

Phenotypic Variability of *Polistes albellus* Giordani Soika, 1976 (Hymenoptera: Vespidae)

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Received July 2, 2021; revised November 14, 2021; accepted November 14, 2021

Abstract—Variability in the coloration and melanin patterns of the social wasp *Polistes albellus* Giordani Soika, 1976 (Hymenoptera: Vespidae), distributed from Western Europe (France) to the Pacific coast of Russia (Primorskii Territory), Mongolia, and China, is described. Altogether, 590 females and 101 males were examined. Phenotypic variability in *P. albellus* females was expressed on the mesoscutum, metasomal tergites 1 and 2, and metasomal sternites 4–6, and in males, also on the clypeus and coxae. The coloration elements and their relationships with the spatial and temporal nesting features were analyzed in three local populations of *P. albellus* in the Meshchera Lowlands (Ryazan Province, Russia). Overwintered foundresses of different morphotypes were shown to differ in the timing of nest initiation, the height of nests on plants, and the tendency to nest in clusters. The samples of queens from different settlements were phenotypically different both each other and from the samples of workers. The mesoscutum pattern appears to be related to habitat humidity, with darker variants being more common in workers from dry habitats. The heterogeneity of environmental conditions may facilitate higher variability of the melanin patterns in wasps.

Keywords: social wasps, Vespidae, *Polistes albellus*, phenotypic variability, melanin patterns

DOI: 10.1134/S0013873821080042

Paper wasps of the genus *Polistes* are widespread throughout the world and are among the most intensively studied resocial insects (Reeve, 1991; Röseler, 1991). Their black-and-yellow pattern is highly variable and provides simple and reliable characters that can be conveniently used in research of population ecology and behavior (Tibbets and Dale, 2004; Rusina, 2009).

One of the main features of temperate-zone *Polistes* species is the presence of three periods in their life cycle: (1) mating of males and future foundresses in late summer and early autumn, (2) overwintering of fertilized foundresses, and (3) nesting of foundresses and development of colonies in spring and summer (the founding, worker, and reproductive phases). It would be interesting to study such a life cycle by methods of popula-

tion morphology (Yablokov, 1976; Yablokov and Larina, 1985; Sergievsky, 1985, 1987; Novozhenov, 1989, etc.), in particular, to search for the traits of melanin pattern (phenes) marking functionally different individuals in the wasp population.

The variability of melanin pattern was earlier described in a number of *Polistes* species, and the phenotypic structure of local settlements, its seasonal and long-term dynamics, and the choice of mates by the future foundresses were studied in detail on this basis (Rusina et al., 2004a, 2004b, 2006, 2007a, 2007b, 2007c, 2009; Firman and Rusina, 2009; Rusina and Lopatin, 2009; Rusina and Orlova, 2009). The phenotypic structure was shown to change cyclically over the season under the changing weather conditions (Rusina et al., 2004a, 2007a,

Table 1. Sampling localities of males and females of *Polistes albellus* Giordani Soika

Samples	Locality	Coordinates	Number of specimens
Russia			
<i>Ryazan Province</i>			
1st local settlement	Klepikovskii District, Utkino	55°08'N, 40°32'E	110 ♀ (live wasps)
2nd local settlement	Snokhino	55°08'N, 40°36'E	302 ♀, 101 ♂ (live wasps)
Solitary nests	Grishino	55°04'6"N, 40°21'18"E	158 ♀ (live wasps)
	Savino	55°06'47"N, 40°33'33"E	
		55°06'35"N, 40°33'32"E	
	Korenevo	55°09'20"N, 40°34'52"E	
	Tuma	55°09'30"N, 40°32'47"E	
	Snokhino	55°08'40"N, 40°36'07"E	
		55°08'40"N, 40°36'12"E	
	55°08'40"N, 40°36'03"E		
<i>Bashkortostan</i>			
	Ishimbaiskii District, Ziganovka	53°36'57"N, 56°34'14"E	3 ♀ (photos by V.A. Valuev)
	Blagovarskii District, Udryakbash	54°31'41"N, 54°57'28"E	
	Buzdyakskii District, Novokilimovo	54°29'57"N, 54°37'14"E	
<i>Zabaikalskii Territory</i>			
	Duldurginskii District, Alkhanay National Park	50°41'50"N, 113°27'6"E	1 ♀ (photos by R.Yu. Abashev; Osy Rossii, 2011–2018)
<i>Orenburg Province</i>			
	Sakmarskii District, Donskoe	52°3'28"N 55°25'12,6"E	1 ♀ (Neumeyer et al., 2015)
Switzerland			
	Bauma	47°23'00"N, 08°50'49"E	8 ♀ (photos by R. Neumeyer and C. Dobler Gross)
Kazakhstan			
	Zaysan	47°14'N, 84°56'	1 ♀ (Neumeyer et al., 2015)

2011). The phenotypic composition of the population was considerably affected by the rates of infestation with parasites and parasitoids (Rusina, 2009; Rusina and Orlova, 2011). Foundresses of different morphotypes clearly differed in the preferred modes of nest foundation and the level of aggressiveness (Rusina et al., 2007b, 2007c, 2009). For instance, females of *Polistes dominula* (Christ, 1791) (Hymenoptera, Vespidae) with dark variants of the clypeal pattern preferred nesting singly (haplometrotically) and became dominant in pleometrotic colonies, while those with lighter pattern variants more often nested in groups (pleometrotically) (Rusina et al., 2007b). According to some authors, the clypeal pattern in this species serves a social function, signaling the rank of an individual (Tibbets, 2002; Tibbets and Dale, 2004).

Widespread species are adapted to a great variety of living conditions and often show a high level of variability and intraspecific phenotypic differentiation

(Rusina et al., 2008). A promising object of population ecological research is the wasp *P. albellus* Giordani Soika, 1976, distributed from Western Europe (France) to Primorskii Territory of Russia, Mongolia, and China (Neumeyer et al., 2014, 2015).

The objectives of our research were to describe the phenotypic variability of *P. albellus* wasps from local settlements in Central Meshchera and to study the relationships between the melanin patterns of foundresses and the spatial and temporal features of their nesting.

MATERIALS AND METHODS

Most of the material on the variability of coloration and melanin pattern in *P. albellus* was collected in June–August 2019 in Central Meshchera (Russia, Ryazan Province), from two local settlements in the environs of Utkino (Table 1; Fig. 1) and Snokhino (Table 1; Fig. 2). Wasps from solitary nests were collected near Grishino, Tuma, Savino, Snokhino, and Korenevo. In addition,



Fig. 1. Humid grass-forb meadow (environs of Utkino, 55°08'N, 40°32'E, 1.VII.2019). Photo by A. Yu. Kosyakova.



Fig. 2. Fallow overgrowing with *Pinus sylvestris* L. (environs of Snokhino, 55°08'N, 40°36'E, 28.IX.2019). Photo by A. Yu. Kosyakova.



Fig. 3. *Polistes albellus* Giordani Soika. Left: future foundresses on the nest in Switzerland (ZH, Bauma: Joggelisböl, 47°23'00"N, 08°50'49"E, 7.IX.2012), photo by R. Neumeyer. Right: a foundress (red arrow) and workers on the nest in Central Meshchera (environs of Korenevo, 55°08'44"N, 40°36'00"E, 26.VI.2019), photo by A.Yu. Kosyakova.

the melanin pattern of wasps was analyzed using photos taken by R. Neumeyer and C. Dobler Gross in the vicinity of Bauma (Switzerland), by V.A. Valuev in Bashkortostan, by R.Yu. Abashev in Zabaikalskii Territory of Russia (Osy Rossii, 2011–2018), and those previously published (Neumeyer et al., 2015). Altogether, 590 females and 101 males were examined.

The variability of melanin pattern on different body parts of *P. albellus* was described using the schemes proposed earlier for other species, in particular *P. dominula* and *P. nimpha* (Christ, 1791) (Rusina et al., 2004b, 2006; Rusina, 2009). The patterns were arranged by the degree of melanization (Filippov, 1961).

Seasonal changes in the phenotypic structure of local settlements were studied in Central Meshchera.

