

Modes of Colony Foundation by Females of Different Morphotypes in the Paper Wasps (Hymenoptera, Vespidae, *Polistes* Latr.)

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Abstract—Paper wasps of the genus *Polistes* exhibit wide variability both of the color and size of foundresses, and the mode of colony foundation. The colony foundation and social hierarchy were studied in populations of two Palearctic species, *Polistes dominulus* (Christ) and *P. nimphus* (Christ) (April–May 2006, the Crimean Peninsula, Ukraine), and one Neotropical species, *P. lanio* (F.) (October 2004–January 2005, Trinidad Island). It was shown that foundresses of various color and size morphs tended to found nests in a peculiar way: singly (haplometrosis), by groups (pleometrosis), or occupying several nests simultaneously (polycaly). The relationship between coloration, size, and mode of colony foundation was species-specific. *P. dominulus* foundresses with a darker clypeus and a paler mesonotum preferred to found nests alone and had a dominant position in pleometrosis. The haplometrotic *P. nimphus* foundresses more often displayed darker variants of the clypeus and paler variants of the mesonotum than did foundresses from pleometrotic colonies. *P. lanio* foundresses from pleometrotic colonies differed from those from polycalic colonies in the coloration variability of the scutum, propodeum, and the 2nd metasomal tergite. The dominant and subordinate *P. nimphus* and *P. lanio* foundresses differed in the size of head and wings. The possible significance of the subdivision of foundresses into the “generalists” and “specialists” for the variability structuring in the population is considered.

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In the course of evolution, the social polistine wasps have acquired various adaptations aimed at colony survival and increasing population stability. Adaptations to particular ecological situations are mostly manifested in changes in the spatio-ecological population structure and the colony life cycle (including the time of nesting), modes of colony foundation, duration of the nesting period, and the colony size (Strassmann, 1983; Gobbi and Zucchi, 1985; Jeanne and Morgan, 1992; Rusina, 2006). Studies of the population structure at early stages of the life cycle have shown that in the temperate latitudes, a nest can be founded either by a single female (haplometrosis) or by several foundresses (pleometrosis) (West-Eberhard, 1969; Röseler, 1985; Reeve, 1991). The colonies with several foundresses are known to be more viable and productive, and to start producing workers earlier (Gamboa, 1980; Grechka and Kipyatkov, 1984); such colonies are less frequently usurped by conspecific females and can better protect the brood from invertebrate predators (Gamboa, 1978; Gibo, 1978; Strassmann, 1981a; Röseler, 1991; Rusina, 2003). In addition, several fe-

males can more effectively restore the nest if it is destroyed (Gibo, 1978). Pleometrosis is the prevalent mode of nest foundation in the tropical zone (West-Eberhard, 1969; Giannotti and Mansur, 1993); in some species, several nests are founded and used by a group of females (Jeanne, 1979; Giannotti and Machado, 1994). This phenomenon can be regarded as polycaly in an expanded meaning of the term (which commonly refers to one colony using several nests simultaneously—Zakharov, 1991). At early stages of colony formation, all the females lay eggs even though the individual fecundity varies. Later, the dominant female establishes reproductive control over the others (Pardi, 1948; West-Eberhard, 1969). The dominant individuals in a pleometrotic colony have more strongly developed ovaries and a higher level of endocrine activity (Turillazzi and Pardi, 1977; Röseler et al., 1980, 1984, 1985, 1986; Turillazzi et al., 1982; Sullivan and Strassmann, 1984). In some species the dominant females are usually larger than the subordinate ones (*Polistes dominulus* (Christ), Turillazzi and Pardi, 1977; *P. metricus* Say, Dropkin and Gamboa, 1981;

P. fuscatus (F.), Noonan, 1981). However, in *P. dominulus* this trend was found to vary from year to year (Turillazzi and Pardi, 1977) or was not observed at all (Cant and Field, 2001). No such trend was observed in *P. annularis* (L.) (Sullivan and Strassmann, 1984).

The population organization of paper wasps is poorly studied. This is true, for example, of those behavioral differences among *P. dominulus* foundresses that are marked with coloration characters. The spatio-ethological structure (distribution of nesting females in the microhabitats, nest density within an aggregation, and the number of subordinate females in a colony) was shown to be correlated with the phenotypic structure, and that both can change depending on the ecological situation. During the depression and population growth phases, pleometrotic colonies can be formed by females of different coloration morphs. At the population peak, however, there are distinct differences in the frequencies of mesonotal patterns between the females nesting in aggregates and the solitary ones, and also between the females from haplo- and pleometrotic colonies (Rusina et al., 2007). Long-term studies of the spatio-temporal variability in *P. dominulus* and *P. gallicus* (L.) have shown that the coloration and pattern polymorphism is dynamically stable: the proportion of morphs among the prospective foundresses in autumn remains nearly the same, but changes strongly in spring and in the course of seasonal development (Rusina et al., 2005, 2006). Although coloration variability was recorded in many species of polistine wasps (Enteman, 1904), its signal role in the family was studied only in *P. fuscatus* and *P. dominulus* (Tibbets, 2002; Tibbets and Dale, 2004), while its organization at the population level remains little known.

The aim of this work was to study the interrelations between the coloration and body size of the foundresses and the mode of colony foundation in two Palaearctic and one Neotropical species of polistine wasps.

MATERIALS AND METHODS

Foundresses of *P. dominulus* were captured in Kurortnoe settl. (Theodosia District, the Crimea, Ukraine, 44°59'N, 34°21'E) in late April, 2006, and transferred into cages together with their nests. Foundresses of *P. nimphus* (Christ) were captured in Yalta (44°29'N, 34°08'E) and Simferopol (44°57'N, 34°06'E) in the first ten days of May, 2006. The nesting of *P. lanio*

(F.) was studied in the environs of St. Augustine (Trinidad Island, 10°38'N, 61°26'W), in Lopino (10°42'N, 61°09'W) and Cora (10°41'N, 61°22'W) settlements, and also at the University of the West Indies agricultural station (10°38'N, 61°26'W) in October 2004–January 2005.

The coloration variants of the clypeus, mesosoma (functional thorax), and metasoma (functional abdomen) were recorded visually in 106 females of *P. dominulus*, 126 females of *P. nimphus*, and 58 females of *P. lanio*, with standard drawings as reference (Figs. 1–3). The correlation between the coloration of foundresses and the preference for a particular mode of colony foundation was estimated using a χ^2 test. Analysis of the mode of colony foundation included the quantitative composition of females in the colony and the number of nests used. In addition, we recorded the cases of haplometrosis (one female building one nest), pleometrosis (a group of females founding one nest), and polycolony in the broad sense (a group of females founding several nests). The hierarchy of dominance was studied by laboratory observation of the behavior of females from pleometrotic colonies of *P. dominulus* (18 colonies), *P. nimphus* (23), and *P. lanio* (9). Each colony was observed for 30–60 min every day during 2–3 days, within the time interval from 10 a.m. to 4 p.m. The total duration of observations was 108 h. The dominant females were recognized by specific forms of their behavior related to the reproductive monopoly at the level of oogenesis (dominant behavior), oviposition (filling of empty cells), and embryogenesis (differential oophagy) (West-Eberhard, 1969). The hierarchical structure of the colony was determined based on the interactions of females, considering the linear hierarchy. The female showing dominant behavior toward any other female by feeling its head, mesosoma, metasoma, and wings, was regarded as an α -individual; the wasp acting as a dominant toward all other members of the colony except the α -female was considered a β -female; the γ -females behaved as a dominant toward all individuals except α and β , and so on (Pardi, 1948; Röseler, 1991, Rusina, 1999). The subordinate status of a female was expressed by a specific posture (with body pressed to the substrate and antennae lowered) and by avoiding contacts.

The sizes of foundresses of different ranks and coloration morphs were compared in wing and head preparations of 88 ind. of *P. dominulus*, 95 ind. of *P. nimphus*, and 34 ind. of *P. lanio*, made according to

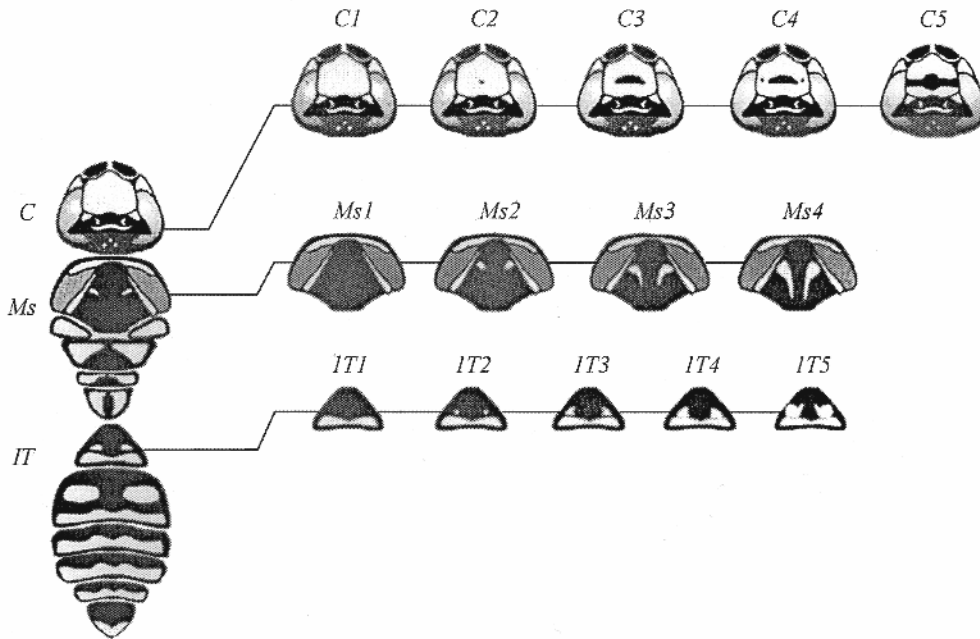


Fig. 1. Coloration variants in the female of *Polistes dominulus* (Christ): variants of the clypeus (C), mesonotum (Ms), and the first abdominal tergite (IT).

