workers were 1.5 times as frequent in *P. gallicus* and 4 times as frequent in *P. dominula*. The frequency of this event was found to be positively correlated with the colony size in *P. gallicus* (r_s = 0.69; $p < 0.05$) and with a number of workers in the nest in *P. dominula* (r_s = 0.73; $p < 0.01$).

The effect of nesting density on specialization of workers. No cases of building material being taken away from workers were observed. The relative abundance of workers of different polyethic groups changed during the experiment (χ^2 = 11.41; df = 5; $p < 0.05$) (see table).

The workers which had hunted and delivered building material in almost equal proportions before the experiment, switched to bringing material into the nest. The active builders almost completely stopped



The ways of handling nest material in colonies of social wasps (after Jeanne, 2003, with additions). (*I*) Independent-founding species of the subfamily Polistinae: *Polistes fuscatus* (F.) (after Downing and Jeanne, 1987) (*1*, *2*), *P. instabilis* Saussure (after Downing and Jeanne, 1987) (*3*), *P. gallicus* (L.) (*4*, *5*), *P. dominula* (Christ) (*6*, *7*), *P. nimpha* (Christ) (*8*, *9*) (Lugansk Nature Reserve, Ukraine, July 2009), *P. versicolor* (Olivier) (*10*), *P. lanio* (F.) (*11*), *Mischocyttarus drewseni* (Saussure) (after Jeanne, 1972) (*12*), *M. mastigophorus* Richards (after O'Donnell, 1998) (*13*), *M. injucundus* (Saussure) (*14*), *M. alfkeni* (Ducke) (*15*). (*II*) Swarm-founding species of the subfamily Polistinae: *Polybia occidentalis* (Olivier) (after Jeanne, 1986) (*16*, *17*), *Protopolybia exigua* (Saussure) (*18*, *19*), *Metapolybia aztecoides* Richards (after Karsai and Wenzel, 1998) (*20*), *M. mesoamerica* Smethurst et Carpenter (after Karsai and Wenzel, 1998) (*21*), *M. cingulata* (F.) (*23*). (*III*) Species of the subfamily Vespinae: *Vespula atropilosa* (Sladen) (here and below, after Jeanne, 2005) (*24*), *V. germanica* (F.) (*25*), *V. pensylvanica* (Saussure) (*26*), *V. squamosa* (Drury) (*27*), *V. vulgaris* (L.) (*28*). (*5*, *7*) The original data, the Black Sea Biosphere Reserve, Ukraine, June–July 2003–2009; (*10*, *11*, *14*, *15*, *19*, *23*) Trinidad Island, October–January 2004–2005. Ordinate: frequency of complete transfer of building material, %.

hunting. For example, before the experiment the foragers brought 4–12 loads of nest material and 1–4 loads of prey, whereas after the experiment they delivered 9–18 loads of nest material and only 0–1 loads of prey. Five cases of oviposition were observed in the nest-building workers; 345 out of a total of 494 acts of dominant behavior (69.8%) by the foundresses were directed towards these workers. The tips of their wings were damaged as a result of aggressive attacks by the foundresses. Dissection of 3 builders from nest no. 80 revealed well-developed ovaries and mature eggs; however, these individuals had empty spermathecae and therefore did not mate.

The Swarm-founding Species of Polistine Wasps

Among the 75 discovered nests of *Metapolybia cingulata*, 3 (4%) were at the stage preceding the emergence of workers of the new generation (the nests were 5–9 cm long); in 21 nests (28%) the workers had already emerged (15–62 cm); the remaining nests were abandoned (68%). Most of abandoned nests (over 70%) were 3–10 cm long; these colonies must have been founded in the preceding years and died at the early stages of development.

The earliest foragers leave the nests of *M. cingulata* and *Protopolybia exigua* at about 6 a.m. local time, and the foraging stops after 7 p.m. The maximum foraging activity was recorded from 11 to 12 a.m. For large colonies of *M. cingulata* this parameter reached on average 42 departures and 34 arrivals for 10 min of observation, and for small colonies, 12 and 10, respectively. The corresponding parameters for *P. exigua* were 37, 29 and 16, 14. Although the activity of wasps decreased in rainy weather, the delivery of food and nest material did not stop completely.