Local settlements of *P. albellus* were found in two plots differing in the soil structure and humidity: the first settlement was located in a humid grass-forb meadow, mostly of *Glyceria maxima* (Harm.) Holmb, on sod-podzolic soil with humic gley patches; the second settlement was located in a forb-reedgrass fallow with a coppice of the Scots pine *Pinus sylvestris* L. on well-drained sod-podzolic soil composed of sands with isolated layers of loam (Annenskaya et al., 1983).

For each nest, we described the spatial characteristics (the species and height of the plant on which the nest was built, the height of the nest itself, the distance to the

nearest neighboring nest, and the density of nests within a 10 × 10-m area), the demographic parameters (the number of cells, IV and V instar larvae, pupae, and workers), and also the melanin patterns of 76 queens captured and ringed at their nests (Fig. 3). The demographic parameters were determined before the emergence of workers, on the same day for all the nests within each settlement. In the first settlement, the melanin patterns were described on 4.VI.2019 for 36 queens from 35 haplometrotic and 1 pleometrotic colonies; in the second settlement, 40 queens from 40 haplometrotic colonies were described on 8.VI.2019.

Correlations between the morphological parameters of the queens and the size of their colonies as well as the spatial characteristics of the nests were determined for each settlement. The colony size was used as an indirect estimate of its relative age, assuming that larger colonies were initiated earlier. In addition, correlations were calculated between the melanin pattern variants of the queens and the spatial characteristics of their colonies.

Altogether, 54 nests were found in the first settlement and 168 nests, in the second settlement during our research (May–August 2019); besides, there were 19 solitary nests. The nests were examined once or twice a week; on every such occasion, the survival and composition of the colony was recorded (Fig. 4), the newly emerged workers, males, and future foundresses were



Fig. 4. Males (blue arrows) and workers of *Polistes albellus* Giordani Soika on the nest destroyed by birds (environs of Korenevo, 55°08'43"N, 40°36'07"E, 28.VI.2019). Photos by A.Yu. Kosyakova.

ringed, their melanin patterns were described, and the presence of parasites and parasitoids was recorded. The mites *Sphexicozela connivens* Mahunka, 1970 (Acari, Astigmata: Winterschmidtidae) and the endoparasites *Xenos vesparum* Rossi, 1793 (Strepsiptera, Stylopidae) were detected by examination of the larvae, late workers, males, and future foundresses.

Signs of brood infestation with parasitoids were recorded during the mapping of nests. Infestation with the parasitoid wasp *Latibulus argiolus* (Rossi, 1790) (Hymenoptera: Ichneumonidae) was detected by the presence of ovally slanted, light yellow or light orange remains of the larval cuticle and/or cocoons (Makino, 1983), and infestation with *Elasmus schmitti* Ruschka, 1920 (Hymenoptera, Eulophidae), by the presence of a dark gray cover which the larvae of this gregarious parasitoid make of their meconia before pupation (Gumovsky et al., 2007).

Multiple comparison of independent samples of nest parameters was performed using the Kruskal-Wallis H test and Dunn's Q test. Pairwise comparisons of two independent samples were performed using the Mann-Whitney U test (Glantz, 1999).

Correlation between the features of melanin patterns of queens and the spatial and/or temporal parameters of their nesting was estimated by the Spearman's correlation coefficient r_s .

The significance of differences between the samples in the frequencies of pattern variants was estimated by χ^2 test. Comparison was performed both between the local settlements at similar stages of development and

during the seasonal development of colonies in each settlement. However, since the regular χ^2 test is insufficiently sensitive to rare variants (Zhivotovsky, 1991), the phenotypic differences between local settlements were additionally estimated using special measures, such as the Cavalli-Sforza chord distances taking rare traits into account (Cavalli-Sforza and Edwards, 1967; Zhivotovsky, 1991; Weir, 1995). To visualize the differences between the samples, the distance matrices were processed by the non-metric multidimensional scaling methods.

All the calculations were made in Microsoft Excel 2019, Statistica v. 10.0 (StatSoft Inc., 1984–2020), and Biostatistica v. 4.03 (Glantz, 1999). The distribution of the studied parameters was tested for normality using the Shapiro-Wilk test. In the case of normal distribution the sample was described as the mean $M \pm$ standard deviation SD, and in the case of non-normal distribution, as the median, the 1st and 3rd quartiles, and the minimum and maximum values: Me [25; 75] [min; max] (Glantz, 1999).

RESULTS

Melanin Pattern of Polistes albellus Females

The general picture of the melanin pattern variability in females and males of *P. albellus* is shown in the schemes (Fig. 5; Fig. 6). The pattern variants found on practically all the body parts represented only part of the total variability spectrum typical of the *Polistes* wasps studied in this respect (Rusina, 2009). Analysis of pattern variability on some body parts allowed us to make diagrams showing the full spectrum of variants and the

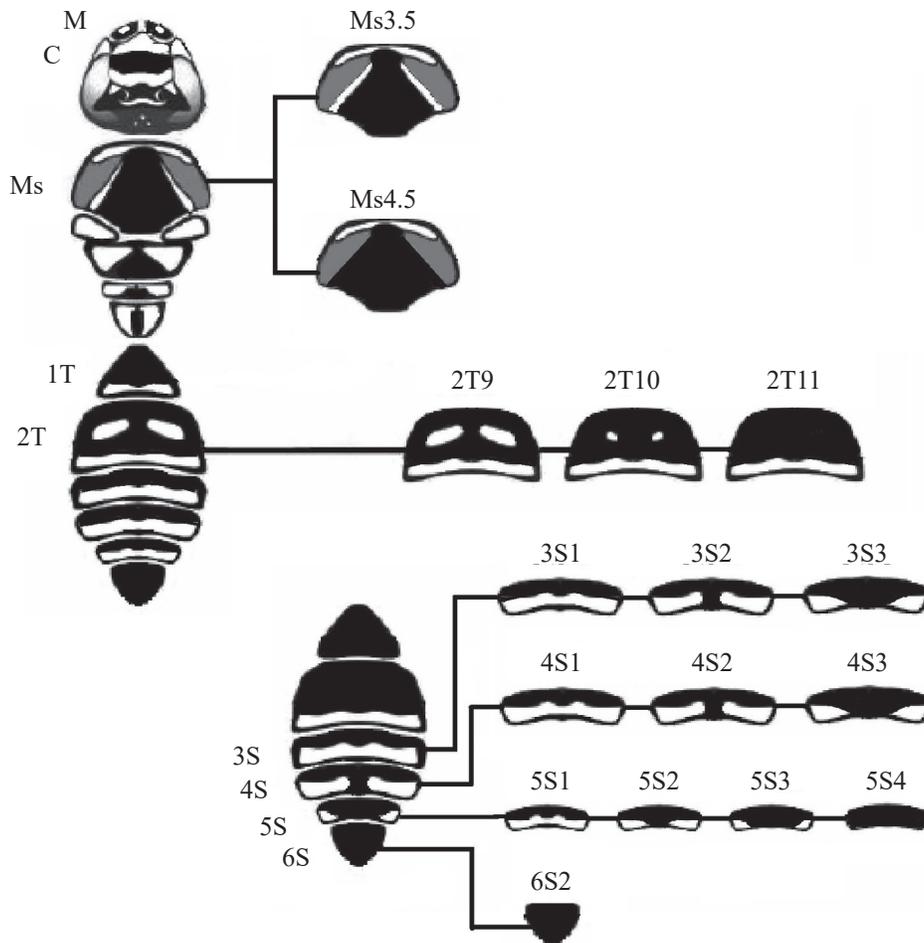


Fig. 5. Pattern variants in females of *Polistes albellus* Giordani Soika: M, mandibles; C, clypeus; Ms, mesoscutum; 1T and 2T, metasomal tergites 1 and 2; 3S–6S, metasomal sternites 3–6.

trends in their development (Fig. 7; Fig. 8; Fig. 9; Fig. 10; Fig. 11; Fig. 12; Fig. 13).

The pattern variability in *P. albellus* was similar to that in *P. dominula* and *P. nimpha* but showed some specific features. In the females of these species, variability could be observed on the mandibles, clypeus, mesosoma, metasomal tergites 1 and 2, and metasomal sternites 4–6 (see Fig. 5).

