

The Role of Parasitoids in Regulation of *Polistes* Wasp Population (Hymenoptera, Vespidae: Polistinae)

L. Yu. Rusina

Kherson State University, Kherson 73000, Ukraine

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Abstract—The study conducted in 2005–2010 analyzes the behavioral response of the parasitoids *Latibulus argiolus* (Rossi) (Hymenoptera, Ichneumonidae) and *Elasmus schmitti* Ruschka (Hymenoptera, Eulophidae) to the distribution of their host, *Polistes* wasps (Hymenoptera, Vespidae). Various conditions of the parasitoid-host system and conditions of regulation of the host abundance are discussed. The parasitoid females are more active in wasp colony clusters and tend to infest larger nests. If the parasitoids are abundant, infestation of host colonies starts earlier, sometimes before the worker emergence; therefore, density-dependent behavioral response of parasitoids is caused primarily by the impact of the aggregation component. Thus, the host population density factor appears to be mediated not only by the non-uniform development rates of colonies and their spatial distribution, but also by the seasonal (temporal) aspect of their development. Low density of the host population, at which the parasitoids regulate the wasp abundance, corresponds to a certain phase of the seasonal colony development, namely to the period before the emergence of workers. On the whole, we are dealing with a host-parasitoid system in which the spatial and temporal factors are closely interrelated.

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The functional and numerical responses of parasitoids are considered among the main stabilizing factors affecting the population dynamics of solitary insects (Solomon, 1964; Hassell and May, 1974; Viktorov, 1975, 1976; Khorkhordin, 1975, 1977; Morrison and Strong, 1980; Guryanova, 1984; Hassell and Waage, 1984; Reznik and Umarova, 1991; Comins et al., 1992; Hassell, 2000; May and McLean, 2007, etc.). In this connection, of considerable interest is the study of responses of parasitoids infesting social insects to the host distribution. The functional response of parasitoids to an increasing density of the host population may include an increase of both the number of infested larvae in the nest and the number of colonies infested. In turn, the functional response creates prerequisites for intra- and intergenerational numerical responses (Hassell, 1964). The former type of numerical response results in aggregation of parasitoids in the areas of high density of their hosts, and the latter type, in the number of parasitoids growing together with the host population density in the subsequent generations.

The regulatory significance of the numerical and functional responses has been demonstrated for parasitoids infesting wasps of the genera *Polistes* and *Belonogaster* (Hymenoptera, Vespidae, Polistinae), despite the difficulties in differentiating between the

various components of their behavior and the specific traits of seasonal development of the host colony and the changing number of larvae suitable for infestation (Strassmann, 1981; Keeping and Crewe, 1983; Makino, 1989; Makino and Sayama, 1994; Rusina, 2008, 2009, 2010, 2011a).

Long-term studies of the host-parasitoid relations have shown that the infestation rates of individual colonies and the entire population vary greatly from season to season (Strassmann, 1981; Makino, 1983, 1989; Makino and Sayama, 1994; Rusina, 2006, 2008, 2009; Gumovsky et al., 2007). The fraction of infested larvae was positively correlated with the colony size in some host species and populations (Strassmann, 1981; Keeping and Crewe, 1983; Rusina, 2008, 2009, 2010, 2011a), and negatively correlated in others (Makino and Sayama, 1994). The observed tendency of parasitoids to infest the largest host colonies may be interpreted as manifestation of the behavioral response to the food resource density (the number of larvae which can be infested). Such a response was observed in two generations of the parasitoids *Latibulus argiolus* (Rossi) (Hymenoptera, Ichneumonidae) and *Elasmus schmitti* Ruschka (Hymenoptera, Eulophidae) infesting the colonies of *Polistes dominula* (Christ) and *P. nimpha* (Christ) (Rusina, 2009, 2010, 2011a). In

addition, the fraction of infested brood was shown to increase with the density of *P. dominula* nests built in shelters (Rusina, 2008). Females of *L. argiolus* were found to be more active in clusters of host colonies, in which they tended to infest larger nests. At high abundance of the parasitoid, infestation of the host colonies starts earlier, sometimes even before the emergence of workers. The latter case results in development of the smallest nests in which no less than 5%, and sometimes more than 10% of cells reveal traces of parasitoid infestation (Rusina, 2008, 2009).