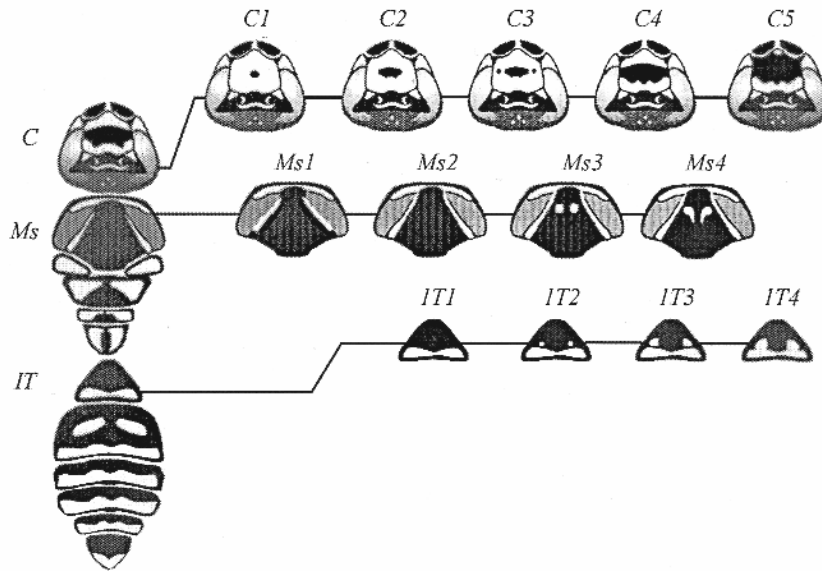


Fig. 2. Coloration variants in the female of *Polistes nimphus* (Christ): variants of the clypeus (C), mesonotum (Ms), and the first abdominal tergite (IT).

special techniques (Dlusskii et al., 1998; Perfil'eva, 2000). The scanned drawings of the heads and wings were measured within the Corel Draw 8.0 software to determine the following parameters: the length (CL) and width (CW) of the clypeus, the maximum width of the head (HW), and the length and width of fore and hind wings (WgIL, WgIW, WgIIL, WgIIW, respectively) (Fig. 4). In case of a normal distribution of characters, the data are shown in the text and tables as

the mean M (with a 95% confidence interval in parentheses) and the mean square deviation s ; in case of a non-normal distribution, the data are presented as the median Me [25; 75] (where 25 and 75 are the 1st and the 3rd quartiles). The body sizes of females from two independent samples were compared using the Student test (for normal distribution) or the Mann-Whitney test (for non-normal distribution); the related samples were compared using the Wilcoxon test; the multiple com-

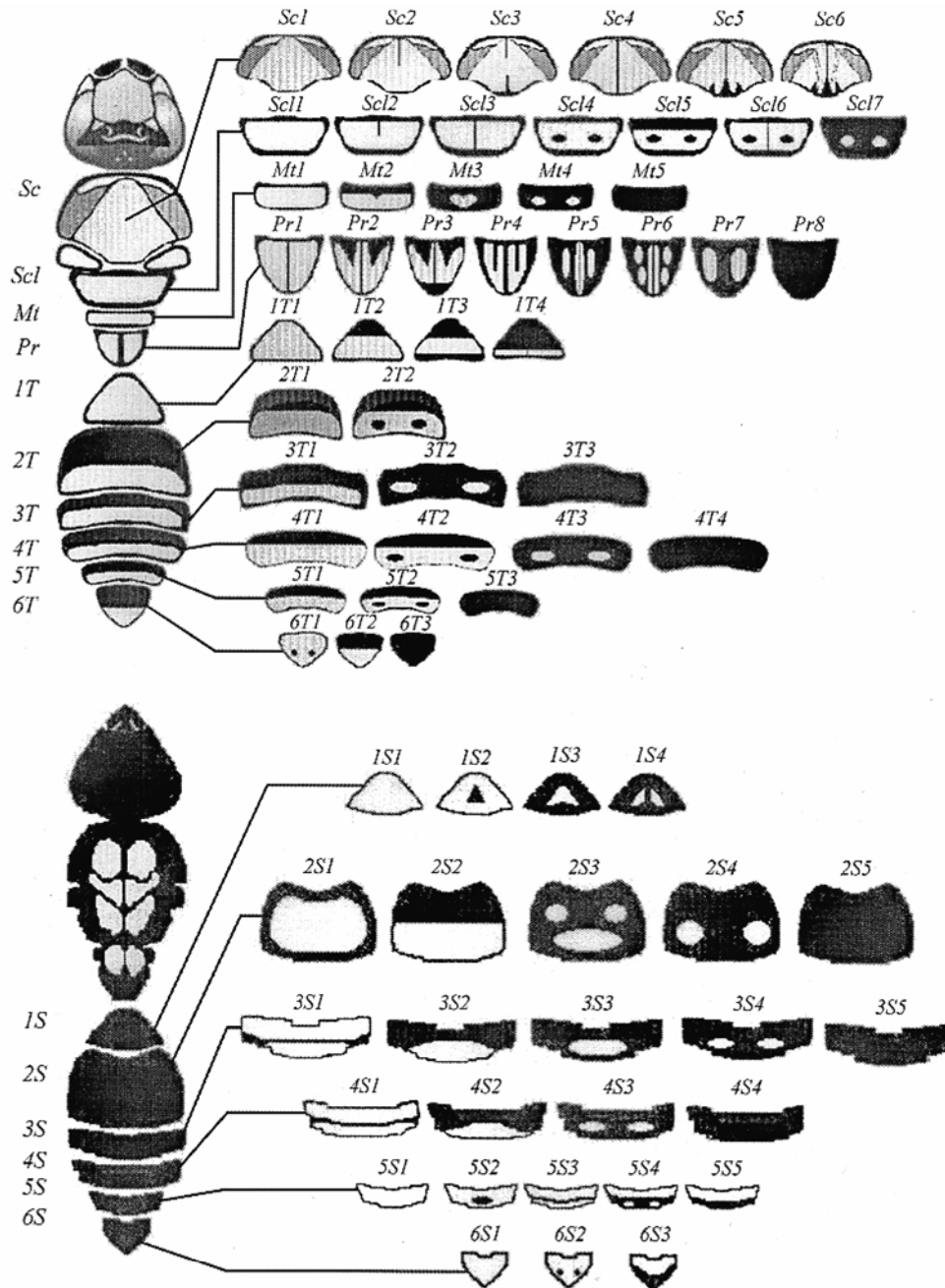


Fig. 3. Coloration variants in the female of *Polistes lanio* (F.): variants of the scutum (*Sc*), scutellum (*Scl*), metanotum (*Mt*), propodeum (*Pr*), first to sixth abdominal tergites (*1T*–*6T*), and the first to sixth abdominal sternites (*1S*–*6S*).

parison was made using the Dunn's test (Glantz, 1999). The distribution of social ranks among females of different coloration morphs was compared using the χ^2 test. In order to reveal the possible relation between the morphological and ethological characters, the Spearman's rank correlation coefficient was calculated: (a) between body size and rank of females, (b) between coloration and rank, and (c) between coloration and size of females within the population and

within a colony. The data were processed using the Statistica 6.0 package (StatSoft Inc., 1984–2001) and the Biostatistica 4.03 software (S.A. Glantz, McGraw Hill; Russian translation by Praktika, 1998).