The mandibular pattern in *Polistes* wasps is characterized by the presence (M1) or absence of yellow spots (M2). The mandibles of *P. albellus* were always only partly pigmented.

The variants of the clypeal pattern are determined by the appearance and subsequent merging of pigmented spots (Fig. 7). The clypeus of *P. albellus* had only one

strongly melanized variant with a wide central transverse band (C5).

On the mesosoma there are paired unpigmented areas (gaps) along the promesonotal suture and in the center of the mesoscutum. Correspondingly, the mesoscutal pattern is described by a combination of two numbers separated by a dot (see Fig. 8), with the first number designating the pattern variant for the first gap area, and the second number, for the second area. The gaps along the promesonotal suture in *Polistes* wasps can be characterized by four variants reflecting the degree of their development: the gaps reach the anterior margin, with the anterior part of the pronotum remaining non-melanized (Ms1); the gaps reach (Ms2) or do not reach (Ms3) the margin of the mesoscutum; the gaps are absent (Ms4).

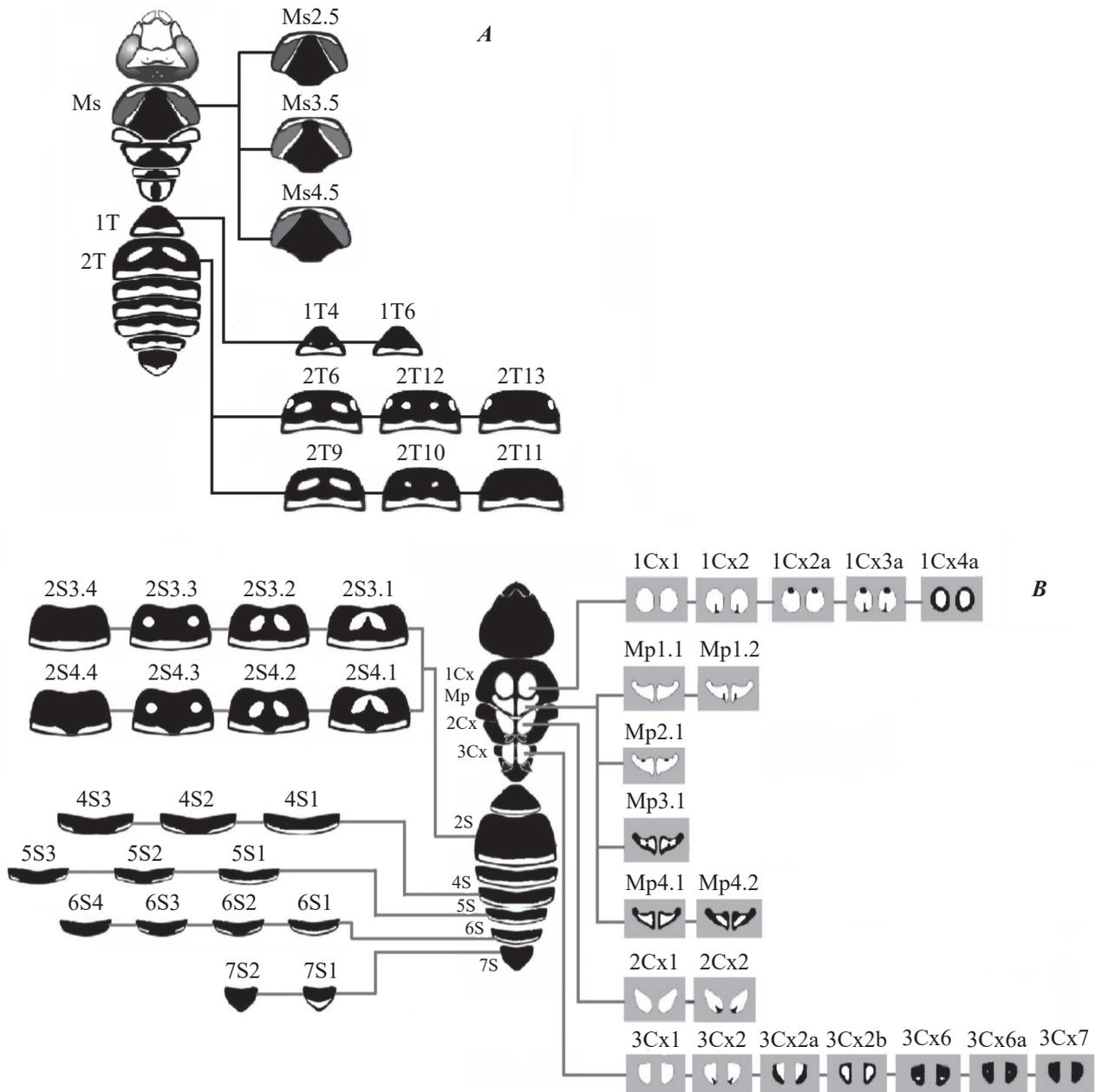


Fig. 6. Pattern variants in males of *Polistes albellus* Giordani Soika: (A) dorsal view; (B) ventral view; 2S, metasomal sternite 2; 1Cx–3Cx, fore, middle, and hind coxae; Mp, mesopleura; other designations as in Fig. 5.

The gaps in the center of the mesoscutum can be described as five variants arranged by increasing melanization: gaps shaped as large elongate commas (Ms1–4.1), as small commas (Ms1–4.2), as small triangles (Ms1–4.3), as dots (Ms1–4.4), or gaps can be absent (Ms1–4.5). In females of *P. albellus*, no gaps were found in the center of the mesoscutum, and two pattern vari-

ants were recorded for the promesonotal suture: Ms3.5 and Ms4.5 (see Fig. 5).

The pattern variants of metasomal tergite 1 in *Polistes* wasps are differentiated by the level of melanization of its dorsal part, while its distal margin always has a yellow band (Fig. 9). In the lightest variants, the gaps have

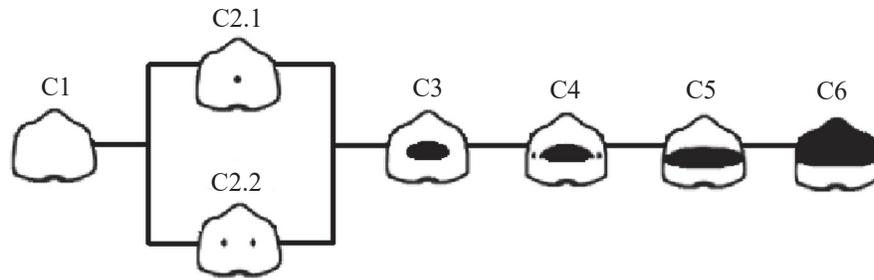


Fig. 7. Variants of the clypeal pattern in female *Polistes* wasps.

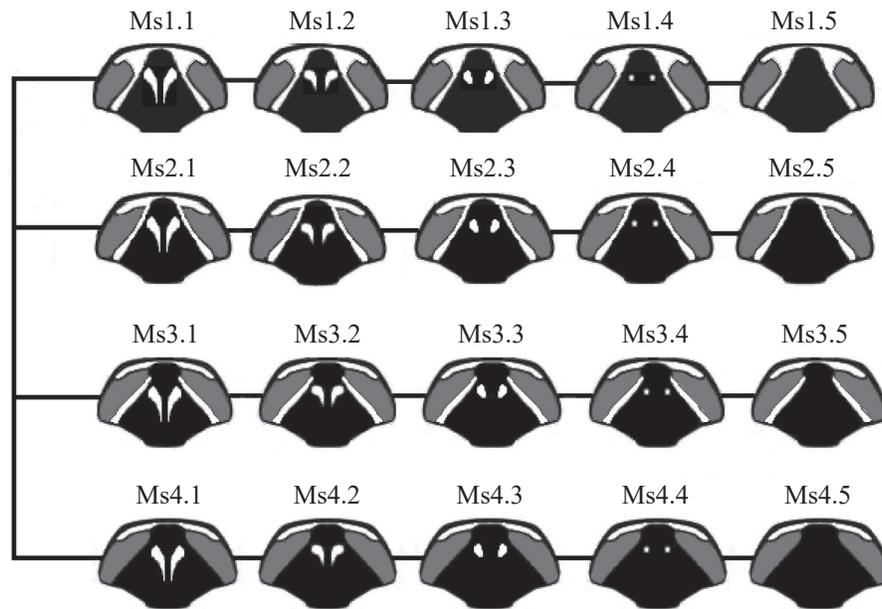


Fig. 8. Variants of the mesoscutal pattern in *Polistes* wasps.

a complex shape and merge with the distal yellow band. Further pattern development leads to separation and reduction of the gaps. A new pattern variant, unknown in other species, was recorded for metasomal tergite 1 of *P. albellus*. In this variant the distal yellow band becomes narrower, and the spots are absent (1T6).