Judging by the results of previous research, the size of the nest and the colony inhabiting it depended considerably on the phase of colony development during which it had been infested (Makino, 1989; Makino and Sayama, 1994; Rusina, 2008, 2011a). In particular, colonies of *P. nimpha* strongly infested with the 1st generation of the parasitoid (with more than 5% of cells containing infested brood) had fewer cells and workers as compared to weakly infested colonies (Rusina, 2011a).

Further studies of interrelations between two species of parasitoids and the wasp *P. dominula* nesting on plants in the Black Sea Biosphere Reserve (Kherson Province, Ukraine) showed that an increase in the absolute and relative number of infested host individuals within the examined range of densities was characteristic only of the chalcid wasp *E. schmitti*. The ichneumonid wasp *L. argiolus* also demonstrated a behavioral response under these conditions, since its females laid more eggs in areas of the greatest density of the host (Rusina, 2008). However, the latter species did not regulate the host abundance; such regulation implies that the infestation rate should depend on the host density (Viktorov, 1976), which was not observed in the above case.

Negative correlations between the number of cells with infested brood and the colony size were observed in a population of *P. snelleni* Saussure, whose rate of infestation with the parasitoid *E. japonicus* Ashmead often reaches 100% (Makino and Sayama, 1994). Under the conditions of Hokkaido Island (Japan) with its cold summers, the foundress raises a single cohort of workers, which in turn raise the reproductives. Unlike the polistine wasps inhabiting warmer regions, *P. snelleni* has a somewhat simplified life cycle: its colony does not contain workers raised by other workers. Therefore, the first generation of *E. japonicus* infests the first cohort of workers; in species inhabit-

ing regions with higher summer temperatures, this would mean an early infestation. In addition, *E. japonicus*, unlike *E. schmitti*, overwinters in the host nests. Under such conditions, infestation with parasitoids was shown to reduce the efficiency of rearing workers by 18–35%, and that of reproductives, by 17–22% (Makino and Sayama, 1994).

Infestation of a colony before the emergence of workers may also result from specific weather conditions during the colony foundation period. For example, the cold spring of 2004 delayed the onset of nesting (and the subsequent phases of nest development) of *P. dominula* in the Black Sea Biosphere Reserve (Rusina, 2008). Since infestation with the chalcid parasitoid *E. schmitti* was not delayed by the weather, this event coincided with an earlier phase of the host colony development, so that the parasitoid affected already the first cohort of workers. The same phenomenon was observed in the ichneumonid wasp *L. argiolus* which infested *P. nimpha* in the spring of 2007 in the territory of Lugansk Nature Reserve (Lugansk Province, Ukraine) (Rusina, 2009).

The stable coexistence of the parasitoid and host populations may be facilitated not only by annual fluctuations of their life cycles, but also by the specific traits of the host habitat which, in turn, may affect the intensity of predation (Nelson, 1968; Strassmann, 1981; Keeping and Crewe, 1983; Makino and Sayama, 1994; Rusina, 2008).

In addition, the effect of parasitoids on the abundance of polistine wasps depends on the defensive behavior of the host (Strassmann, 1981; Lutz et al., 1984; Makino, 1989; Makino and Sayama, 1994; Rusina, 2008) as well as on the intra- and interspecific competition of the parasitoids (Rusina, 2011b).

Below, I will consider some aspects of the behavioral response of the natural populations of parasitoids under the conditions of free choice of naturally distributed host colonies, and determine the conditions of regulation of the host abundance.