RESULTS

Mode of Colony Foundation and Type of Nesting

P. dominulus. The period of colony sampling and observations coincided with the initial stages of nest-

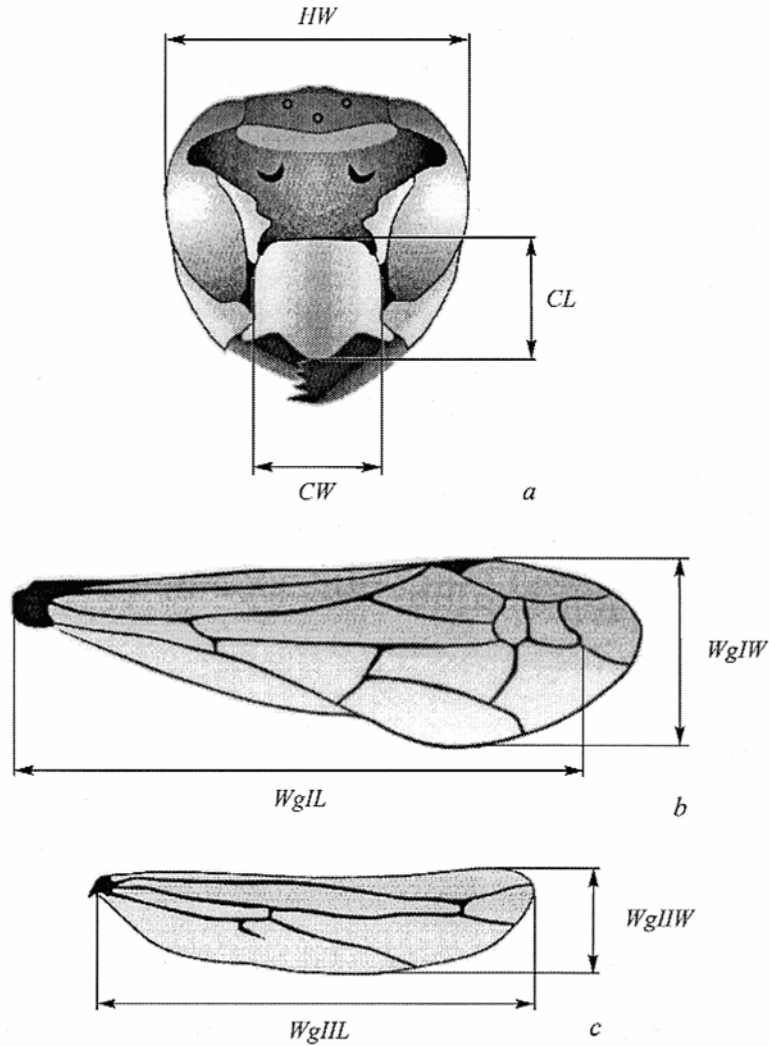


Fig. 4. Measurements of the head and wings of paper wasp females (*Polistes*): head (a), fore wing (b), and hind wing (c). The abbreviations *HW*, *CL*, *CW*, *WgIL*, *WgIW*, *WgIIL*, and *WgIIW* are explained in the *Materials and methods* section.

ing. In all, 57 nests were found in shelters and one on a plant. The preferred nesting shelters were metal pipes used as frames for fences; 8 nests (14%) were found under the roofs. The fraction of pleometrotic colonies was 31.6% (18/57) (Table 1). Some females (18/122, 14.8%) had not started nesting but occurred near those building the nests. The maximum number of females in a pleometrotic colony was 10, and the fraction of large colonies, comprising 5 or more females, was 11.1 % (2/18). The nest size varied from 2 to 13 cells; eggs were present in the brood.

P. nimphus. In all, 85 colonies of this species were found in the attics of 6 apartment buildings in Simferopol and Yalta during the first ten days of May. The fraction of pleometrotic colonies was 27.1% (23/85) (Table 1). The nests comprised on the average 10 (4–20) cells, containing eggs and young instar lar-

vae. Two colonies did not build their own nests but used old ones, remaining from the preceding year. These nests were small (92 and 104 cells) and contained wintering cocoons of the parasitoid wasp *Lati-bulus argiolus* Rossi (Hymenoptera, Ichneumonidae) (7 and 6 cocoons, respectively). The maximum number of females in a pleometrotic colony was 10, and the fraction of large colonies, comprising 5 or more females, was 4.3% (1/23).

P. lanio. In all, 80 nests were found in various anthropogenic shelters and 3 on plants. The colonies were at different stages of development: 42 before and 41 after emergence of workers (Table 2). At the agricultural station of the University of West Indies, mass nesting was recorded in the middle ten days of November. The wasps nested under the roof, in utility rooms, and under the floors of buildings standing on

Table 1. Colony foundation in *Polistes dominulus* and *P. nimphus* in the Crimea (April and early May, 2006)

Species	Haplometrosis	Pleometrosis				Total
		2 females	3 females	4 females	≥ 5 females	
<i>P. dominulus</i>	39	12	2	2	2	57
<i>P. nimphus</i>	62	14	6	2	1	85

Table 2. Composition of *Polistes lanio* colonies on Trinidad Island

Collection site and date	Before emergence of workers						After emergence of workers
	1 female	2 females	3 females	4 females	≥ 5 females	polycaly	
University of the West Indies agriculture station, 30.X.2004	4	3	6	1	4	2	2*
Trinidad, Lopino settl., 9.I.2005	1	1	3	–	2	1	22
Environs of St. Augustine, 24–26.XII.2004	–	1	3	3	–	–	12
Cora settl., 17.XI.2004	1	1	2	1	2	–	5

Note: * no brood; adult males present in the nest.

piles. The nests contained eggs and young instar larvae. The maximum number of females in a pleometrotic colony was 6, and in a polycalic colony, 8. The latter category included colonies using 2–3 nests each.

Coloration of Foundresses and the Type of Nesting

The coloration variants of foundresses of the species studied are given in Tables 3 and 4. The females from colonies founded in different ways showed different frequencies of coloration morphs. The females of *P. dominulus* founding haplometrotic colonies showed a higher frequency of mesosomal variant *M2*, as compared to the females from pleometrotic colonies (Tables 3, 5). This trend became even more evident when foundresses from small (2–3 females) and large (more than 3 females) colonies were compared (Tables 3, 5). Females from small colonies differed significantly from haplometrotic females in the frequencies of coloration morphs. The non-nesting females resembled haplometrotic ones in the frequencies of coloration characters, but differed considerably from pleometrotic ones in having a larger fraction of mesosomal character *IT4* (Tables 3, 5).

The haplo- and pleometrotic females of *P. nimphus* differed in the frequencies of color morphs of the mesonotum and clypeus. The solitary nesting females of *P. nimphus* had a significantly larger fraction of the dark variant of the clypeus *C5* and a paler variant of the mesonotum *Ms2* than did pleometrotic females (Tables 3, 5). Females from small colonies (2–3 ind.)

did not differ from haplometrotic ones, whereas females from larger colonies (4–40 ind.) differed from haplometrotic ones in the coloration of the clypeus and mesosoma: they had a larger fraction of variant *C3*, while that of the mesosomal variant *Ms2* was smaller, and the frequency of *Ms1* was higher (Tables 3, 5). Females from small colonies more often showed clypeal variant *C5* and less often *C3*, as compared to females from large colonies; no differences were observed in the coloration of the mesosoma and abdomen (Tables 3, 5).

Females of *P. lanio* from pleometrotic colonies and those founding polycalic colonies, collected at the University of the West Indies agricultural stations, differed in the frequencies of color morphs of the scutum, propodeum, and the 2nd abdominal tergite (Tables 4, 5). Females from polycalic colonies more often showed variants *Sc5* of the scutum, *Pr2* of the propodeum, and *2T1* of the 2nd abdominal tergite, and less often, the corresponding variants *Sc6*, *Pr3*, and *2T2*.

Size and Coloration of Females in the Colony

The foundresses of *P. dominulus* and *P. nimphus* with different color morphs showed no difference in size in the colonies studied. However, such differences were observed in pleometrotic *P. dominulus* females but not in haplometrotic ones (Table 6). The wings and heads were smaller in females with pale variants of the clypeus (*C1* and *C2*) than in those with darker variants (*C3*, *C4*, and *C5*). Individuals with mesonotum variant *Ms4* exceeded those with *Ms2* in the

Table 3. Incidence of different coloration variants (%) in *Polistes dominulus* and *P. nimphus* foundresses from haplometrotic and pleometrotic (large and small) colonies

Clypeus					Mesonotum				Abdomen				
<i>Cl</i>	<i>C2</i>	<i>C3</i>	<i>C4</i>	<i>C5</i>	<i>Ms1</i>	<i>Ms2</i>	<i>Ms3</i>	<i>Ms4</i>	<i>IT1</i>	<i>IT2</i>	<i>IT3</i>	<i>IT4</i>	<i>IT5</i>
<i>P. dominulus</i> , haplometrosis (<i>N</i> = 41)													
7.3	19.5	53.7	7.3	12.2	0	22.0	58.5	19.5	0	2.4	80.5	14.6	2.5
<i>P. dominulus</i> , pleometrosis (<i>N</i> = 47)													
2.1	10.7	68.1	2.1	17.0	2.1	14.9	61.7	21.3	0	0	91.5	8.5	0
Non-nesting <i>P. dominulus</i> females (<i>N</i> = 18)													
5.6	22.2	55.5	11.1	5.6	0	44.4	44.4	11.2	0	0	66.7	33.3	0
<i>P. dominulus</i> females from small colonies (<i>N</i> = 26)													
3.8	11.5	65.4	3.8	15.5	3.8	19.2	73.2	3.8	0	0	100	0	0
<i>P. dominulus</i> females from large colonies (<i>N</i> = 21)													
0	9.5	71.5	0	19.0	0	9.5	47.6	42.9	0	0	81.0	19.0	0
High rank <i>P. dominulus</i> females (<i>N</i> = 28)													
3.6	10.7	60.7	3.6	21.4	0	10.7	78.6	10.7	0	0	96.4	3.6	0
Low rank <i>P. dominulus</i> females (<i>N</i> = 9)													
0	22.2	55.6	0	22.2	0	22.2	44.4	33.4	0	0	66.7	33.3	0
<i>P. nimphus</i> , haplometrosis (<i>N</i> = 62)													
0	0	6.5	3.2	90.3	43.5	51.6	4.9	0	11.3	27.4	56.5	4.8	0
<i>P. nimphus</i> , pleometrosis (<i>N</i> = 64)													
0	0	26.6	0	73.4	71.9	25	3.1	0	21.9	37.5	39.1	1.5	0
<i>P. nimphus</i> females from small colonies (<i>N</i> = 46)													
0	0	19.6	0	80.4	67.4	30.4	2.2	0	17.4	45.7	34.8	2.1	0
<i>P. nimphus</i> females from large colonies (<i>N</i> = 18)													
0	0	44.4	0	55.6	83.3	11.1	5.6	0	33.3	16.7	50	0	0
High rank <i>P. nimphus</i> females (<i>N</i> = 41)													
0	0	24.4	0	75.6	68.3	26.8	4.9	0	14.6	46.4	36.6	2.4	0
Low rank <i>P. nimphus</i> females (<i>N</i> = 17)													
0	0	29.4	0	70.6	82.4	17.6	0	0.1	41.2	23.5	35.3	0	0

Notes: *Cl*–*C5* are the coloration variants of the clypeus, *Ms1*–*Ms4*, those of the mesonotum, and *IT1*–*IT5*, those of the abdomen.

clypeus and head width and in the length of both wing pairs.