The degree of worker specialization correlated with the colony age. The young colonies of *M. cingulata* and *P. exigua* included 2–5 gatherers of nest material, which comprised over 5% of individuals. Besides the nest material, these foragers also brought water. The nest material was completely passed from one individual to another in 82.2% of cases in *P. exigua* (37 out of 45 cases observed), more frequently than in *M. cingulata* (69.7%, 46 of 66) (see figure). This may be related to the size of the freshly swarmed colony of *P. exigua* that included over 90 ind. In two weeks, the workers constructed an open nest with 303 cells on a leaf of *Dracaena fragrans* (L.).

The composition of polyethic groups of workers of *Polistes dominula* before (1) and after (2) an experimental increase in the nesting density

Polyethic groups	Occurrence of workers, %			
	colony no. 80		colony no. 53	
	1	2	1	2
Builders	11.54	42.87	8.33	29.63
Prey foragers	23.08	10.71	16.67	14.81
Generalized foragers	46.15	28.57	33.33	25.93
Nectar foragers	15.38	10.71	25	18.52
Water foragers	3.85	3.57	4.17	7.41
In-nest workers	0	3.57	12.5	3.70
Total	26	28	24	27

After the emergence of workers in large colonies, the foragers usually become specialized in delivering only one type of material. The gatherers of nest material do not build the nest themselves but pass the material to 1–3 builders which distribute it among several workers. The frequency of transfer of complete batches of nest material was higher after the appearance of the new generation of workers in all the species studied: 97.6% (84 of 86 cases) in *P. exigua* and 98.3% (238 of 242) in *M. cingulata* (see figure).

When the envelopes were removed from nests of 3 small colonies of *M. cingulata*, only one, the largest nest was restored. The remaining two nests were abandoned, 6–8 workers remaining in each of them. In 3 large nests containing workers of the new generation, the experimentally removed envelopes were restored. The swarming colonies seem to be more sensitive to nest damage.

In the second experiment, when the pulp foragers were removed from large colonies, they were functionally replaced by workers 15–17 days old which had previously nursed the brood; some of them had also participated in nest construction.

DISCUSSION

The most complex organization of communities and regulation of foraging activity among wasps are observed in the swarm-founding species characterized by swarm-founded colonies, decentralized control, and separation of the two functional spheres (Jeanne, 1991a, 1991b, 2003; Zakharov, 1991). The colonies of independent-founding species mostly display centralized regulation of the workers' activities, including the nest construction (Jeanne, 2003). The previous publications and our original data (see figure) show that the pulp foragers seldom pass their loads to other individuals. In such cases the wood pulp is usually taken by the foundress. Since the frequency of such behavior of the foundress is positively correlated with the colony size, it may be determined by individual parameters of the foundress, in particular its fecundity.

Our experiments show that the workers of *Polistes dominula* have a low level of individual specialization and that the colony activity in this species is regulated by redistribution of foraging tasks between individuals. For example, an experimental increase in the nesting density led to an increase in the fraction of workers gathering paper pulp, and also to development of ovaries in some of them. This fact also indicates an incomplete separation of the reproductive and support spheres.

In general, an increase in the functional group of builders and more frequent aggressive contacts between them and the foundress may serve as a mechanism of density regulation at the colony level of organization.

The intra- and interspecific differences in the polyethic groups of workers, and also the relation between polyethism and dominance hierarchy seem to represent adaptations to the particular nesting place (Jeanne, 1972; Strassmann et al., 1984; Downing and Jeanne, 1987; Post et al., 1988; O'Donnell, 1995, 1996b; Rusina, 2006). The colonies of swarm-founding wasp species do not pass through the independent-founding phase; their nests have envelopes and are founded by swarms consisting of the reproductive individuals and workers. The functioning of such colonies is not limited by the lifespan of the reproductives; they are char-

acterized by preimaginal caste differentiation, a complete separation of the two functional spheres, and decentralized forms of control of foraging activity.