MATERIALS AND METHODS

The host-parasitoid relations were studied based on analysis of 908 nests from 12 local settlements of *Polistes nimpha* (Christ), 9 settlements of *P. dominula* (Christ), and 5 settlements of *P. gallicus* (L.), collected by myself and kindly provided by my colleagues and students of Kherson, Chernovtsy, and

Yekaterinburg universities. The collection localities and sample parameters are listed in table.

The polistine wasps studied share the following traits of the life cycle. The overwintered fertilized foundresses build nests during the first decade of May and raise the first generation of workers which emerge during the first half of June. In the process of colony development, it switches from rearing workers to raising the sexual individuals (males and prospective foundresses). The future foundresses of these species appear in August, after the mass emergence of the males. Mating of the sexual individuals and disintegration of the colony take place at the end of summer and in autumn. The future foundresses overwinter whereas the males and workers die in autumn.

The history of colony infestation was described by the nest mapping method, recording the number of meconia and traces of the presence of the parasitoids whose larvae had consumed the host pupae (Grechka and Kipyatkov, 1983; Rusina, 2006). Infestation with *Latibulus argiolus* was determined by the presence of ovaly slanted, light yellow or light orange remains of the larval cuticle on the cell margins (Makino, 1983). Infestation with *Elasmus schmitti* was determined by the presence of dark gray covers in the cells, formed of the parasitoid's meconium prior to pupation (Gumovskiy et al., 2007). Both parasitoids develop in two generations: females of the first generation infest the host nests from the end of May to mid-June, and those of the second generation, from the second half of July to the beginning of August (Rusina, 2009).

In addition, two circumstances were taken into account: first, that the parasitoids tend to infest the largest colonies in the settlement, and second, that the colonies that get infested earlier in the season are smaller (Rusina, 2009, 2010). The following temporal variants of infestation were distinguished.

(1) Parasitoids of the first generation infest the colony before the emergence of workers; the nest consists of up to 50 cells at the end of the life cycle; cells with traces of parasitoid infestation are located in the center of the nest.

(2) Parasitoids of the first generation infest the colony after the emergence of workers; the nest consists of 50–120 cells at the end of the life cycle. Cells with parasitoids occur both in the center and in the periphery of the nest.

(3) Parasitoids of the second generation infest the colony while it is raising the reproductive generation.

The nest consists of 90–340 cells at the end of the life cycle; cells with parasitoids occur both in the center and in the periphery of the nest.

The relation between parasitoid infestation, determined by the absolute and relative number of cells with infested brood, and the colony size (considering the total number of cells, the number of cells with one, two, or three meconia, and the total number of the adults reared) was estimated by the Kendall correlation coefficient (Strassmann, 1981). The relation between the absolute and relative brood infestation (the fraction of cells with parasitoids related to the total number of cells in the nest, %) and the spatial parameters of the colony (the distance to the nearest neighboring colony and the level of aggregation) was estimated by the Spearman correlation test. The level of aggregation was estimated by Lloyd's index of patchiness, within areas of 0.5×0.5 m for nests built in the attics of buildings, and within areas of 5×5 m for openly located nests.

The fraction of infested colonies in the settlement (below referred to as settlement infestation) was used as a measure of the relative abundance of the parasitoid. This method does not allow one to determine the absolute number of parasitoid females and the nature of their response (functional, numerical, or combined), but still provides the means for assessing certain behavioral traits of the parasitoids.

In the table, data for each sample were presented as the median and the 1st and 3rd quartiles: Me [25; 75] (Glantz, 1999). The results obtained were statistically processed using the Statistica v. 6.0 software package (Statsoft Inc., USA, 1984–2001).

RESULTS AND DISCUSSION

The interrelations between the parasitoids and the host species can manifest themselves by one of the following variants.