In *P. nimphus*, pleometrotic females with abdomen variants *IT1* and *IT2* had smaller wings but a larger head and clypeus as compared to those with variant *IT3* (Table 7). In case of haplometrosis, females with abdomen variants *IT1* exceeded those with variant *IT3* in the width of head and hind wings (Mann-Whitney test for *HW*: $p = 0.036$; for *WgIIW*: $p = 0.036$).

The pleometrotic females of *P. lanio* with propodeum variants *Pr2*, *Pr3*, and *Pr4* exceeded those with variant *Pr6* in the width of head and hind wings (Table 8).

The haplo- and pleometrotic females of *P. dominulus* and *P. nimphus* differed in size (Tables 9, 10). The haplometrotic females of *P. dominulus* had smaller heads (*CL*) than did the females from pleometrotic colonies (Mann-Whitney test for *CL*: $p < 0.05$). The haplometrotic females of *P. nimphus* had larger wings but smaller heads than did pleometrotic ones (Mann-Whitney test for *WgIW*: $p < 0.01$; for *HW*: $p < 0.01$; for *CW*: $p < 0.04$). *P. nimphus*, unlike *P. dominulus*, revealed statistically significant correlations between the mode of colony foundation and the size of the foundresses (for *WgIW*: $r_s = 0.29$, $n = 95$, $p < 0.01$; for *CW*: $r_s = 0.38$, $n = 95$, $p < 0.05$; for *HL*: $r_s = -0.38$, $n = 95$, $p < 0.01$).

Table 4. Incidence of different coloration variants (%) of *Polistes lanio* foundresses in cases of pleometrosis and polycaly, and also in females of different ranks

Groups of females or type of colony foundation	Scutum						Scutellum							Metanotum					
	1	2	3	4	5	6	1	2	3	4	5	6	7	1	2	3	4	5	
Pleometrosis (N = 14)	0	0	0	0	14.3	85.7	0	0	100	0	0	0	0	0	28.6	71.4	0	0	
Polycaly (N = 10)	0	0	0	0	70	30	0	0	100	0	0	0	0	0	80	10	10	0	
High rank females (N = 9)	0	0	0	88.9	0	11.1	0	0	100	0	0	0	0	0	33.3	66.7	0	0	
Low rank females (N = 25)	0	0	0	60	4	28	0	0	100	0	0	0	0	0	48	48	4	0	
	Propodeum							1st abdominal tergite				2nd abdominal tergite		3rd abdominal tergite					
	1	2	3	4	5	6	7	8	1	2	3	4	1	2	1	2	3		
Pleometrosis (N = 14)	0	7.2	50	28.6	0	7.2	0	0	0	100	0	0	50	50	64.3	0	35.7		
Polycaly (N = 10)	0	80	10	10	0	0	0	0	0	100	0	0	90	10	80	0	20		
High rank females (N = 9)	0	22.2	22.2	22.2	0	33.4	0	0	0	100	0	0	77.8	22.2					
Low rank females (N = 25)	0	24	32	16	4	16	8	0	0	100	0	0	88	12					
	4th abdominal tergite				5th abdominal tergite			6th abdominal tergite			1st abdominal sternite				2nd abdominal sternite				
	1	2	3	4	1	2	3	1	2	3	1	2	3	4	1	2	3	4	5
Pleometrosis (N = 14)	92.9	7.1	0	0	71.4	28.6	0	0	7.1	92.9	28.6	0	0	71.4	0	0	0	100	0
Polycaly (N = 10)	100	0	0	0	90	10	0	0	0	100	50	0	0	50	0	0	0	100	0
	3rd abdominal sternite					4th abdominal sternite				5th abdominal sternite					6th abdominal sternite				
	1	2	3	4	5	1	2	3	4	1	2	3	4	5	1	2	3		
Pleometrosis (N = 14)	0	0	0	100	0	0	0	100	0	0	0	0	85.7	14.3	0	100			
Polycaly (N = 10)	0	0	0	100	0	0	0	100	0	0	0	0	100	0	0	100			

Notes: For the cases of pleometrosis (6 colonies) and polycaly (2 colonies), the frequencies of color variants of foundresses collected at the agricultural station of the University of West Indies are given. The frequencies of color variants of females of different ranks were determined from 9 colonies collected before the emergence of workers near St. Augustine and in Cora and Lopino settlements; 1–8 are the coloration variants.

Dominant Rank, Size, and Coloration of Females in the Colony

The rank of foundresses in the species studied revealed no dependence on their coloration: a low rank individual from one colony and an α -female from another colony could be of the same color morph. *P. dominulus* females of high (α and β) and low ranks (γ and below) did not differ from haplometrotic fe-

males in the frequencies of color variants. The high rank females of *P. dominulus* showed a significantly higher frequency of abdomen variant *IT3* and a significantly lower frequency of variant *IT4* (Tables 3, 10). No statistically significant correlations were observed between the rank and coloration or between the rank and size in pleometrotic *P. dominulus* females. However, the color variants of the mesonotum and the

Table 5. Comparison of the coloration pattern of foundresses in different groups of paper wasps (*Polistes*): χ^2 test

Female groups or types of colony foundation	Pattern characters		
	Clypeus	Mesonotum	Abdomen
Haplo- and pleometrosis, <i>P. dominulus</i>	3.06; <i>df</i> = 4; <i>p</i> = 0.548	12.94; <i>df</i> = 4; <i>p</i> = 0.012	1.49; <i>df</i> = 3; <i>p</i> = 0.685
Haplo- and pleometrosis, <i>P. nimphus</i>	10.81; <i>df</i> = 2; <i>p</i> = 0.005	10.45; <i>df</i> = 2; <i>p</i> = 0.005	6.16; <i>df</i> = 3; <i>p</i> = 0.104
Haplometrosis and colonies with 2 females, <i>P. dominulus</i>	0.93; <i>df</i> = 4; <i>p</i> = 0.920	5.63; <i>df</i> = 2; <i>p</i> = 0.060	4.49; <i>df</i> = 3; <i>p</i> = 0.213
Haplometrosis and colonies with 2 females, <i>P. nimphus</i>	4.30; <i>df</i> = 2; <i>p</i> = 0.116	4.98; <i>df</i> = 2; <i>p</i> = 0.083	3.09; <i>df</i> = 3; <i>p</i> = 0.379
Haplometrosis and colonies with 5–9 females, <i>P. dominulus</i>	5.12; <i>df</i> = 4; <i>p</i> = 0.276	4.27; <i>df</i> = 2; <i>p</i> = 0.118	1.19; <i>df</i> = 3; <i>p</i> = 0.755
Haplometrosis and colonies with 5–9 females, <i>P. nimphus</i>	16.04; <i>df</i> = 2; <i>p</i> < 0.001	9.60; <i>df</i> = 2; <i>p</i> = 0.008	5.79; <i>df</i> = 3; <i>p</i> = 0.122
Colonies with 2 females and those with 3–8 females, <i>P. dominulus</i>	2.79; <i>df</i> = 4; <i>p</i> = 0.593	11.00; <i>df</i> = 2; <i>p</i> = 0.004	
Colonies with 2–4 females and those with 5–9 females, <i>P. nimphus</i>	4.11; <i>df</i> = 1; <i>p</i> = 0.042	2.86; <i>df</i> = 2; <i>p</i> = 0.239	5.56; <i>df</i> = 3; <i>p</i> = 0.135
Haplometrosis and non-nesting females, <i>P. dominulus</i>	0.87; <i>df</i> = 4; <i>p</i> = 0.929	3.17; <i>df</i> = 2; <i>p</i> = 0.240	3.34; <i>df</i> = 3; <i>p</i> = 0.342
Pleometrosis and non-nesting females, <i>P. dominulus</i>	5.59; <i>df</i> = 4; <i>p</i> = 0.232	6.72; <i>df</i> = 3; <i>p</i> = 0.081	6.16; <i>df</i> = 1; <i>p</i> = 0.013
	Scutum	Propodeum	2nd abdominal tergite
Pleometrosis and polycaly, <i>P. lanio</i>	7.73; <i>df</i> = 1; <i>p</i> = 0.005	9.29; <i>df</i> = 2; <i>p</i> = 0.01	13.31; <i>df</i> = 4; <i>p</i> = 0.004

Note: Statistically significant differences are shown in bold.

size of wings and heads were found to be correlated (for *WgIL*: $r_s = 0.55$, $n = 47$, $p < 0.05$; for *WgILL*: $r_s = 0.64$, $n = 47$, $p < 0.01$; for *HW*: $r_s = 0.55$, $n = 47$, $p < 0.05$).