The workers of nomosocial species of ants compete for particular functions in the colony (Zakharov, 1991). In-nest activity was shown to be the preferred function (Zakharov, 1981, 1991). For example, after experimental removal of hunters from the colony of *Cataglyphis setipes* F. they were functionally replaced by some in-nest workers. When the hunters were returned to the colony, they resumed their former activity whereas some of the new foragers reverted to in-nest activities (Zakharov, 1975). Thus, a certain hierarchy of individuals is present not only in the reproductive sphere but also in the support sphere in these ants. Nobody has yet raised the question whether such a phenomenon is typical of wasps as well, since the attention of most researchers remains focused on the reproductive competition and kin selection.

According to Jeanne (2003), the principal difference between independent-founding and swarm-founding species lies in the ways of handling the loads. A complete transfer of material in swarm-founding polistine wasps allows the development of age-related polyethism and a more complex colony organization.

Anderson and co-authors (Anderson and McShea, 2001; Anderson et al., 2001) considered the degree of required cooperation and coordination as a measure of complexity of the colony organization. The lowest level of complexity distinguished by these researchers is an individual one; it includes some tasks performed by an individual that do not require cooperation or coordination with other individuals (for example, nest construction by independent-founding wasps). At the group level of complexity, two or more individuals perform the same task and should act in a coordinated manner to reach their goal (for example, several ants dragging the same load). The team level also implies the activity of two or more individuals; however, in this case the work is subdivided into a certain number of subtasks which should be performed in a coordinated manner (for example, nest construction by weaver ants). Finally, at the level of partitioned activity, two or more subtasks should be performed not simultaneously (as at the team level) but consecutively (for example, the foragers collect nectar while the in-nest workers process and store it). This scheme was used by Jeanne (2003) for comparative analysis of groups of wasps. Since all the foraging acts in independent-founding polistine wasps are performed at the individual level, the social structure of their colonies is simpler. Even though *Ropalidia marginata* (Lepeletier), unlike other independent-founding species, displays a distinct age-related polyethism, its foragers still utilize the pulp and prey themselves, at least partly (Naug and Gadagkar, 1998; Gadagkar, 2001; Naug, 2001), i.e., the subdivision of building tasks is optional in these wasps. It is only in case of complete separation of labor that some workers may become specialized to foraging, and others, to in-nest activities (Jeanne, 1986a; Anderson and Ratnieks, 1999).

The building activity in swarm-founding polistine wasps is not only subdivided into delivery of paper pulp and construction proper, but also involves the transport of water by specialized workers. This work may thus be regarded as activity at the team level. Moreover, the loads of pulp delivered by the gatherers are usually too large to be used directly in construction, so that the foragers have to pass at least part of the pulp to the in-nest workers which then distribute it among themselves (Jeanne, 1986b; O'Donnell and Jeanne, 1990; Karsai and Wenzel, 1998).

The quantitative differences between the independent-founding and swarm-founding species in the frequency of complete transfer of building materials are shown in figure. In *Polybia* and *Metapolybia* wasps, the load of material brought to the nest by a forager is 6–8 times as large as the batch that can be processed by a single builder. The high efficiency of material transportation would be impossible without sharing the load with the builders (Jeanne, 1986b; Karsai and Wenzel, 2000; our data). The delays resulting from the foragers of *Polybia* waiting for their turn to pass the load are compensated for by lower energy costs of transportation (Jeanne, 1986b). The queues facilitate regulation of the number of foragers and "storekeepers" in response to the changing external conditions (Ratnieks and Anderson, 1999). It is interesting that in *Metapolybia* the building activity is regulated by water carriers (Karsai and Wenzel, 2000).