(1) There is no correlation between the colony size and the absolute and relative number of infested cells. This condition can be observed when colonies in the wasp settlement become infested with only the 2nd generation of one or several species of parasitoids, apparently as the result of their migration (*a*). As an example, the coefficients of correlations for *P. dominula* and two parasitoid species infesting it in the Solenoozernyi sector of the Black Sea Biosphere Reserve are shown in table. Sample 1 corresponds to the combined infestation with the two parasitoid spe-

cies, while samples 2 and 3 correspond to each of the two species separately.

In some cases, the correlation may be statistically non-significant for each parasitoid species considered separately but significant for the two species combined (a local settlement of *P. dominula* examined in 2009, located in the attics of two nearby buildings in Kherson: samples 28 and 29).

This variant can also be observed in the case of weak infestation with the 1st generation of parasitoids; no colonies infested before the emergence of workers were found in such settlements (*b*: sample 5). If the settlement is infested with two parasitoid species, the above situation may be observed for only one of them (samples 13 and 36).

Finally, the correlation is absent when the colonies are infested with the 1st generation of parasitoids before the emergence of workers but are positioned far apart (*c*: samples 4 and 6 in table).

In some cases, the samples are too small to confirm the presence or absence of any correlation (*d*: sample 7).

As a rule, all the above samples were characterized by the absence of strongly parasitized colonies, i.e., those with more than 10% of cells infested with parasitoids.

(2) The number of parasitoids in the nest is positively correlated with the host colony size, whereas the nest density and the parasitoid abundance are higher. The fraction of infested colonies is high, reaching ~85%. There are two variants of this state.

In the first case, the colonies are infested with the 1st generation of parasitoids after the emergence of the first cohort of workers (late infestation: sample 8 in table).

In the second case, the settlement includes some colonies infested with the 1st generation of parasitoids before the emergence of workers (samples 9–12 and 14–19 in table). The fraction of such colonies in some settlements may reach 22%. Even though some colonies are strongly infested, their productivity is not considerably affected, so that the infested and intact colonies remain similar in size.

In general, it may be concluded that under such conditions, parasitoids can only modify the abundance of the host.

(3) Both the absolute number and the fraction of infested cells are positively correlated with the colony size (samples 20–27). The nest density is high. The colonies are infested by both the 1st and the 2nd generation of parasitoids. The fraction of strongly infested colonies is greater. The weakly infested colonies, with less than 5% of cells containing infested brood, are the largest, whereas those infested by 10% and more are the smallest. This condition was previously described for *P. dominula* nesting in attics in Kherson Province of Ukraine (Rusina, 2008). The different productivity of colonies with different rates of infestation clearly indicates that the host abundance is regulated by the parasitoid. This effect depends on the time of infestation and the activity of parasitoids in the host colonies. The influence of the time of infestation is mediated by the intergenerational numerical response of the parasitoid (a high relative abundance of the 1st generation of the parasitoid is combined with an earlier infestation of the host colony).

This group also includes settlements in which all the colonies were infested, except for orphaned ones which had lost the foundresses soon after the emergence of workers (e.g., a settlement of *P. nimpha* from the Venevitinovo Research Station, Voronezh Prov., 2008: samples 20–22 in table). The number of nests founded in 2008 was almost half as great as in 2007 (93 and 178, respectively) (Rusina et al., 2009). At the same time, the survival rate and spatial parameters of the nests were similar in the two seasons, even though the fraction of successful colonies decreased by 10% in 2008 as compared to 2007, whereas the fraction of orphaned colonies increased. In addition, not only the total fraction of colonies infested with parasitoids, mostly with *L. argiolus*, but also the fraction of those infested with the 1st generation increased in 2008 as compared to 2007, indicating a greater relative abundance of parasitoids. Almost all the successful colonies in the settlement were infested with parasitoids in 2008, only the orphaned ones remaining intact. It was for this reason that the intact colonies were smaller than infested ones in 2008, whereas the colony productivity was generally lower in 2008 as compared to 2007 (Rusina et al., 2009).