P. nimphus females of both high (α and β) and low rank (γ and below) differed from haplometrotic females in the frequencies of color variants of the clypeus and mesonotum: they had smaller fractions of variants *C5* of the clypeus and *Ms2* of the mesonotum, and larger fractions of variants *C3* and *Ms1*. However, α -females of *P. nimphus* resembled the haplometrotic ones in the coloration characters but differed considerably from the low rank individuals in the coloration

of clypeus and mesonotum (Tables 3, 10). The rank was correlated with the color of mesonotum ($r_s = -0.41$, $n = 42$, $p < 0.05$) and with the clypeus width ($r_s = -0.46$, $n = 42$, $p < 0.05$). In addition, in each particular colony of *P. nimphus* the relative intensity of abdomen coloration was correlated with the female's position in the hierarchy: $\chi^2 = 7.54$, $df = 2$, $p = 0.021$.

Foundresses of different ranks from *P. nimphus* and *P. dominulus* colonies comprising 2 females each (14 and 12 colonies, respectively) did not differ in size.

In *P. dominulus* colonies with several foundresses (6 colonies), no difference in size was observed be-

Table 6. Size of the head and wings of the pleometrotic foundresses of *Polistes dominulus* with different coloration variant of the clypeus and mesonotum

Parameters	Coloration characters			Multiple group comparison (Dunn's test)		
	clypeus			C1–C2 vs. C3	C1–C2 vs. C4–C5	C3 vs. C4–C5
	C1–C2, <i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 13)	C3, <i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 32)	C4–C5, <i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 10)			
<i>WgIL</i>	10.8 (10.61–11.06); 0.692	11.4 [11.1; 11.6]	11.2 (10.89–11.48); 0.594	**	*	<i>n. s.</i>
<i>WgIW</i>	3.9 (3.82–3.96); 0.218	4.0 [3.9; 4.2]	4.0 (3.95–4.14); 0.188	**	*	<i>n. s.</i>
<i>WgIIL</i>	8.1 [7.6; 8.4]	8.3 [8.3; 8.5]	8.3 (8.08–8.57); 0.459	**	*	<i>n. s.</i>
<i>WgIIW</i>	2.1 (2.07–2.17); 0.156	2.3 [2.2; 2.3]	2.2 (2.09–2.25); 0.161	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CL</i>	1.5 (1.44–1.52); 0.105	1.5 (1.48–1.59); 0.075	1.6 (1.51–1.59); 0.086	<i>n. s.</i>	*	<i>n. s.</i>
<i>CW</i>	1.6 (1.59–1.65); 0.079	1.7 (1.65–1.72); 0.067	1.7 (1.63–1.70); 0.073	**	*	<i>n. s.</i>
<i>HW</i>	3.7 (3.69–3.70); 0.145	3.8 (3.78–3.91); 0.123	3.8 (3.75–3.9); 0.113	*	*	<i>n. s.</i>
	Mesonotum					
	<i>Ms2</i> (<i>N</i> = 12)	<i>Ms3</i> (<i>N</i> = 33)	<i>Ms4</i> (<i>N</i> = 10)	<i>Ms2</i> vs. <i>Ms3</i>	<i>Ms2</i> vs. <i>Ms4</i>	<i>Ms3</i> vs. <i>Ms4</i>
<i>WgIL</i>	10.5 [10.2; 11.3]	11.2 [10.8; 11.6]	11.3 [11.0; 11.4]	**	***	<i>n. s.</i>
<i>WgIW</i>	4.0 [3.9; 4.0]	4.0 (3.94–4.12); 0.205	4.1 (4.04–4.14); 0.103	*	***	*
<i>WgIIL</i>	8.0 [7.4; 8.1]	8.1 [7.7; 8.5]	8.2 [8.0; 8.5]	*	**	<i>n. s.</i>
<i>WgIIW</i>	2.3 [2.0; 2.3]	2.2 [2.0; 2.3]	2.2 (2.11–2.22); 0.117	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CL</i>	1.5 [1.4; 1.5]	1.5 (1.47–1.52); 0.104	1.5 (1.48–1.53); 0.057	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CW</i>	1.6 (1.55–1.63); 0.090	1.6 (1.58–1.63); 0.103	1.7(1.64–1.71); 0.073	<i>n. s.</i>	**	*
<i>HW</i>	3.6 (3.57–3.71); 0.154	3.7 (3.63–3.72); 0.190	3.8 (3.72–3.84); 0.122	<i>n. s.</i>	**	*

Notes: *HW*, *CL*, *CW*, *WgIL*, *WgIW*, *WgIIL*, *WgIIW* are explained in the *Materials and Methods* section; *C1–C5* and *Ms2–Ms4* are 11 coloration variants; statistically non-significant differences are designated as *n. s.*; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

tween α - and β -females and between α - and γ -females (Table 11). In the colonies of *P. nimphus* and *P. lanio* comprising several foundresses (8 and 6 colonies, respectively), wasps of different rank differed in size (Table 11): γ -females (as well as β -females of *P. nimphus*, in some characters) had smaller head (*CW* and *HW* in *P. nimphus*; *HW* in *P. lanio*) and wings (*WgIL* and *WgIW* in *P. lanio*) than α -female did. The pleometrotic females of *P. nimphus* revealed statistically significant correlations between the length and width of fore wings, length of hind wings, and the abdomen coloration variants (for *WgIL*: $r_s = 0.37$, $n = 42$, $p < 0.01$; for *WgIW*: $r_s = 0.33$, $n = 42$, $p < 0.01$; for *WgIIL*: $r_s = 0.26$, $n = 42$, $p < 0.05$), and also between the length of clypeus, width of heads, and the mesonotum coloration variants (for *CL*: $r_s = -0.33$, $n = 42$, $p < 0.05$; for *HW*: $r_s = -0.31$, $n = 42$, $p < 0.05$).

The haplometrotic *P. nimphus* females had longer and wider wings as compared to the subordinate individuals (β , γ and below) from pleometrotic colonies

(Dunn's test for *WgIL* between haplo- and α -females: $p > 0.05$; between haplo- and β -females: $p = 0.05$; between haplo- and γ -females: $p = 0.02$; for *WgIW* between haplo- and α -females: $p > 0.05$; between haplo- and β -females: $p < 0.01$; between haplo- and γ -females: $p < 0.01$; for *WgIIW* between haplo- and α -females: $p > 0.05$; between haplo- and β -females: $p = 0.03$; between haplo- and γ -females: $p = 0.02$). The haplometrotic *P. dominulus* females almost did not yield to α -females in the length of clypeus (Dunn's test for *CL*: $p = 0.05$) and resembled β - and γ -females ($p > 0.05$ for all the characters).

DISCUSSION

Stable functioning of biological system is known to be based on their structuring (Setrov, 1971; Svirezhev and Logofet, 1978) and dynamic processes within the non-equilibrium range (Setrov, 1975; Prigogine and Nikolis, 2003; Khlebovich, 2007). According to the theory of functional systems (Setrov, 1975), "organi-

Table 7. Size of the head and wings of the pleometrotic foundresses of *Polistes nimphus* with different coloration variants of the clypeus, mesonotum, and abdomen

Parameters	Coloration characters			Pairwise comparison (Mann-Whitney or Student test); multiple comparison (Dunn's test)		
	Clypeus					
	<i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 17)	<i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 47)		<i>C3</i> vs. <i>C5</i>		
<i>WgIL</i>	10.1 (9.87–10.41); 0.539	10.0 (9.88–10.18); 0.549		<i>n. s.</i>		
<i>WgIW</i>	3.9 [3.8; 4.0]	3.9 (3.80–3.92); 0.216		<i>n. s.</i>		
<i>WgIIL</i>	7.8 (7.59–8.02); 0.429	7.7 (7.57–7.83); 0.457		<i>n. s.</i>		
<i>WgIIW</i>	2.2 (2.13–2.27); 0.146	2.2 (2.11–2.20); 0.168		<i>n. s.</i>		
<i>CL</i>	1.4 (1.37–1.50); 0.089	1.4 [1.4; 1.5]		<i>n. s.</i>		
<i>CW</i>	1.6 (1.52–1.60); 0.058	1.6 [1.5; 1.6]		<i>n. s.</i>		
<i>HW</i>	3.5 (3.38–3.58); 0.137	3.4 (3.39–3.50); 0.149		<i>n. s.</i>		
	Mesonotum					
	<i>Ms1</i> (<i>N</i> = 46)	<i>Ms2</i> (<i>N</i> = 16)				
<i>WgIL</i>	10.1 (9.94–10.30); 0.503	9.9 (9.71–10.18); 0.612		<i>n. s.</i>		
<i>WgIW</i>	3.9 (3.85–3.98); 0.192	3.8 (3.70–3.87); 0.226		<i>n. s.</i>		
<i>WgIIL</i>	7.8 (7.65–7.94); 0.416	7.8 [7.4; 7.9]		<i>n. s.</i>		
<i>WgIIW</i>	2.2 (2.14–2.24); 0.140	2.2 [2.0; 2.3]		<i>n. s.</i>		
<i>CL</i>	1.4 (1.39–1.46); 0.090	1.5 (1.41–1.52); 0.107		<i>n. s.</i>		
<i>CW</i>	1.6 [1.5; 1.6]	1.5 (1.55–1.58); 0.680		<i>n. s.</i>		
<i>HW</i>	3.5 (3.39–3.52); 0.147	3.5 (3.28–3.42); 0.125		<i>n. s.</i>		
	Abdomen					
	<i>IT1</i> (<i>N</i> = 14)	<i>IT2</i> (<i>N</i> = 24)	<i>IT3</i> (<i>N</i> = 25)	<i>IT1</i> vs. <i>IT2</i>	<i>IT2</i> vs. <i>IT3</i>	<i>IT1</i> vs. <i>IT3</i>
<i>WgIL</i>	9.7 (9.15–10.26); 0.527	9.9 (9.70–10.12); 0.569	10.2 (10.07–10.42); 0.476	<i>n. s.</i>	*	*
<i>WgIW</i>	3.8 (3.57–3.98); 0.198	3.8 (3.72–3.89); 0.229	3.9 (3.88–4.00); 0.173	<i>n. s.</i>	<i>n. s.</i>	*
<i>WgIIL</i>	7.5 (7.08–7.94); 0.407	7.7 (7.48–7.84); 0.475	7.8 [7.6; 8.1]	<i>n. s.</i>	*	<i>n. s.</i>
<i>WgIIW</i>	2.1 (1.88–2.34); 0.221	2.2 [2.0; 2.3]	2.2 (2.15–2.260); 0.154	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CL</i>	1.5 (1.39–1.60); 0.103	1.4 [1.4; 1.5]	1.4 (1.40–1.48); 0.066	*	<i>n. s.</i>	*
<i>CW</i>	1.6 (1.51–1.66); 0.072	1.6 (1.53–1.60); 0.077	1.5 [1.5; 1.6]	<i>n. s.</i>	*	*
<i>HW</i>	3.6 (3.37–3.76); 0.183	3.5 (3.40–3.51); 0.020	3.4 (3.25–3.52); 0.050	<i>n. s.</i>	*	**