The pattern variants of metasomal tergite 2 are differentiated by the presence of paired gaps and their size and shape (Fig. 10). In the lightest variants, the gaps may merge with the distal yellow band or remain separate, but they are large and have a complex shape. In the variants recorded in *P. albellus*, the central gaps were either present as large spots (2T9) or dots (2T10), or absent (2T11; see Fig. 5).

On the metasomal sternites of *Polistes* wasps, variability is observed in the transverse yellow band (see Fig. 5), which may be either continuous or divided into two parts by a pigmented wedge. Metasomal sternite 6 may be completely black or have a small gap in some species. In *P. albellus* pattern variability was recorded on sternites 3–5. In particular, sternites 3 and 4 had three pattern variants each: a solid yellow band (S1) and a more (3S2 and 4S2) or less (3S3 and 4S3) pronounced band divided by a pigmented area into two parts. Sternite 5 had some of the variants described above (5S1, 5S2, 5S3) and also a variant without the yellow band (5S4). Sternite 6 in *P. albellus* females was always completely black (6S2).



Fig. 9. Variants of the pattern of metasomal tergite 1 in *Polistes* wasps.

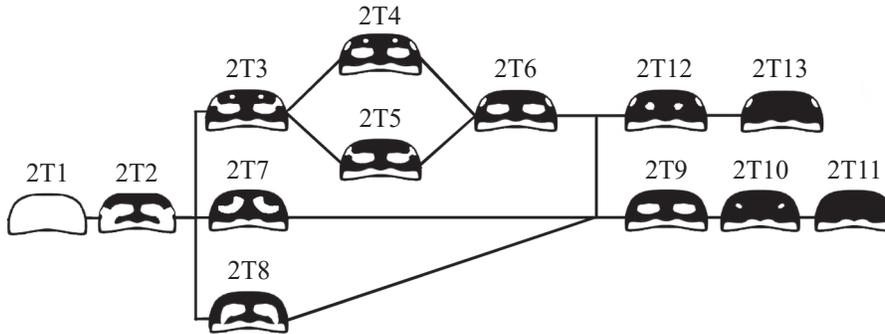


Fig. 10. Variants of the pattern of metasomal tergite 2 in *Polistes* wasps.

Melanin Pattern of Polistes albellus Males

Males of *P. albellus* are much more variable than females and in general have a noticeably lighter coloration. Pattern variability in males of this species was recorded on the clypeus, mesoscutum, all the coxae, metasomal tergites 1 and 2, and metasomal sternites 2 and 4–7 (see Fig. 6).

As in other *Polistes* species, the variability of the mesosomal pattern in *P. albellus* males is similar to that in females (Fig. 8). Most males in our material had the same variants of mesoscutal pattern as females, i.e., with gaps along the promesonotal suture (Ms3.5) or without such gaps (Ms4.5). Occasional specimens had variant Ms2.5, with the gaps extending along the promesonotal suture as far as the anterior margin of the mesoscutum and without the paired central gaps.

The mesopleural pattern of male *Polistes* wasps is highly variable (Fig. 11) and reveals an almost complete spectrum, from completely yellow coloration to the darkest variant without gaps. The pigment spots vary in shape and can occur in different places.

Six pattern variants were recorded on the mesopleura of *P. albellus*. Three of them also occur in other *Polistes* species: the lightest variant (Mp1.1), the variant with a posterior pigmented focus (Mp1.2), and the pigmented

variant with a central gap (Mp4.2). In addition, three previously undescribed variants were found in *P. albellus*. In the first variant, a pigment point appeared at the upper margin of the mesopleuron (Mp2.1). In the second variant, pigmentation spread onto the entire outer margin (Mp4.1). The third variant (Mp3.3) was similar to the preceding one, differing from it in two protrusions in the inner part of the pigmented band.

The pattern of metasomal tergites in males follows the same scheme as that in females. Metasomal tergite 1 of *P. albellus* had two variants. The most common variant was the one with a yellow band along the tergite margin (1T6); it was also found in females of this species. Besides, males also had the variant with paired dot-like gaps (1T4).

Six pattern variants were recorded for metasomal tergite 2 of *P. albellus* (see Fig. 10). Three of them were similar to those found in females of this species and were characterized by a pair of central spots (2T9), which could be reduced to dots (2T10) or completely absent (2T11). In addition, there was one lighter variant with two pairs of spots (2T6). Further development of this pattern in *P. albellus* consisted in reduction of the large central spots to dots (2T12) and their complete disappearance, with the lateral spots preserved (2T13). The last two pattern variants were not recorded in *P. dominula* and *P. nimpha*.

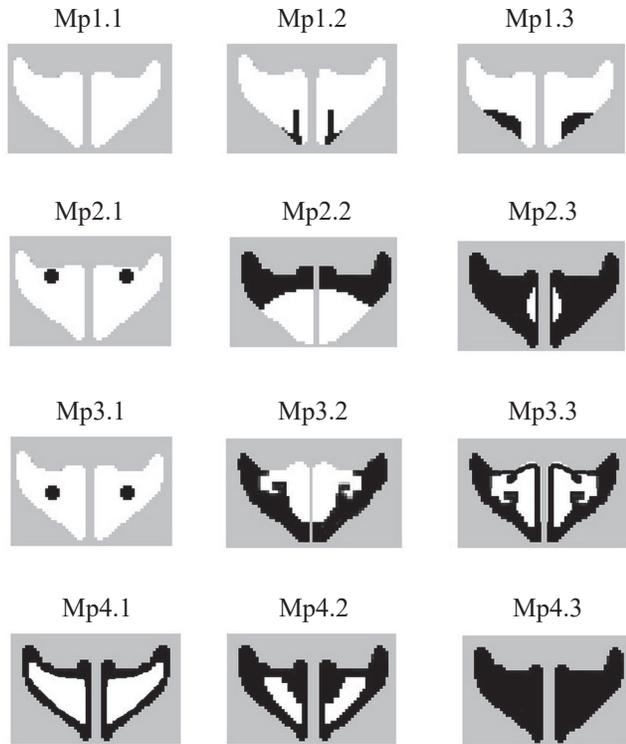


Fig. 11. Variants of the mesopleural pattern in male *Polistes* wasps.

The main changes in the pattern on metasomal sternite 2 in *Polistes* wasps involve the central gaps (Fig. 12). In particular, males of *P. nimpha* possess the lightest variant and the variant with paired pigmented spots that are not found in *P. dominula*. As many as six pattern variants are known in *P. dominula*, and only two have been found in *P. nimpha*.

Considerable variability of metasomal sternite 2 in *P. albellus* males was manifested in the presence or absence, number, size, and shape of gaps. In addition, variability involved the yellow band running along the distal sternite margin. This band could be entire or divided into two parts by a pigmented area. The patterns of sternite 2 can be divided into two groups.

The first group unites the patterns with an entire yellow band. The brightest variant was characterized by two large merging spots in the center (2S3.1); in other variants they split into two separate spots (2S3.2), which then decreased in size (2S3.3) and disappeared completely (2S3.4).