(4) The colony size is positively correlated with the absolute number of cells with infested brood but negatively correlated with the fraction of infested brood (samples 30 and 31). In some cases, only the negative correlation between the colony size and the fraction of infested brood may be revealed (samples 32–34). This

Infestation of colonies and settlements of polistine wasps with the parasitoids *Latibulus argiolus* (Rossi) and *Elasmus schmitti* Ruschka in Ukraine and Russia in 2006–2010

Sample (on the right: sample number referred to in the text)	Nestling place	Host/ parasitoid	Kendall coefficient of correlation between the number/fraction of infested cells and the number of:		Fraction of colonies (%)		Distance to the nearest neighboring colony, m	Aggregation level
			infested adults	infested cells	infested with 1 meconium	cells with 2 meconia	infested with 2 meconia	
Kherson Prov., Black Sea Biosphere Reserve, 2007, <i>N</i> = 23	P	<i>P. dominula</i> / <i>L. argiolus</i> + <i>E. schmitti</i>	0.41 NS 0.35 NS	0.42 NS 0.36 NS	-0.01 NS -0.06 NS	0.35 NS 0.29 NS	0.34 NS 0.27 NS	4 [3; 5] [2; 6]
	P	<i>P. dominula</i> / <i>L. argiolus</i>	0.34 NS 0.34 NS	0.30 NS 0.29 NS	0.04 NS 0.04 NS	0.18 NS 0.18 NS	0.16 NS 0.16 NS	
	P	<i>P. dominula</i> / <i>E. schmitti</i>	0.15 NS 0.14 NS	0.19 NS 0.19 NS	-0.08 NS -0.09 NS	0.23 NS 0.21 NS	0.23 NS 0.21 NS	
Lugansk, ravines Ploskaya and Kalmyskii Yar, 2007, <i>N</i> = 51	P	<i>P. gallicus</i> / <i>L. argiolus</i>	-0.08 NS -0.22 NS	-0.01 NS -0.15 NS	0.00 NS -0.15 NS	-0.01 NS -0.15 NS	-0.10 NS -0.23 NS	5.9
	P	<i>P. gallicus</i> / <i>E. schmitti</i>	0.23 NS 0.04 NS	0.14 NS 0.01 NS	0.27 NS 0.14 NS	0.19 NS 0.04 NS	0.13 NS 0.00 NS	2
Krasnodar Territory, Golubitskaya, 2007, <i>N</i> = 25	P	<i>P. gallicus</i> / <i>L. argiolus</i>	-0.01 NS -0.11 NS	0.01 NS -0.08 NS	0.04 NS -0.07 NS	0.13 NS 0.03 NS	-0.03 NS -0.12 NS	0
Krasnodar Territory, Sea of Azov coast, 2007, <i>N</i> = 14	Sh	<i>P. nimpha</i> / <i>L. argiolus</i>	-0.07 NS -0.20 NS	0.10 NS 0.00 NS	-0.26 NS -0.28 NS	0.07 NS -0.04 NS	0.00 NS -0.01 NS	14.3
Kurgan Prov., Ketovo Distr., Sychevo, 2007, <i>N</i> = 14	P	<i>P. gallicus</i> / <i>L. argiolus</i>	0.12 NS -0.09 NS	0.28* 0.08 NS	0.04 NS -0.09 NS	0.27 NS 0.09 NS	0.17 NS -0.01 NS	0
Krasnodar Territory, Dubovyi Rynok tract, 2007, <i>N</i> = 26	P	<i>P. nimpha</i> / <i>L. argiolus</i>	0.45* 0.25 NS	0.50** 0.30 NS	0.32 NS 0.23 NS	0.51** 0.32 NS	0.51* 0.24 NS	72.7
Donetsk Prov., Kramatorsk, 2008, <i>N</i> = 22	Sh	<i>P. nimpha</i> / <i>L. argiolus</i>	0.45* 0.25 NS	0.50** 0.30 NS	0.32 NS 0.23 NS	0.51* 0.32 NS	4.5	22.7
Sunny, 2010, <i>N</i> = 18	Sh	<i>P. nimpha</i> / <i>L. argiolus</i>	0.30 NS 0.22 NS	0.40* 0.34 NS	0.55* 0.50*	0.39* 0.32 NS	50.0 0.32 NS	Not measured

Table (Contd.)