Note: For designations, see Table 3.

zation is a set of phenomena whose properties manifest themselves as functions of preservation and development of this set.” The self-organization mechanisms of a system can be understood by (1) studying the structural localization of processes, (2) analysis of the internal stability or instability of processes at certain stages of their development, (3) studying the al-

ternation of stable and critical stages, and (4) building a holistic evolutionary model (Zakharov, 1991; Knyazeva and Kurdyumov, 1994).

At the population level, these properties are manifested in the specific spatial distribution of individuals and groups (the spatial structure) and in the system of

Table 8. Size of the head and wings of the foundresses of *Polistes lanio* with different coloration variants of the scutum, propodeum, and second abdominal tergite

Parameters	Coloration characters				Pairwise comparison (Mann-Whitney or Student test); multiple comparison (Dunn's test)
	Scutum				
	<i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 23)		<i>M</i> (95% CI); <i>s</i> or <i>Me</i> [25; 75] (<i>N</i> = 8)		4 vs. 6
<i>WgIL</i>	18.2 (17.83–18.65); 0.953		17.9 (17.45–18.32); 0.521		<i>n. s.</i>
<i>WgIW</i>	6.0 (5.86–6.13); 0.303		5.9 (5.75–6.12); 0.216		<i>n. s.</i>
<i>WgIIL</i>	12.3 (12.01–12.57); 0.655		12.2 (11.73–12.73); 0.596		<i>n. s.</i>
<i>WgIIW</i>	3.2 (3.14–3.28); 0.163		3.3 (3.08–3.50); 0.253		<i>n. s.</i>
<i>HW</i>	4.3 [4.2; 4.5]		4.4 (4.32–4.55); 0.141		<i>n. s.</i>
<i>HL</i>	4.0 (3.92–4.14); 0.256		4.1 [4.1; 4.1]		<i>n. s.</i>
	Propodeum				
	2 (<i>N</i> = 8)	3 (<i>N</i> = 10)	4 (<i>N</i> = 6)	6 (<i>N</i> = 7)	
<i>WgIL</i>	18.4 (17.83–19.05); 0.725	18.1 (17.52–18.67); 0.805	18.3 (17.39–19.20); 0.859	18.1 [17.7; 18.3]	All multiple comparisons: <i>n. s.</i>
<i>WgIW</i>	6.0 (5.81–6.28); 0.280	6.0 (5.82–6.17); 0.244	6.1 (5.84–6.32); 0.231	5.8 (5.56–6.06); 0.270	All multiple comparisons: <i>n. s.</i>
<i>WgIIL</i>	12.5 (12.26–12.75); 0.297	12.2 (11.72–12.76); 0.729	12.5 (11.67–13.34); 0.795	12.1 (11.57–12.57); 0.538	All multiple comparisons: <i>n. s.</i>
<i>WgIIW</i>	3.2 (3.14–3.35); 0.127	3.3 (3.11–3.40); 0.202	3.4 (3.18–3.56); 0.180	3.1 (2.95–3.22); 0.145	2 vs. 6 **; 3 vs. 6 *; 4 vs. 6 **
<i>HW</i>	4.4 (4.25–4.52); 0.165	4.3 (4.23–4.42); 0.131	4.5 (4.36–4.66); 0.144	4.2 [4.1; 4.4]	2 vs. 6 **; 3 vs. 4 *; 4 vs. 6 **
	Second abdominal tergite				
<i>WgIL</i>	18.1 (17.80–18.46); 0.875		18.2 (17.45–18.91); 0.591		<i>n. s.</i>
<i>WgIW</i>	6.0 (5.88–6.10); 0.287		5.9 (5.71–6.10); 0.156		<i>n. s.</i>
<i>WgIIL</i>	12.3 (12.01–12.51); 0.650		12.5 (12.19–12.84); 0.260		<i>n. s.</i>
<i>WgIIW</i>	3.2 (3.15–3.29); 0.183		3.3 (3.05–3.52); 0.187		<i>n. s.</i>
<i>HW</i>	4.3 (4.28–1.40); 0.162		4.3 (4.01–1.63); 0.249		<i>n. s.</i>

Note: The coloration variants are designated by numbers in italics; other designations as in Table 6.

interactions between the individuals (the ethological structure) (Shilov, 1977, 1991a, 1991b; Panov, 1983). The integration mechanism of a population is based on the individuals obtaining information about the spatial localization of other individuals, colonies, and assemblages, and also on the innate behavioral stereotype forcing each individual to seek and maintain a certain level of olfactory, visual, acoustic, and tactic interrelations with other individuals. Many researchers have

described the behavioral stereotypes of paper wasps consisting in seeking contacts, and also realized as nesting within the “signal field” (sensu N.P. Naumov, 1977) of other individuals. This behavior comprises the contacts between females even before nesting (on the old nest), relocation of females from nest to nest within a colony, a weak association between a female and a particular nest at the early stages of the colony development, and periodical visits to neighboring

Table 9. Size of the head and wings of the foundresses of *Polistes dominulus* and *P. nimphus* from haplometrotic colonies

Parameters	<i>P. dominulus</i> (N = 33)	<i>P. nimphus</i> (N = 31)
<i>WgIL</i>	10.8 (10.81–10.92); 0.560	10.1 (9.92–0.18); 0.345
<i>WgIW</i>	4.0 (3.96–4.08); 0.183	3.9 (3.88–3.98); 0.134
<i>WgIIL</i>	2.27 (2.22–2.31); 0.138	7.6 (7.49–7.71); 0.299
<i>WgIIW</i>	8.2 [7.9; 8.5]	2.2 (2.16–2.21); 0.088
<i>CW</i>	1.5 [1.4; 1.6]	1.5 (1.47–1.56); 0.113
<i>CL</i>	1.5 [1.4; 1.6]	1.5 (1.46–1.55); 0.121
<i>HW</i>	3.6 [3.5; 3.7]	3.4 (3.32–3.41); 0.119

Note: for designations, see Table 3.

Table 10. Comparison of coloration patterns of *Polistes* foundresses of different ranks (χ^2 test)

Groups of females and type of colony foundation	Coloration of body parts		
	Clypeus	Mesonotum	Abdomen
<i>P. dominulus</i>			
Haplometrosis vs. high rank females (α and β)	2.65, <i>df</i> = 4, <i>p</i> = 0.618	3.01, <i>df</i> = 2, <i>p</i> = 0.221	3.86, <i>df</i> = 3, <i>p</i> = 0.278
Haplometrosis vs. low rank females (γ and below)	0.96, <i>df</i> = 3, <i>p</i> = 0.811	1.41, <i>df</i> = 3, <i>p</i> = 0.702	0.45, <i>df</i> = 1, <i>p</i> = 0.521
High rank females vs. low rank females	1.34, <i>df</i> = 4, <i>p</i> = 0.854	3.95, <i>df</i> = 2, <i>p</i> = 0.139	6.26, <i>df</i> = 1, <i>p</i> = 0.012
High rank females vs. non-nesting females	3.87, <i>df</i> = 4, <i>p</i> = 0.424	7.17, <i>df</i> = 2, <i>p</i> = 0.028	7.52, <i>df</i> = 1, <i>p</i> = 0.006
Low rank females vs. non-nesting females	3.01, <i>df</i> = 4, <i>p</i> = 0.558	2.40, <i>df</i> = 2, <i>p</i> = 0.301	–
<i>P. nimphus</i>			
Haplometrosis vs. high rank females (α and β)	7.80, <i>df</i> = 2, <i>p</i> = 0.020	6.46, <i>df</i> = 2, <i>p</i> = 0.039	0.51, <i>df</i> = 3, <i>p</i> = 0.163
Haplometrosis vs. α -females	3.42, <i>df</i> = 2, <i>p</i> = 0.181	3.52, <i>df</i> = 2, <i>p</i> = 0.172	5.57, <i>df</i> = 3, <i>p</i> = 0.135
Haplometrosis vs. low rank females (γ and below)	12.71, <i>df</i> = 2, <i>p</i> = 0.001	12.26, <i>df</i> = 2, <i>p</i> = 0.002	4.83, <i>df</i> = 3, <i>p</i> = 0.185
α -female vs. low rank females	26.19, <i>df</i> = 4, <i>p</i> < 0.001	11.53, <i>df</i> = 3, <i>p</i> = 0.009	3.48, <i>df</i> = 3, <i>p</i> = 0.324
	Scutum	Propodeum	2nd abdominal tergite
<i>P. lanio</i>			
High rank females vs. low rank females	2.70, <i>df</i> = 3, <i>p</i> = 0.441	1.12, <i>df</i> = 2, <i>p</i> = 0.572	2.41, <i>df</i> = 5, <i>p</i> = 0.789