The patterns of the second group generally resembled the variants of the first group, but differed from them

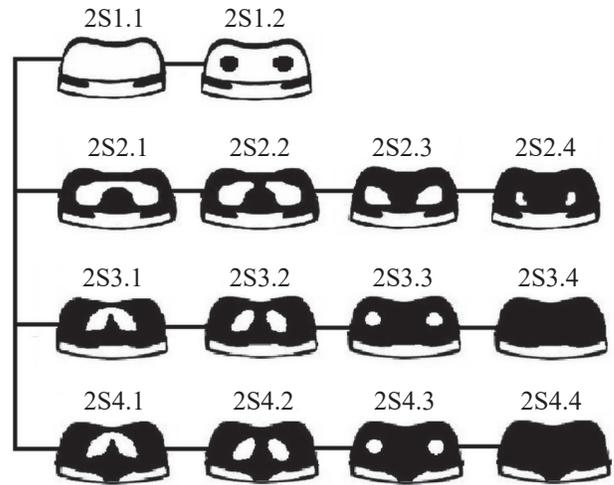


Fig. 12. Variants of the pattern of metasomal sternite 2 in *Polistes* wasps.

in the yellow band divided into two parts by a central pigmented area (2S4.1–2S4.4).

Variants of the melanin pattern on metasomal sternites 4–7 in *P. albellus* differed in the characteristics of the yellow band (S1–S2–S3). Apart from these variants, sternite 6 could be completely pigmented (S4). The last sternite (7) could have a small yellow gap (7S1) or no such gap (7S2).

Similar to other *Polistes* wasps, the variability of all the coxal patterns in *P. albellus* males was manifested in reduction of the gaps and an increase of pigmentation in various places (Fig. 13). Both completely non-melanized variants (1Cx1, 2Cx1, 3Cx1) and variants with a pigmented patch at the lower margin (1Cx2, 2Cx2, 3Cx2) could be found on all the coxae. The fore and hind coxae revealed some pattern variants previously unknown in males of *P. dominula* and *P. nimpha*. For instance, besides variants 1Cx1 and 1Cx2, the fore coxae revealed a variant with a spot in the upper position (1Cx2a). One more variant was characterized by a lower pigmented focus in addition to the rounded upper spot (1Cx3a). There was also a variant with pigmented bands along the outer margins of the coxae and with unpigmented central parts (1Cx4a).

The pattern variability on the hind coxae included variants 3Cx1 and 3Cx2, and also a pattern previously unknown in other species, with a pigmented band along the outer margin (3Cx2a). In a more pigmented variant,

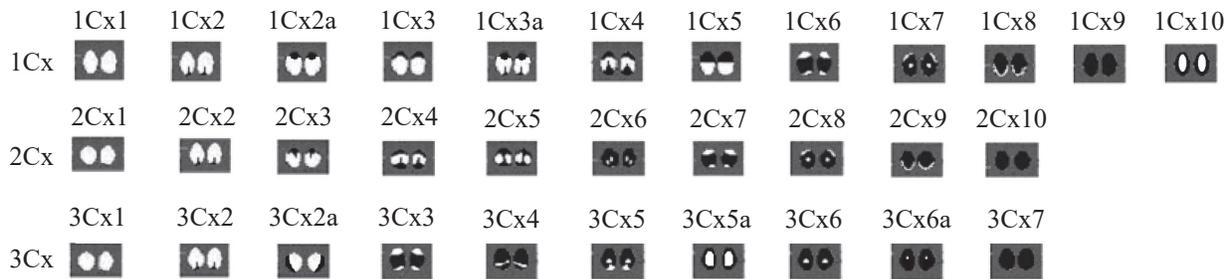


Fig. 13. Variants of the coxal pattern in male *Polistes* wasps.

the band extended over the entire margin of the coxa (3Cx2b); increased melanization in this case resulted in a variant with a small central gap (3Cx6). Non-melanized gaps in *P. albellus* were preserved as small dots (3Cx6a). Finally, in the darkest variant the hind coxae were completely pigmented (3Cx7).

*Nesting Places and Phenology
of Colony Development of Polistes albellus
in Central Meshchera*

The overwintered foundresses of *P. albellus* in Central Meshchera built nests on plants in spring ($N = 222$; see Table 2). Most of the nests occurred in two settlements, in which some nests were positioned very close together, and others occurred in small sparse groups. In addition, some solitary nests were found outside the settlements.

In the first settlement, nests of *P. albellus* were most often attached to dry stems of herbaceous plants of the previous year (77.8%, 42 out of 54), less often to the stems of low vegetating young trees and shrubs. In the second settlement, most nests (80.95%, 136 out of 168) were built on young trees of the Scots pine *Pinus sylvestris* (on average 0.62 ± 0.30 m tall), less often on deciduous shrubs and trees and on the stems of herbaceous plants.

The overwintered females nested singly in May. On one occasion on June 2, a female European hornet *Vespa crabro* L. (Hymenoptera, Vespidae) was observed landing on a nest of *P. albellus*, extracting a larva and chewing it; on that day the hornet visited the nest several times and severely damaged it. On the next day, the ringed foundress of the damaged nest moved to a neighboring nest located 8 m away. No aggressive interactions between this female and the foundress of

the neighboring nest were observed, and the two foundresses subsequently inhabited the nest together.

Comparative analysis of the spatial and temporal parameters of the nests revealed statistically significant differences between settlements in the height of nest attachment. In particular, in the first settlement, located in a more humid biotope, the nests were attached higher than the solitary nests and those in the second settlement (Fig. 14).

The earliest workers emerged in the beginning third of June, on average on June 10 ± 3 days ($N = 39$). Males were recorded in some nests on June 15, and their mass emergence occurred on average on July 9 ± 6 days. The future foundresses appeared after the emergence of males, in the last third of July. They were recorded only in part of the nests in the second settlement and in solitary nests, because all the colonies in the first settlement were destroyed by cattle grazing.

No differences were found between the settlements in the timing of emergence of workers, males, and future foundresses in 2019.

No parasitic mites *Sphexicozela connivens* and strepsipterans *Xenos vesparum* were found on the examined adult wasps ($N = 671$). No covers of the parasitoid wasp *E. schmitti* were found in the nests, either.

Signs of infestation with the parasitoid wasp *Latibulus argiolus* were found in 10.81% of the nests (24 out of 222). Only the first generation of the parasitoid was detected in 5.36% of nests (3 out of 54) in the first settlement. In the second settlement, the rate of infestation with the first generation of *L. argiolus* was 3.57% (6 out of 168 primary nests); that with the second generation was 41.4% (12 out of 29 surviving nests). Two colonies were infested with both generations of *L. argiolus*.

Table 2. Species composition of plants used for nesting by *Polistes albellus* Giordani Soika

Plant species	Frequency of nesting, %			
	first settlement (N = 54)	second settlement (N = 168)	solitary nests (N = 19)	total (N = 241)
Family Pinaceae				
<i>Pinus sylvestris</i> L.	–	79.17	42.11	58.5
Family Betulaceae				
<i>Betula pendula</i> Roth	–	1.19	10.53	1.66
Family Compositae				
<i>Tanacetum vulgare</i> L.	3.7	0.59	–	1.24
Family Elaeagnaceae				
<i>Hippophaë rhamnoides</i> L.	–	–	10.53	0.83
Family Fagaceae				
<i>Quercus robur</i> L.	–	–	5.26	0.42
Family Gramineae				
<i>Calamagrostis epigeios</i> (L.) Roth	18.52	0.59	–	4.56
<i>Dactylis glomerata</i> L.	–	1.79	–	1.24
Family Onagraceae				
<i>Epilobium</i> sp.	–	–	5.26	0.42
Family Polygonaceae				
<i>Rumex confertus</i> Willd.	16.67	2.38	–	5.39
Family Ranunculaceae				
<i>Ranunculus acris</i> L.	1.85	–	–	0.42
Family Rhamnaceae				
<i>Frangula alnus</i> Mill.	–	2.98	–	2.07
Family Rosaceae				
<i>Amelanchier spicata</i> (Lam.) C. Koch	1.85	–	–	0.42
<i>Malus domestica</i> Borkh.	7.41	5.37	15.79	6.64
<i>Rosa majalis</i> Herrm.	1.85	–	5.26	0.83
<i>Rubus idaeus</i> L.	1.85	–	–	0.42
Family Rubiaceae				
<i>Galium mollugo</i> L.	–	0.59	–	0.42
Family Salicaceae				
<i>Populus alba</i> L.	–	0.59	–	0.42
<i>Salix cinerea</i> L.	9.26	3.57	5.26	4.98
Family Sapindaceae				
<i>Acer negundo</i> L.	1.85	1.19	–	1.24
Unidentified plants	35.19	–	–	7.88
<i>N</i> is the number of nests				