Sample (on the right: sample number referred to in the text)	Nestling place	Host/ parasitoid	Kendall coefficient of correlation between the number/fraction of infested cells and the number of:			Fraction of colonies (%)		
			cells with 1 meconium	cells with 2 meconia	adults total number of meconia	infested with 2 parasites of the 1st generation	the emergence of workers infested before the first generation	strongly infested colonies, m
Voronezh Prov., Venevitinovo Research Station, 2007, N = 111	11	Sh <i>P. nimpha</i> / <i>L. argiolus</i> + <i>E. schmitti</i>	0.17 NS 0.13 NS	0.19* 0.15 NS	0.03 NS 0.02 NS	0.18* 0.13 NS	0.16 NS 0.12 NS	19.8
	12	P. nimpha / <i>L. argiolus</i>	0.18* 0.14 NS	0.20* 0.16 NS	0.07 NS 0.06 NS	0.19* 0.15 NS	0.18* 0.14 NS	6.3
	13	P. nimpha / <i>E. schmitti</i>	0.10 NS 0.10 NS	0.08 NS 0.07 NS	0.00 NS 0.00 NS	0.05 NS 0.05 NS	0.04 NS 0.04 NS	10.8
Kherson, Tavricheskii neighborhood unit, 2006, N = 20	14	P <i>P. gallicus</i> / <i>L. argiolus</i>	0.27 NS -0.03 NS	0.35* -0.04 NS	0.20 NS -0.11 NS	0.35* 0.05 NS	0.32* 0.03 NS	25.0
	15	Sh <i>P. dominula</i> / <i>L. argiolus</i>	0.58*** 0.24 NS	0.57*** 0.23 NS	0.35 NS 0.25 NS	0.60*** 0.31 NS	0.60** 0.31 NS	15.0
Kirovograd Prov., Bobritnets, 2006, N = 41	16	Sh <i>P. dominula</i> / <i>L. argiolus</i>	0.51*** -0.04 NS	0.54*** -0.01 NS	0.15 NS -0.05 NS	0.50*** 0.01 NS	0.47** -0.03 NS	41.5
Kirovograd Prov., Bobritnets Distr., Chariivnoe, 2007, N = 23	17	Sh <i>P. dominula</i> / <i>L. argiolus</i>						17.1
Same locality, 2008, N = 22								34.1
Kherson Prov., Genichesk Distr., Rovnoe, 2010, N = 32	18	Sh <i>P. dominula</i> / <i>L. argiolus</i> + <i>E. schmitti</i>	0.44* 0.19 NS	0.55** 0.31 NS	0.25 NS 0.04 NS	0.46** 0.22 NS	0.44* 0.20 NS	9.4
	19	Sh <i>P. dominula</i> / <i>L. argiolus</i> + <i>E. schmitti</i>	0.38* 0.16 NS	0.43** 0.20 NS	0.25 0.04 NS	0.39* 0.17 NS	0.23 0.01 NS	64.9
Sumy Prov., Lipovaya Dolina, 2010, N = 37								24.3
								13.5
								10.8
								Not measured

Table (Contd.)