nests (West-Eberhard, 1969; Pratte, 1980; Strassmann, 1983; Itô, 1984, 1993; Starr, 1991; Giannotti and Mansur, 1993; Rusina, 2000, 2006). It should be noted that the formation and development of the spatial structure of *P. dominulus* and *P. nimphus* settlements is affected by direct and indirect communication between the overwintering females on the old nests (Rusina, 2006). Such females either found a nest collectively, or settle close to each other and to the old nest, forming an assemblage. In the peak population season, the nests are located closer together than during the

phases of population growth or depression (Rusina, 2006). Relocation of nesting females, observed in *P. dominulus* and *P. nimphus* during the population peak, reduces the fraction of single-female nests, increases the degree of pleometrosis, and decreases the nesting density (Rusina, 2000). In case of haplometrosis all the females participate in reproduction, whereas in case of pleometrosis their reproductive success becomes differentiated due to competition. The self-organization processes at the colony level include periods with a varying level of aggression, alternating

Table 11. Size of paper wasps (*Polistes*) of different ranks

Parameters	Ranks			Group comparison (Dunn's test)		
<i>P. dominulus</i>						
	α-female (<i>N</i> = 6)	β-female (<i>N</i> = 6)	γ-female (<i>N</i> = 19)	α vs. β	β vs. γ	α vs. γ
<i>WgIL</i>	11.1 [10.6; 11.8]	10.9 (10.39–11.56); 0.965	10.9 (10.42–11.44); 0.665	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>WgIW</i>	4.1 (3.92–4.27); 0.289	4.1 (3.94–4.30); 0.298	4.0 (3.887–4.22); 0.225	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>WgIIL</i>	8.2 (7.68–8.73); 0.869	8.2 (7.78–8.62); 0.699	8.4 (7.96–8.77); 0.532	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>WgIIW</i>	2.3 (2.14–2.37); 0.191	2.3 (2.18–2.39); 0.172	2.3 (2.17–2.50); 0.213	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CL</i>	1.5 (1.41–1.55); 0.107	1.5 (1.43–1.56); 0.103	1.5 (1.44–1.58); 0.091	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CW</i>	1.6 (1.56–1.71); 0.118	1.6 (1.59–1.67); 0.069	1.6 (1.53–1.70); 0.111	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>HW</i>	3.7 (3.63–3.83); 0.158	3.7 (3.59–3.80); 0.166	3.6 (3.42–3.71); 0.187	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>P. nimphus</i>						
	α-female (<i>N</i> = 9)	β-female (<i>N</i> = 9)	γ-female (<i>N</i> = 46)	α vs. β	β vs. γ	α vs. γ
<i>WgIL</i>	9.9 (9.75–10.21); 0.427	9.7 (9.42–9.95); 0.498	9.7 [9.4; 9.8]	*	<i>n. s.</i>	*
<i>WgIW</i>	3.8 (3.74–3.93); 0.183	3.8 (3.65–3.85); 0.191	3.7 (3.41–3.98); 0.230	*	<i>n. s.</i>	*
<i>WgIIL</i>	7.6 (7.42–7.85); 0.408	7.4 (7.16–7.68); 0.502	7.1 (6.33–7.97); 0.659	*	<i>n. s.</i>	*
<i>WgIIW</i>	2.2 (2.13–2.23); 0.098	2.1 (2.00–2.17); 0.168	1.9 (1.71–2.28); 0.226	*	<i>n. s.</i>	*
<i>CL</i>	1.5 (1.44–1.52); 0.078	1.5 (1.41–1.53); 0.118	1.5 (1.36–1.55); 0.094	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>CW</i>	1.6 [1.6; 1.6]	1.6 (1.48–1.60); 0.109	1.5 (1.42–1.66); 0.117	*	<i>n. s.</i>	*
<i>CH</i>	3.5 (3.44–3.58); 0.148	3.5 (3.39–3.54); 0.153	3.4 (3.24–3.54); 0.140	<i>n. s.</i>	<i>n. s.</i>	*
<i>P. lanio</i>						
	α-female (<i>N</i> = 6)	β-female (<i>N</i> = 6)	γ-female (<i>N</i> = 16)	α vs. β	β vs. γ	α vs. γ
<i>WgIL</i>	19.0 [17.8; 18.7]	18.1 (17.71–18.40); 0.833	18.1 (17.64–18.51); 0.569	<i>n. s.</i>	<i>n. s.</i>	*
<i>WgIW</i>	6.1 (5.88–6.28); 0.259	5.9 (5.83–6.05); 0.271	5.9 (5.81–6.07); 0.230	<i>n. s.</i>	<i>n. s.</i>	*
<i>WgIIL</i>	12.5 (12.09–12.97); 0.571	12.2 (11.96–12.47); 0.614	12.2 (11.91–12.50); 0.593	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>WgIIW</i>	3.3 (3.22–3.41); 0.122	3.2 (3.12–3.28); 0.192	3.2 (3.11–3.29); 0.181	<i>n. s.</i>	<i>n. s.</i>	<i>n. s.</i>
<i>HW</i>	4.4 (4.29–4.48); 0.125	4.3 (4.24–4.40); 0.186	4.3 (3.93–4.17); 0.142	<i>n. s.</i>	<i>n. s.</i>	*

Note: For designations, see Table 6.

with peaceful contacts; the degree of reproductive monopoly of the dominant female also varies. The extent of the dominant reproductive monopoly in the colony is species-specific (Reeve, 1991; Rusina, 1999). When the subordinate females of *P. nimphus* resume oviposition they are expelled from the colony by the dominant female. In *P. dominulus* the relations in the colony and the degree of reproductive monopoly depend on the nesting density. In sheltered nests, the subordinate *P. dominulus* females only rarely participate in reproduction when eggs of the sexual generation are laid (Rusina, 2006). According to genetic analysis, the subordinate females from nest built in shelters produce only 0.2 to 2.6% of sexual progeny (Queller et al., 2000). When nests are built on plants, the nesting density is considerably lower (Rusina, 2006). In this case, the subordinate individuals lay

eggs, while the α -female displays a low level of aggression towards them; according to the genetic analysis, the subordinate females produce up to 10% of the progeny (Rusina, Firman, Paxton, unpubl.). In general, transition from critical regimes to relatively stable structures is achieved in the population by means of various stereotype responses and information processes (Knyazeva and Kurdyumov, 1994).

Thus, on the one hand, the pattern of the spatial distribution of individuals reduces the competition, and on the other hand, it maintains stable informational and functional contacts among the individuals. Therefore, the existence of a population as an integral system requires a combination of mechanisms of spatial differentiation and functional integration of individuals, which determine the specific type of spatio-

ethological structure that serves as the basis of population homeostasis in complex and dynamic environment (Shilov, 1967).

Stable interactions within the system “population–environment” are known to be regulated and maintained by the system of polymorphism (Kreslavskii, 1984; Sergievskii, 1987). Polymorphic populations consist of several groups of individuals displaying different strategies and responding differently to environmental conditions as well as population density. It should be noted that settlement formation and establishment of the dominant hierarchy in pleometrotic colonies are not random. These processes, while varying between species, are determined by individual heterogeneity in the population and within the colony with respect to a number of morpho-physiological and behavioral parameters: size, coloration, hormonal activity, and aggressiveness (Turillazzi and Pardi, 1977; Dropkin and Gamboa, 1981; Noonan, 1981; Sullivan and Strassmann, 1984; Röseler et al., 1984; Rusina et al., 2007). In particular, our results show that females of different morphs prefer different modes of colony foundation. Females of *P. nimphus* with large wings, showing coloration variants *C5* of the clypeus, *Ms1* and *Ms2* of the mesonotum, and *IT1–IT3* of the abdomen, tend to nest singly. Pleometrosis is more commonly observed in the females having a larger head and showing the mass phenotypes *C3* and *C5* of the clypeus and mostly *Ms1* of the mesonotum, and also in the small females with rare coloration morphs. The coloration of the dominant females is the same as that of the haplometrotic ones, which indicates that the dominant individuals have been the actual foundresses. The small females with rare combinations of color characters form the group of subordinate individuals.