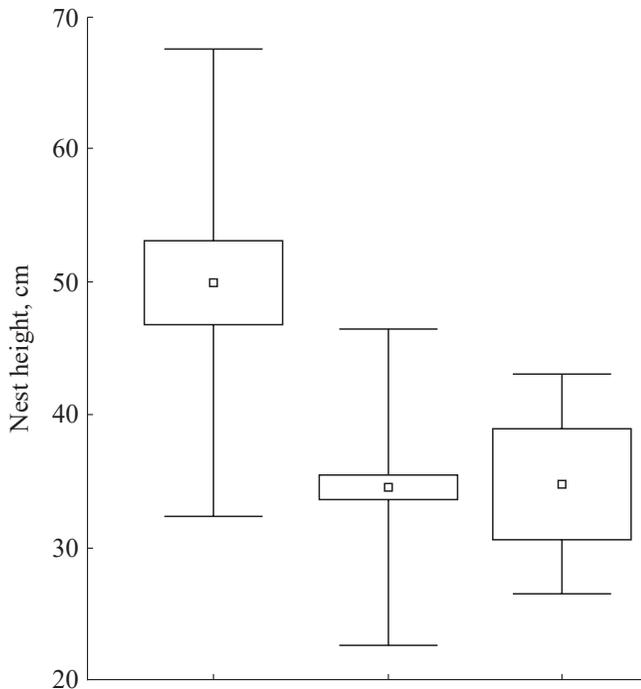


Fig. 14. Initial height of attachment of *Polistes albellus* nests in Central Meshchera. Groups of nests: (1) the first local settlement, (2) the second local settlement, (3) solitary nests. Kruskal-Wallis test: $H = 27.9$, $p < 0.001$. Pairwise comparisons by Dunn's test: (1) vs (2): $Q = 27.7$, $p < 0.001$; (1) vs (3): $Q = 4.3$, $p < 0.05$; (2) vs (3): $Q = 0.02$, $p > 0.05$.

Brood infestation was observed in a small secondary nest, built by the workers after destruction of the primary nest and containing only 38 cells.

Among the 8 solitary nests that survived, 1 showed signs of infestation with the first generation, and 3 nests, with the second generation of *L. argioides*.

The intact colonies and those infested with *L. argioides* were similar in size in each settlement.

Formation of Local Settlements by Polistes albellus Queens of Different Morphotypes in Central Meshchera

Phenotypic differences between the queens in two settlements were found in the frequencies of pattern variants of metasomal sternites 3 and 5: $\chi^2 = 15.85$, $p < 0.001$ and $\chi^2 = 13.52$, $p < 0.01$, respectively (Table 3; Table 4). Females with phenotype Ms3.5–1T9 clearly predominated in both settlements, comprising 58.34% and 35%, respectively.

At the same time, the choice of nesting places and the dates of colony initiation by foundresses of different morphotypes were found to be non-random in each settlement. The colonies of the first settlement had the following mean demographic parameters (here and below, they are expressed as Me [25; 75] [min; max]): the number of cells: 56 [49; 61] [26; 72]; pupae: 6 [4; 8] [0; 17]; IV instar larvae: 2 [1; 3] [0; 5]; V instar larvae: 2 [0; 3] [0; 7]. The colonies of the second settlement had the following mean parameters: the number of cells: 47 [28; 58] [4; 93]; pupae: 0 [0; 9] [0; 14]; IV instar larvae: 0 [0; 2] [0; 6]; V instar larvae: 0 [0; 0] [0; 5].

In the first settlement, queens with lighter variants of metasomal sternite 5 had more cells in their nests: $r_s = -0.39$, $p < 0.05$. Besides, queens with more melanized sternite 4 attached their nests at a greater height: $r_s = 0.42$; $p < 0.05$. In the second settlement, a negative correlation was revealed between the level of melanization of metasomal sternite 3 and the nest crowding: $r_s = -0.41$; $p < 0.05$, i.e., foundresses with lighter variants of sternite 3 showed a greater preference for nesting in clusters.

No correlation was observed between the degree of melanization of the queens and the rate of infestation of their brood with *Latibulus argioides* in either settlement.

Queens of different morphotypes did not differ in their choice of plants or orientation of the nests.

Seasonal Dynamics of the Phenetic Composition of Polistes albellus in Central Meshchera

Queens and workers in both settlements showed identical pattern variants of the mandibles (M1), clypeus (C5), metasomal tergite 1 (1T6), and sternite 6 (6S2). At the same time, the females differed in the frequencies of pattern variants of the mesoscutum, tergite 2, and sternites 3–5 (Table 3).

In the first settlement, the frequencies of 2T pattern variants were similar in the queens and workers. The lightest variants were the most common in both castes. In addition, the two castes had similar frequencies of 3S pattern variants, this sternite being strongly pigmented in most females.

Table 3. Frequencies of different pattern variants (%) in queens, workers, and future foundresses of *Polistes albellus* Giordani Soika in the local settlements in Central Meshchera

Body part	Pattern variant	1 (N = 36)	2 (N = 74)	3 (N = 40)	4 (N = 248)	5 (N = 14)	6 (N = 106)	7 (N = 48)
Mesoscutum	Ms 3.5	80.56	72.97	70	68.14	78.57	80.19	89.58
	Ms 4.5	19.44	27.03	30	31.86	21.43	19.81	10.42
Tergite 2	2T9	66.67	36.49	55	33.47	0	24.53	14.58
	2T10	19.44	36.49	35	36.69	71.43	38.68	31.25
	2T11	13.89	27.02	10	29.84	28.57	36.79	54.17
Sternite 3	3S1	2.78	1.35	5	0	0	0	0
	3S2	38.89	27.03	2.5	25	0	8.49	12.5
	3S3	58.33	71.62	92.5	75	100	91.51	87.5
Sternite 4	4S1	2.78	1.35	0	0	0	0	0
	4S2	16.67	0	2.5	0.81	0	0.94	2.08
	4S3	80.55	98.65	97.5	99.19	100	99.06	97.92
Sternite 5	5S2	5.56	0	2.5	0	0	0	0
	5S3	66.66	8.11	27.5	6.45	0	1.89	14.58
	5S4	27.78	91.89	70	93.55	100	98.11	85.42

1, queens of the first settlement; 2, workers of the first settlement; 3, queens of the second settlement; 4, workers of the second settlement; 5, future foundresses of the second settlement; 6, workers from solitary nests; 7, future foundresses from solitary nests; *N* is the number of specimens.

Table 4. Differences in the frequency of pattern variants in queens and workers of *Polistes albellus* Giordani Soika from the local settlements in Central Meshchera: χ^2 test

Pattern variant	1 vs 2	3 vs 4	1 vs 3	2 vs 4
Ms	0.75	0.06	1.13	0.62
2T	8.87	9.41**	2.33	0.31
3S	2.01	21.73***	15.85***	3.53
4S	13.46**	–	5.84	3.95
5S	48.60***	24.59***	13.52**	–

1, queens of the first settlement; 2, workers of the first settlement; 3, queens of the second settlement; 4, workers of the second settlement; ** $p < 0.01$; *** $p < 0.001$.

In the second settlement, queens were similar to workers in the frequency of mesoscutal pattern variants. The prevalent variant in both castes was Ms3.5 with a gap along the promesonotal suture. Similarity was also observed in metasomal sternite 4, which most often had dark pattern variants.

Queens and workers in the first settlement showed statistically significant differences in the frequencies of pattern variants of metasomal sternites 4 and 5 (Table 4): variant 4S2 with pronounced gaps was recorded in

queens but not in workers; the darkest variant of this sternite (4S3) was the most common in both groups. Sternite 5 most often had gaps in queens, but it was completely pigmented in the great majority of workers. In addition, the lightest variant 5S2 was never recorded in workers. The mesoscutum of both female castes most often had the lightest variant Ms3.5, but its proportion was noticeably lower in workers than in queens. In general, workers differed from queens in the prevalence of more melanized variants of all the studied traits.