The nests of *Metapolybia* wasps have envelopes with translucent windows, possibly made of exocrine secretions (Vesey-FitzGerald, 1938). If we assume that the secretion is produced by young workers, this will explain the restoration of the envelope in large colonies that have raised offspring of the new generation. In our opinion, each swarm of *M. cingulata* has a unique age composition of workers, similar to what was observed in *M. azteca* Araujo (Forsyth, 1981).

Relatively high mortality of colonies before emergence of the new generation of workers is related to the elimination of pulp foragers and the absence of young workers in the swarm.

The mechanisms of organization of building activity in swarm-founding wasps have been studied in two genera only. The representatives of the genera *Protopolybia* Ducke, *Agelaia* Lepeletier, *Brachygastra* Perty, and *Parachartergus* von Ihering, which are the most diverse and the most important for understanding the evolution of sociality in wasps, should also be studied from this viewpoint.

ACKNOWLEDGMENTS

The authors are very grateful to the management and staff of the Black Sea Biosphere Reserve and the Lugansk Nature Reserve for their help in carrying out this research. We are grateful to O. Maksimova, E. Orlova, and A. Gulak (Kherson State University), and also to Sarah Bharat, Bobby and Susanne Bissoondial (Trinidad).

REFERENCES

1. Anderson, C., Franks, N.R., and McShea, D.W., "The Complexity and Hierarchical Structure of Tasks in Insect Societies," Anim. Behav. **62**, 643–651 (2001).
2. Anderson, C. and McShea, D.W., "Individual versus Social Complexity, with Particular Reference to Ant Colonies," Biol. Rev. **76**, 211–237 (2001).
3. Anderson, C. and Ratnieks, F.L.W., "Task Partitioning in Insect Societies. 1. Effect of Colony Size on Queuing Delay and Colony Ergonomic Efficiency," Amer. Nat. **154**, 521–535 (1999).
4. Downing, H.A. and Jeanne, R.J., "A Comparison of Nest Construction Behavior in Two Species of *Polistes* Paper Wasps (Insecta, Hymenoptera: Vespidae)," J. Ethol. **5**, 53–66 (1987).
5. Forsyth, A.B., "Swarming Activity of Polybiine Social Wasps (Hymenoptera: Vespidae: Polybiini)," Biotropica **13**, 93–99 (1981).
6. Gadagkar, R., *The Social Biology of Ropalidia marginata: Toward Understanding the Evolution of Eusociality* (Harvard Univ. Press, Cambridge, MA, 2001).
7. Glantz, S.A., *Primer of Biostatistics*, 4th Ed. (McGraw-Hill Inc., New York, 1997; Praktika, Moscow, 1999) [in Russian].
8. Jeanne, R.L., "Social Biology of the Neotropical Wasp *Mischocyttarus drewseni*," Bull. Mus. Comp. Zool. Harvard Univ. **144**, 63–150 (1972).
9. Jeanne, R.L., "The Evolution of the Organization of Work in Social Insects," Monit. Zool. Ital. N. S. **20**, 119–133 (1986a).
10. Jeanne, R.L., "The Organization of Work in *Polybia occidentalis*: Costs and Benefits of Specialization in a Social Wasp," Behav. Ecol. Sociobiol. **19**, 333–341 (1986b).
11. Jeanne, R.L., "The Swarm-Founding Polistinae," in *The Social Biology of Wasps*, Ed. by K.G. Ross and R.W. Matthews (Cornell Univ. Press, New York, 1991a), pp. 191–231.
12. Jeanne, R.L., "Polyethism," in *The Social Biology of Wasps*, Ed. by K.G. Ross and R.W. Matthews (Cornell Univ. Press, New York, 1991b), pp. 389–425.
13. Jeanne, R.L., "Regulation of Nest Construction Behavior in *Polybia occidentalis*," Anim. Behav. **52**, 473–488 (1996).
14. Jeanne, R.L., "Social Complexity in the Hymenoptera with Special Attention to the Wasps," in *Genes, Behaviors and Evolution of Social Insects*, Ed. by T. Kikuchi, N. Azuma, and S. Higashi (Hokkaido Univ. Press, Sapporo, 2003), pp. 81–130.
15. Karsai, I. and Wenzel, J.W., "Productivity, Individual-Level and Colony-Level Flexibility, and Organization of Work as Consequences of Colony Size," Proc. Natn. Acad. Sci. USA **95**, 8665–8669 (1998).
16. Karsai, I. and Wenzel, J.W., "Organization and Regulation of Nest Construction Behavior in *Metapolybia* Wasps," J. Insect Behav. **13**, 111–140 (2000).
17. Naug, D., "Ergonomic Mechanisms for Handling Variable Amounts of Work in Colonies of the Wasp *Ropalidia marginata*," Ethology **107**, 1115–1123 (2001).
18. Naug, D. and Gadagkar, R., "The Role of Age in Temporal Polyethism in a Primitively Eusocial Wasp," Behav. Ecol. Sociobiol. **42**, 37–47 (1998).
19. O'Donnell, S., "Division of Labor in Post-Emergence Colonies of the Primitively Eusocial Wasp *Polistes instabilis* de Saussure (Hymenoptera: Vespidae)," Insectes Soc. **42**, 17–29 (1995).
20. O'Donnell, S., "RAPD Markers Suggest Genotypic Effects on Forager Specialization in a Eusocial Wasp," Behav. Ecol. Sociobiol. **38**, 83–88 (1996a).
21. O'Donnell, S., "Reproductive Potential and Division of Labor in Wasps: are Queen and Worker Behavior Alternative Strategies?" Ethol. Ecol. Evol. **8**, 305–308 (1996b).
22. O'Donnell, S., "Dominance and Polyethism in the Eusocial Wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae)," Behav. Ecol. Sociobiol. **43**, 327–331 (1998a).
23. O'Donnell, S., "Genetic Effects on Task Performance, but Not on Age Polyethism, in a Swarm-Founding Eusocial Wasp," Anim. Behav. **55**, 417–426 (1998b).
24. O'Donnell, S. and Jeanne, R.L., "Forager Specialization and the Control of Nest Repair in *Polybia occidentalis* Olivier," Behav. Ecol. Sociobiol. **27**, 359–364 (1990).
25. Post, D.C., Jeanne, R.L., and Erickson, H.E., "Variation in Behavior among Workers of the Primitively Social