Sample (on the right: sample number referred to in the text)	Nestling place	Host/ parasitoid	Kendall coefficient of correlation between the number/fraction of infested cells and the number of:		Fraction of colonies (%)		Distance to the nearest neighboring colony, m	Aggregation level
			infested adults	infested with parasites of the 1st generation	infested with parasites of the 2nd generation	total number of meconia	strongly infested	
Voronezh Prov., Venevitinovo Research Station, 2008, N = 61	Sh	<i>P. nimpfa /</i> <i>L. argiolus +</i> <i>E. schmitti</i>	0.58*** 0.50***	0.63*** 0.55***	0.54*** 0.45***	0.61*** 0.53***	0.60*** 0.52***	2 [0; 4.5] [0; 4]
20								
21		<i>P. nimpfa /</i> <i>L. argiolus</i>	0.51*** 0.48***	0.56*** 0.50***	0.47*** 0.41***	0.54*** 0.48***	0.53*** 0.47***	
22		<i>P. nimpfa /</i> <i>E. schmitti</i>	0.42*** 0.39***	0.42*** 0.39***	0.42*** 0.39***	0.42*** 0.38***	0.41*** 0.38***	
23	Sh	<i>P. nimpfa /</i> <i>L. argiolus</i>	0.75*** 0.47***	0.76*** 0.51***	0.50*** 0.42***	0.82*** 0.59***	0.78*** 0.54***	
Chernovtsy Prov., Khotin Distr., Kruten'ki, 2009, N = 58								
Donetsk Prov., Zuevka, 2008, N = 21	P	<i>P. nimpfa /</i> <i>L. argiolus</i>	0.55*** 0.45*	0.60** 0.50*	0.43* 0.34 NS	0.63** 0.53*	0.54* 0.44*	14.3 [9.5; 23.0] [3.0; 75.0] [1.5; 3.5] [1; 5.0]
Dnepropetrovsk Prov., Pavlograd, 2009, N = 17	Sh	<i>P. dominula /</i> <i>L. argiolus</i>	0.56*** 0.52**	0.57** 0.52**	0.59** 0.54**	0.56** 0.51**	0.56** 0.51**	Not measured
Lugansk Prov., Trekhizbenskii training ground, 2009, N = 16	P	<i>P. nimpfa /</i> <i>L. argiolus</i>	0.33 NS 0.26 NS	0.48** 0.40*	0.19 NS 0.12 NS	0.31 NS 0.24 NS	0.30 NS 0.23 NS	23.5
Kherson, 2009, N = 28	Sh	<i>P. dominula /</i> <i>L. argiolus +</i> <i>E. schmitti</i>	0.90*** 0.82*	0.94*** 0.85*	0.77* 0.89**	0.88** 0.89**	0.88** 0.89**	13.7 [9.5; 23.0] [3.0; 75.0] [1.5; 3.5] [1; 5.0]
27								
28		<i>P. dominula /</i> <i>L. argiolus</i>						
29		<i>P. dominula /</i> <i>E. schmitti</i>						

Table (Contd.)

Sample (on the right: sample number referred to in the text)	Nesting place	Kendall coefficient of correlation between the number/fraction of infested cells and the number of:				Fraction of colonies (%)	Distance to the nearest neighboring colony, m	Aggregation level
		Host/ parasitoid	cells	cells with 1 meconium	total number of meconia			
Crimea, Yalta, 2006, $N = 42$	Sh <i>P. nimphea / L. argiolus</i>	0.37* -0.49**	0.44** -0.42**	0.19 NS -0.57***	0.37* -0.48**	0.31* -0.53**	40.5	42.9
Kherson Prov., Golopristanskii Distr., Tavriiskoe, 2009, $N = 44$	Sh <i>P. nimphea / L. argiolus</i>	0.28* -0.27*	0.28** -0.26**	0.25** -0.29**	0.27** -0.27**	0.24* -0.30**	38.6	31.8
Lugansk, environs, 2007, $N = 51$	P <i>P. nimphea / L. argiolus</i>	-0.15 NS -0.25*	0.03 NS -0.07 NS	0.00 NS -0.06 NS	0.05 NS -0.05 NS	52.9 -0.12 NS	33.3	19.6
Kherson Prov., Ivanovka Distr., Blagodatnoe, 2007, $N = 38$	Sh <i>P. dominula / L. argiolus + E. schmitti</i>	-0.05 NS -0.41**	-0.08 NS -0.43**	-0.19 NS -0.44**	-0.07 NS -0.43**	-0.17 NS -0.51**	65.8	15.8
	P <i>P. dominula / L. argiolus</i>	-0.07 NS -0.42**	-0.10 NS -0.44*	-0.21 NS -0.45**	-0.10 NS -0.44 NS	-0.10 NS -0.43 NS	60.5	28.9
	P <i>P. dominula / E. schmitti</i>	0.16 NS 0.16 NS	0.14 NS 0.14 NS	0.04 NS 0.04 NS	0.13 NS 0.13 NS	0.13 NS 0.13 NS	7.9	0.8 [0.5; 1.1] [0.1; 4.1]
Lugansk Prov., Provalskaya Steppe, 2006, $N = 18$	P <i>P. nimphea / L. argiolus</i>	-0.68* -0.82**	-0.7* -0.88**	0.18 NS 0.43 NS	-0.88*** -0.87*	-0.88*** -0.87**	100	33.3