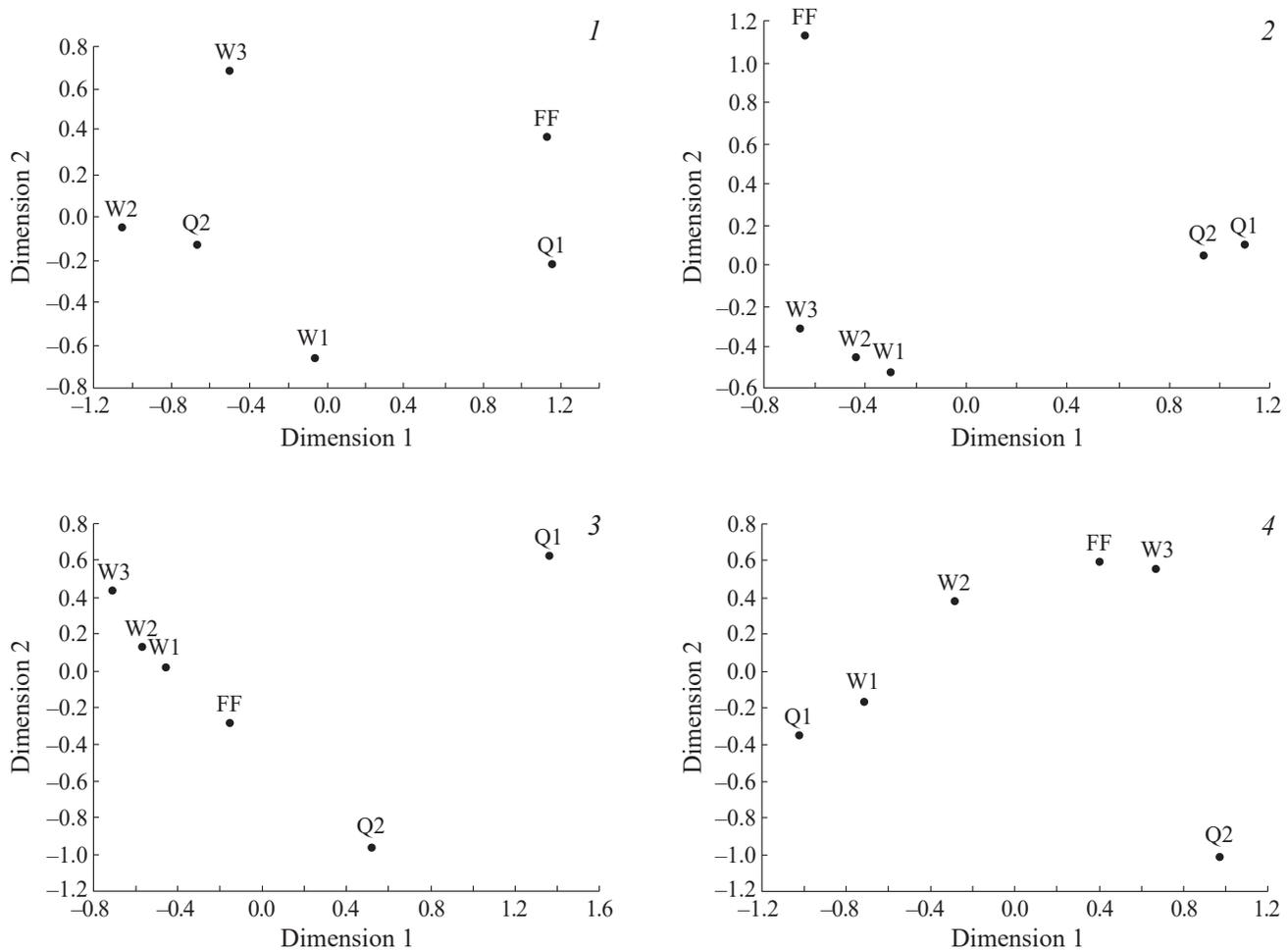


Fig. 15. Phenotypic distances based on the patterns of the mesoscutum (1), metasomal tergite 2 (2), metasomal tergite 5 (3), and metasomal sternite 3 (4). Groups of *Polistes albellus* wasps: Q1, queens in the first local settlement; W1, workers in the first local settlement; Q2, queens in the second local settlement; W2, workers in the second local settlement; W3, workers in solitary nests; FF, future foundresses.

Queens in the second settlement significantly differed from workers in the frequencies of pattern variants of 2T, 3S, and 5S (see Table 4). The lightest variant of metasomal tergite 2 with large spots (2T9) was prevalent in queens, and a darker variant with small gaps (2T10), in workers. The lightest variant of 3S pattern with a continuous band (3S1) was found in the second settlement only in workers. Besides, the variants of sternite 5 with gaps were more common in queens than in workers. The lightest variants 4S1 and 5S2 were not found in workers at all.

Two settlements in Central Meshchera differed in the frequencies of melanin pattern variants in queens and workers of *P. albellus* (see Table 3; Fig. 15). Queens in two settlements had similar frequencies of pattern variants of tergite 2, mesoscutum, and sternite 4, but they

differed considerably in the frequencies of pattern variants of sternites 3 and 5. Queens in the second settlement more often had more melanized variants of these body parts. The relative occurrence of different pattern variants on all the body parts was similar in the workers of both settlements (see Table 4).

On the whole, the samples of workers and future foundresses from different settlements and solitary nests were similar, while the samples of queens phenotypically differed from them and from each other.

It is noteworthy that the samples of workers were arranged in the sequence W1–W2–W3 along one of the axes for almost all the characters (Fig. 15; Fig. 16). The samples of queens were sometimes arranged in the same sequence. This sequence of phenetic compositions cor-

responded to the gradual change from more humid to drier nesting habitats.

For analysis of the combinations of pattern variants, we selected the body parts showing the highest variability, namely the mesoscutum and metasomal tergite 2 (Table 5).

Queens in both settlements most often had the light phenotype variants Ms3.5–2T9 and Ms3.5–2T10. The difference between the settlements was that queens in the second settlement also frequently had the darker variant Ms4.5–2T9.

Workers in both settlements most often had phenotypes Ms3.5–2T9, Ms3.5–2T10, and Ms3.5–2T11. Specimens with phenotype Ms4.5–2T10 were found only in the first settlement.

It should be noted that the samples from Central Meshchera included all the phenotypes described by us based on photos from other, considerably remote parts of the species' range (see Table 1). In particular, workers and future foundresses of *P. albellus* from Switzerland had phenotype Ms3.5–2T9 ($N = 8$). Three females were described from Bashkortostan, of which 2 had phenotype Ms3.5–2T9 and 1 had phenotype Ms3.5–2T10. A female from Orenburg Province had phenotype Ms3.5–2T10. The combination Ms4.5–2T11 was recorded in Zabaikalskii Territory (Osya Rossii, 2011–2018), and Ms3.5–2T11, in Kazakhstan.