Wasp *Polistes fuscatus variatus*," in *Interindividual Behavior Variability in Social Insects*, Ed. by R.L. Jeanne (Westview, Boulder, 1988), pp. 283–321.

26. Ratnieks, F.L.W. and Anderson, C., "Task Partitioning in Insect Societies," Insectes Soc. **46**, 95–108 (1999).
27. Rusina, L.Yu., "Task Partitioning in Polistine Wasps (Hymenoptera, Vespidae)," Vestnik Zool. **33** (1–2), 105–108 (1999).
28. Rusina, L.Yu., *Polistine Wasps in Natural and Anthropogenic Landscapes of the Lower Dnieper Area* (Kherson Gos. Univ., 2006) [in Russian].
29. Strassmann, J.E., Meyer, D.C., and Matlock, R.L., "Behavioral Castes in the Social Wasps, *Polistes exclamans*," Sociobiology **8**, 211–224 (1984).
30. Vesey-FitzGerald, D., "Social Wasps (Hymenoptera, Vespidae) from Trinidad, with a Note on the Genus *Trypoxylon* Latreille," Trans. R. Ent. Soc. London **87**, 181–191 (1938).
31. Zakharov, A.A., "Functional Groups and Competition between Individuals in a Colony of the Ant *Cataglyphis setipes turcomanica*," in *Problems of Zoopsychology, Ethology and Comparative Psychology* (Mosk. Gos. Univ., Moscow, 1975), pp. 47–49 [in Russian].
32. Zakharov, A.A., "Behavioral Organization of an Ant Colony," in *N.A. Kholodkovsky Memorial Lectures* (Nauka, Leningrad, 1981), pp. 34–58 [in Russian].
33. Zakharov, A.A., *Organization of Ant Communities* (Nauka, Moscow, 1991) [in Russian].