Note. Nesting places: P, plants; Sh, shelters; N is the number of nests; NS marks statistically non-significant differences.

* $p < 0.05$;
 ** $p < 0.01$;
 *** $p < 0.001$.

condition was observed at high rates of infestation of colonies and settlements; it may result from high density of the host colonies coinciding with intergenerational numerical response of the parasitoid, for example, due to favorable conditions for development and wintering of the parasitoid in the preceding season. In this case, the regulatory effect is enhanced by the combined action of functional and numerical responses of the parasitoid to the host colony density, because it is due to strong infestation at early stages that parasitoids may significantly reduce the number of workers in the colony. Since the positive effect of the colony productivity regulation was observed in the seasons with high abundance of parasitoids, there are grounds to believe that the density-dependent response of parasitoids is mostly determined by the aggregation component.

(5) The colony size is negatively correlated with both parameters of parasitoid infestation. This variant was observed when all the colonies in the settlement were infested (sample 36).

Similar correlations were also reported for *P. snelleni* (Makino and Sayama, 1994).

Certain correlations between the infestation parameters and spatial characteristics of colonies were observed in some, but not all, wasp settlements. The colonies positioned close together and those showing a high index of congestion were characterized by a greater number of cells with infested brood ($-0.27 < r_s < -0.58$; $0.01 < p < 0.05$) and a greater fraction of such cells, i.e., a higher infestation rate ($-0.26 < r_s < -0.71$; $0.01 < p < 0.05$).

With some reservations, the above phenomenon may be interpreted as a functional response of the parasitoid to an increasing number of host larvae in the nest. A similar response is known in parasitoids of solitary insects, which spend more time and lay more eggs in areas of host aggregation (Khorkhordin, 1975; Guryanova, 1978; Ruberson et al., 1991). In order to understand the exact roles of the functional and numerical responses, one should find out how many parasitoid females infest a single host colony.

It is essential that changes in the system of interacting parasitoid and host populations do not depend on the host species and occur in the same way (with an increasing abundance of the 1st generation of the parasitoid) regardless of the mode of nesting (in shelters or openly on plants).

The behavior of parasitoids of polistine wasps is clearly similar to that of parasitoids infesting solitary hosts. In particular, they tend to select larger "food clusters" (in our case, host colonies). The parasitoids also display a behavioral response to the host population density, being able to regulate the host abundance at low densities (Viktorov, 1976). However, since the principal population unit of polistine wasps is not the individual but the colony, the factor "host population density" is mediated not only by the non-uniform rates of colony development and their spatial distribution but also by the temporal aspect. The low density of the host population, at which the parasitoid can regulate its abundance, corresponds to a certain phase of colony development, namely the one preceding the emergence of workers. On the whole, the spatial and temporal aspects of interrelations between the parasitoid and the host are inextricably intertwined.

Thus, the system of interacting populations of a polistine wasp and its parasitoids may exist in a considerable variety of states. These variants may be specific to particular biocenotic and geographic conditions, or they may represent different phases in the dynamics of the interacting populations.

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