DISCUSSION

The melanin patterns of insects have been studied for more than 100 years, mainly in beetles. At first, the

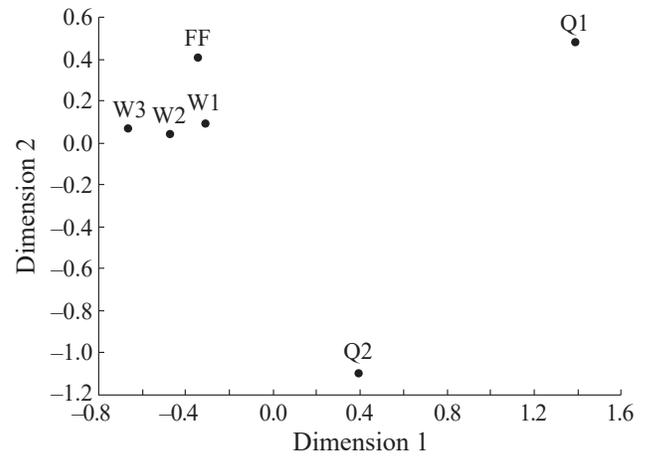


Fig. 16. Total phenotypic distances between different groups of *Polistes albellus* wasps: Q1, queens in the first local settlement; W1, workers in the first local settlement; Q2, queens in the second local settlement; W2, workers in the second local settlement; W3, workers in solitary nests; FF, future foundresses.

known pattern aberrations were relatively few, and they were even given Latin names which, however, had no taxonomic status (e.g., see Plavilstshikov, 1936; Zakharov, 1997, etc.). As the material accumulated, hundreds of pattern variants became known in some species. An important step was made by Filippov (1961), who showed that many aberrations could be arranged into series of forms connected by certain transformations. Further studies showed that the pattern of insects was composed of certain elements whose presence was related to the pigmentation level (i.e., the amount of pigment in the cuticle) and followed certain species-

Table 5. Frequencies of different phenotypes (%) of *Polistes albellus* in the local settlements in Central Meshchera

Phenotype	Queens of first settlement ($N = 36$)	Workers of first settlement ($N = 74$)	Queens of second settlement ($N = 40$)	Workers of second settlement ($N = 248$)
Ms3.5–2T9	58.34	31.08	35	27.02
Ms3.5–2T10	11.11	25.67	27.5	27.82
Ms3.5–2T11	11.11	16.22	7.5	13.31
Ms4.5–2T9	8.33	5.41	20	6.45
Ms4.5–2T10	8.33	10.81	7.5	8.87
Ms4.5–2T11	2.78	10.81	2.5	16.53
Total	100	100	100	100

N is the number of specimens

specific trends (Kreslavsky, 1975, 1977; Vasil'ev, 1988, 2005, etc.).

Our analysis showed the variability of melanin pattern to be similar in *P. dominula*, *P. nimpha*, and *P. albellus* (Rusina et al., 2006, 2007c). Variability was recorded on a greater number of segments with different melanin patterns in *P. nimpha* than in other species, but *P. albellus* had a broader spectrum of pattern variants on some body parts, such as the mesoscutum (see Fig. 8) and the mesopleura and coxae in males (see Fig. 11; Fig. 12).

Polistes albellus, unlike *P. nimpha* and *P. dominula*, nests openly on plants, and its colonies are founded haplometrotically by overwintered foundresses. Among the species that nest not only on plants but also in various shelters of natural and anthropogenic origin, the queens of *P. nimpha* with lighter variants of metasomal tergite 1 prefer nesting in shelters, and those with darker pattern variants, on plants; the queens of *P. dominula* show an opposite tendency (Rusina, 2014). This trend can be traced in *P. nimpha* over a large part of its range, from Crimea to the Trans-Ural region (Rusina et al., 2008).

Our field studies of local *P. albellus* settlements in Central Meshchera showed that the features of melanin pattern in *Polistes* wasps reflected different components of variability (see Table 4). The samples of workers and future foundresses were phenotypically similar. In addition, analysis of phenotypic distances and the multidimensional scaling results indicated that the relative position of the samples corresponded well to the humidity gradient of the microhabitats. The samples of wasps from the humid grass-forb meadow (the first settlement) had the darkest coloration, and those from drier habitats (solitary nests) had the lightest coloration. Wasps from the settlement in a fallow with a pine coppice occupied an intermediate position; pine is known to prefer dry and well-drained soils. The workers and future foundresses developing under different conditions may be affected by the humidity factor both directly and indirectly, via the difference in the trophic spectra of the larvae.

Phenotypic differences between queens from different habitats were recorded earlier in other species of *Polistes* wasps. In particular, studies of *P. nimpha* in different parts of the Luhansk Nature Reserve (LNR) revealed differences between samples in the frequencies

of the pattern variants of metasomal tergite 1 (Rusina et al., 2007a). Besides, *P. nimpha* queens nesting in different plant communities in the Streltsovskaya Steppe part of LNR also differed in this character. Interannual differences between *P. nimpha* queens from LNR and *P. dominula* queens from the Black Sea Biosphere Reserve (BSR) were manifested in the frequencies of the mesoscutal pattern variants (Rusina et al., 2007a; Rusina and Orlova, 2009).

It remains unknown what factors affect the melanin pattern variability in workers, males, and future foundresses of *P. albellus*. We may suppose that, similar to *P. dominula*, the body size and melanin pattern of the adult wasp depend on the parameters of the larval diet that are determined by the morpho-physiological traits of the foundress as well as by the size and history of the colony (Rusina and Orlova, 2010; Firman and Rusina, 2013).

For instance, the darker was the clypeal pattern in *P. dominula* queens in BSR, the darker was the clypeus and the lighter were the mesoscutum and metasomal tergite 1 in the future foundresses in their progeny. In addition, the future foundresses reared in larger colonies had darker patterns of the clypeus and lighter patterns of the mesoscutum and metasomal tergite 1. Colonies of *P. dominula* vary considerably not only in the number of workers per one IV and V instar larva, but also in their foraging activity. These parameters are higher in successful colonies with active queens, as compared to other categories of colonies: orphaned, infested with the first generation of parasitoids, and usurped, i.e., aggressively taken over by alien queens (Rusina, 2009).

Experimental studies of *P. dominula* showed that changes in the diet of V instar larvae affected melanization of metasomal tergite 1 within the colony and the frequencies of mesoscutal pattern variants within the settlement (Rusina and Orlova, 2010). Insufficient feeding of the IV and V instar larvae in the experiment (as the result of a twofold reduction in the number of foragers and nurses) increased melanization of metasomal tergite 1, while the clypeus of the future foundresses became almost unpigmented. Significant shortage of food led to a decrease in the body size of females and a stronger mesoscutal pigmentation.

Some colonies of *P. albellus* in our material were infested with the parasitoid wasp *Latibulus argiolus*.

The intact and infested colonies were similar in size. Infestation of brood with the first generation of *L. argiolus* before the emergence of workers was not detected in any nest. By contrast, nearly 30% of *P. nimpha* colonies were infested with the first generation of *L. argiolus* in LNR in some years (Rusina, 2009). The female parasitoids infested the host colonies before the emergence of workers, preferring larger colonies which had been initiated by *P. nimpha* foundresses with darker pattern variants. *Elasmus schmitti* was not found in the colonies of *P. albellus*; yet this parasitoid wasp is known to infest pupae in the colonies of *P. nimpha* which nest in Central Meshchera not only in shelters (Kosyakova et al., 2020), but also on plants (the second settlement in 2020).

The parasitic mite *Sphexicozela connivens* and the strepsipteran *Xenos vesparum* were not found on males and females of *P. albellus* from Central Meshchera; at the same time, cases of infestation of *P. albellus* with *X. vesparum* were recorded in Switzerland (private collection of R. Neumeyer).

We found *S. connivens* on males and females of *P. nimpha* nesting on plants not far from *P. albellus* within the same local settlements, while *X. vesparum* was recorded on females of *P. dominula* nesting in shelters in Ryazan.

Parasite infestation was also shown to affect the phenotypic variability of males and future foundresses (Rusina and Orlova, 2011). For instance, weak and moderate infestation of *P. nimpha* larvae and pupae with the mite *S. connivens* changed the frequencies of pattern variants of metasomal sternite 4 in the future foundresses but did not affect their body size. Heavy infestation of larvae (more than 5 mites per host) resulted in a smaller body size of the adults and a higher proportion of wasps with a weakly melanized variant of sternite 4 (Rusina and Orlova, 2011).

On the whole, the process of melanization and pattern development in *P. albellus* remains insufficiently studied. The scheme presented herein will be modified and improved as new data become available on the ontogenesis of the pattern elements as well as on the phenetic composition of populations in different parts of the species' range.

ACKNOWLEDGMENTS

The authors are grateful to A.P. Morgachev, E.A. Morgacheva, A.S. Lukina, C.A. Lukin, D.A. Drobot, and D.A. Bovsunovsky for help with material collection, and to V.A. Valuev, A.V. Krutilin, and C. Dobler Gross for permission to use the photos. Thanks are also due to S.A. Belokobylsky, S.Ya. Reznik, A.V. Lopatin, A.V. Fateryga, and B.A. Korotyayev for critical discussion of the manuscript.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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