The females of *P. dominulus* showing variants *C3* and *C5* of the clypeus, *Ms2* and *Ms3* of the mesonotum, and *IT3* of the abdomen nest singly. The larger individuals of this group attract the females with a rare variant *IT4* of the abdomen and occupy dominant positions in the colony hierarchy. *P. dominulus* females that have not nested by the moment of observation include both potentially haplometrotic females and low rank individuals. Females of different rank proved to be similar in size. At the same time, α -females of *P. dominulus* from the colonies comprising two foundresses usually exceeded β -females in the width of head, mesonotum, and scutum, and also in the length of wings (Turillazzi and Pardi, 1977). During the

population peak, the color intensity of the abdomen (in small colonies also of the clypeus) was correlated with a female’s position in the dominant hierarchy in each particular *P. dominulus* colony, nesting on plants in the Lower Dnieper area (Rusina et al., 2007). The difference between the results of our morphometric analysis of *P. dominulus* colonies and the previously published data (Turillazzi and Pardi, 1977; Rusina et al., 2007) can be explained either by the fact that the settlement formation was still incomplete at the moment of our observations, or by the existence of some coloration-related differences between the females in size, phenotypic diversity, and reproductive success, dependent on the phase of the population dynamics. Abundance of the species decreased after a very severe winter of 2005/2006, as indicated by some indirect parameters. For comparison, the following data referring to the populations of this species during an abundance peak in Kherson Province can be considered (Rusina, 2006): (1) the fraction of pleometrosis in the studied population from Kurortnoe settl. was 31.6%, as compared to 48.94% (1991, Kherson house attics) and 14.6% (2004, on plants, the Black Sea Biosphere Reserve, Kherson Prov.); (2) the fraction of large colonies founded by five or more females was 11.1%, as compared to 18.2% (1991, Kherson house attics) and 24.2% (2004, on plants, the Black Sea Biosphere Reserve). It was shown that an increase in the population density of *P. dominulus* in the Lower Dnieper area (during an abundance peak or in case of sheltered nesting) is accompanied not only by the appearance of large pleometrotic colonies, but also by an increase in their phenotypic diversity and, correspondingly, the fraction of “specialist” individuals (Rusina et al., 2007). The Crimean populations of *P. nimphus*, unlike those of the more northern Lower Dnieper area (Rusina, 2006), revealed twice as great a fraction of pleometrotic colonies and a higher phenotypic diversity.

As can be seen from our data, *P. lanio* females with coloration variants *Sc5* of the scutum, *Pr2* of the propodeum, and *2T1* of the second abdominal tergite show preference for group founding of a colony and raising brood in several nests. According to E. Giannotti (1992, cited after Giannotti and Machado, 1994), in southeastern Brazil 60.3% of colonies of this species develop in 2–16 nests. R.L. Jeanne (1979) suggested that the same nesting mode in *P. canadensis canadensis* (L.) might have an adaptive significance for protecting the brood from a parasitoid. J.E. Strassmann (1981a) compared the survival rates in the haplometrotic, pleometrotic, and polycalic (referred to

as satellite) colonies of *P. exclamans* Viereck attacked by predators and demonstrated that the latter category had a better chance of survival. Although the role of polycaly was not studied in this work, indirect data suggest that it may be related to the colony protection from parasitoids. This is indicated by the fact that all the nests abandoned by polycalic colonies revealed traces of parasitoid infestation.

Thus, the results of our work and analysis of the spatio-temporal variability of *P. dominulus* nesting on plants in the Lower Dnieper area (Rusina et al., 2007) allow us to conclude that the population structure of polistine wasps includes individuals of common phenotypes ("generalists") and those marked by less frequent characters ("specialists"). The common coloration variants mark the "generalists," which can nest singly not far from the old nest and occupy a dominant position in case of pleometrosis. These females are characterized by high aggressiveness. The degree of aggressiveness of a dominant female was shown to be correlated with a melanin pattern on the clypeus of the subordinate individual: the more fragmented is the pattern the higher is the aggressiveness (Tibbets and Dale, 2002). The foundress having a dark variant of the clypeus may join an alien colony after its own nest has been destroyed by predators, in which case the resident female is usually forced into a subordinate position (Rusina et al., 2006). Females of low ranks (γ and below) are smaller and less aggressive individuals which show rare coloration variants. Females of this group differ noticeably from haplometrotic individuals in their phenotype; they tend to form a large colony even when free nesting sites and sufficient trophic resources are available. These coloration variants mark the group of "specialists" which clearly prefer nesting in groups. Such females may be more sensitive to the decreasing level of hormonal and ovarial activity, corresponding to their subordinate rank in the colony. It should be noted that in the Lower Dnieper area, the "specialist" females of *P. dominulus* are observed only in dense sheltered nesting sites, and in case of nesting on plants, only at the abundance peak after a mild winter (Rusina et al., 2007). The special group of "generalists" is represented in the Lower Dnieper area by migrant individuals. Females of this group tend to nest singly in a new area. The ecological role of this group becomes evident if we consider the high level of parasitoid infestation in the nesting places used for several years (Starr, 1976, 1978; Rusina, 2006). The phenotypic marking of individuals in the population (size

reduction and/or coloration polymorphism) is known in many groups of animals; it appears to have an adaptive significance, allowing a higher abundance to be maintained despite the restricted resources (Wall and Begon, 1987; Krebs and Davies, 1993). The mechanisms leading to size differentiation of females in the population may be related to the difference in food provided to the prospective foundresses in different colonies (Turillazzi, 1980; Sullivan and Strassmann, 1984). In addition, according to S. Turillazzi (1980), the smallest females in a *P. dominulus* population are infested with the parasite *Xenos vesparum* Rossi (Strepsiptera, Stylopidae). The styloped females have small corpora allata (CA) and are non-aggressive (Röseler et al., 1984). The possible way of maintaining coloration polymorphism may be based on the pleotropic effect of coloration genes on the social behavior.

Already M.J. West-Eberhard suggested that the existence of females with different strategies of colony foundation could be related to polymorphism (West, 1967; West-Eberhard, 1969); however, she applied the concept of polymorphism only to size and fecundity of the females (the subfertility hypothesis). According to this hypothesis, small females with low fecundity tend to join a more fertile one. Other authors opposed this assumption, mentioning that females of different ranks could be similar in size, degree of ovary development, and level of hormonal activity at the initial stages of colony formation, or could differ in only one of these parameters; in addition, relations between these parameters could be non-linear (Turillazzi and Pardi, 1977; Röseler et al., 1984; Sullivan and Strassmann, 1984). For example, P.F. Röseler with co-authors (Röseler et al., 1984) found no relation between the differences in size of differently ranked females and the degree of development of their ovaries and the CA activity. However, the greater the size difference between α - and β -females the stronger is the relation between the activity of their ovaries and CA. The dominant positions are occupied by those females which first arrive at the nesting sites after wintering, because the hormonal activity of their ovaries and CA depends on the time when they recover after hibernation (Röseler et al., 1986). The differences in fecundity manifest themselves later, depending on the position of a female in the colony hierarchy and on the colony size (Strassmann, 1981b; Turillazzi et al., 1982). However, in our opinion, the very idea of M.J. West-Eberhard concerning the heterogeneity of

females in polistine wasps deserves much attention, even though the main focus of polymorphism studies should be shifted from the colony level to that of the population.

V.V. Khlebovich (2007), analyzing the mechanisms of homeostasis, has shown that one of their functions consists in maintaining the biological system within the non-equilibrium zone. In our opinion, at the population level this mechanism comprises various processes concerning the individual, colony, and the entire population, and increasing the morpho-physiological, phenotypic, and behavioral diversity. It should be noted that increasing diversity at the early stages of a wasp settlement formation or during the hierarchy establishment in the colony enhances the non-equilibrium, resulting in broader possibilities of obtaining a relatively stable structure. Indirect manifestations of such mechanisms can be observed during the abundance peak phase. Thus, the mechanisms of system self-organization affect the processes of increasing diversity and regulation near the stability limits, because “abrupt changes of the system properties near the critical points can be caused by a minimum impact” (Khlebovich, 2007), including that of a signal nature.

I.I. Schmalhauzen (1983) and G.A. Viktorov (1975) considered the development of intraspecific mechanisms of abundance regulation in relation to the position of the species in the food chain. The species occupying lower and middle trophic layers are usually characterized by intensive non-selective elimination. Correspondingly, selection in these species favors more intensive reproduction, which may lead to overpopulation. Different types of population dynamics were characterized, and the various regulating mechanisms were discussed based on long-term studies (Viktorov, 1975). According to the cited author, insects with labile population dynamics (including polistine wasps) “can acquire a number of such mechanisms, acting at the different levels of the population abundance.” The hypothesis of stepwise regulation of the population abundance, proposed by G.A. Viktorov, holds much promise with respect to this particular group of insects. The interrelations between phenotypic variability and the mechanisms of population homeostasis can be completely understood only by long-term observations of the population dynamics, covering the periods of population peaks and depressions.

A.S. Severtsov (1990), summarizing data on the intraspecific diversity, considered it to be the main factor of evolutionary stability of species.

In general, it can be concluded that differential choice of environment by individuals of different morphotypes affects the spatio-ethological structure of the population. Strong differences in the phenotype frequencies within small areas can be achieved by behavioral segregation, whereas reproductive differentiation of females of different morphotypes in pleometrotic and polycalic colonies increases the difference in their reproductive success, which may lead to genetic heterogeneity of the population. The specific type of the spatio-ethological population structure, determined by the balanced effect of the species-specific mechanisms of spatial segregation and functional integration (Shilov, 1991a, 1991b), is obviously linked with the mechanisms maintaining intrapopulation polymorphism. Owing to the complex internal structure, multilevel correlations, and the potentials for self-organization, the population systems of paper wasps realize various mechanisms of adaptations to the environment.

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