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ZOOLOGY =

Peculiarities of the Seasonal Biology of Ectoparasites of the Genus *Spinturnix* von Heyden, 1826 (Mesostigmata: Gamasina: Spinturnicidae) in the Boreal Zone of the Palearctic Region

M. V. Orlova^{*a*, *b*, *, O. L. Orlov^{*b*, *c*}, D. V. Kazakov^{*b*}, and A. V. Zhigalin^{*a*, *d*}}

^aNational Research Tomsk State University, Tomsk, 634050 Russia
 ^bTyumen State University, Tyumen, 625003 Russia
 ^cUral State Medical University, Yekaterinburg, 620028 Russia
 ^dCenter for Hygiene and Epidemiology, Tomsk, 634021 Russia
 *e-mail: masha_orlova@mail.ru
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Abstract—The most complete data on the peculiarities of seasonal biology of gamasid mites of the genus *Spinturnix*, which are ectoparasites of bats of the boreal zone of the Old World, are presented. Data on the dynamics of the sex and age structure of superpopulations of parasites throughout the year are presented; the infestation of various bat species is analyzed, and the factors affecting it are discussed. The main differences between the life cycles of the boreal and subboreal Spinturnicidae mites were revealed.

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INTRODUCTION

Parasitic gamasid mites of the genus *Spinturnix* von Heyden, 1826 (Mesostigmata: Gamasina: Spinturnicidae) are specific ectoparasites of bats that form the core of the parasitofauna of vesper bats (Chiroptera: Vespertilionidae) in many regions of the Old and New Worlds (Orlova et al., 2016). The most important feature of sedentary bats of the temperate zone is the long (up to six months) wintering in caves, galleries, and other shelters at a constant temperature of $2-5^{\circ}$ C, which is critically low for most arthropods.

One of the earliest works studying the dynamics of the number of Spinturnicidae mites and the factors affecting it was performed by Deunff and Beaucournu (1981). Later (Estrada-Pena et al., 1991), the dynamics of the number of *Spinturnix psi* (Kolenati, 1856) mites was also described throughout the year; in that article it was noted that the process of parasite multiplication is most active during the breeding season of hosts, but in general reproduction and metamorphosis of the species are observed throughout the year.

In studies at the beginning of the 21th century, it was noted that the peak of infestation of hosts with gamasid mites occurs during pregnancy and lactation of the hosts, and by November the proportion of infected individuals and the average number of parasites per host is significantly reduced (Christe et al., 2000, 2003; Zahn and Rupp, 2004). Lučan, investigating the infestation of bats with spinturnicid mites, described the higher infestation of females and immature specimens of Daubenton's bat (Myotis daubentonii) (Kuhl, 1817) with S. andegavina (Kolenati, 1857) mites in the summer (Lučan, 2006). Subsequently, in a number of works, Lučan's data on infestation were confirmed: in the summer, for several species of bats, it was shown that adult females are more infected with Spinturnix mites than adult males, and there were no sex differences between immature individuals, which were also characterized by significant infectiousness (Christe et al., 2007; Encarnação et al., 2012). In addition, it was found that spinturnicid mites prefer more well-nourished individuals (Christe et al., 2003). In the studies of Lourenço et al. (Lourenço, 2008; Lourenço and Palmeirim, 2008), it was confirmed that the reproductive activity of gamasid mites is synchronized with the reproductive activity of the host and sharply decreases during the wintering period.

However, despite a large-scale study of the parasite—host relationships of palearctic spinturnicid mites (Sharifi et al., 2008; Encarnação et al., 2012; Postawa and Szubert-Kruszyńska, 2014; Postawa and Nagy, 2016; etc.), a number of phenological aspects of the genus *Spinturnix* remain unexplored. This concerns, in particular, the sex—age structure and the dynamics of numbers throughout the wintering period, the complexity of which is caused by the limited availability of

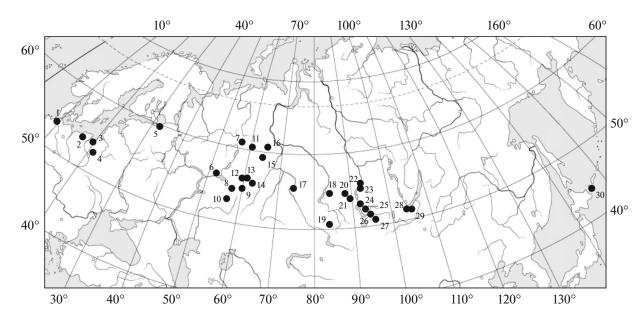


Fig. 1. Map of sampling points. 1–5, Location of Europe and northwestern Russia; 6–17, the Urals and the Trans-Urals; 18–29, western and eastern Siberia; 30, the Far East.

wintering sites and limitations of environmental legislation in most European countries. In addition, in the overwhelming majority of publications on the biology of spinturnicid mites in summer shelters, data on the biology of mites in the boreal zone, under conditions of prolonged wintering at low temperatures, are extremely limited.

Earlier, we noted the synchronization of life cycles of bats and spinturnicid mites (Orlova et al., 2016). At the same time, in the foreign literature, the proportion of females with intrauterine protonymph has virtually not been analyzed. In our opinion, this is an important indicator characterizing the presence/absence of the reproduction process in the parasitic infrapopulation (a population parasitizing one host specimen) (Balashov, 2009)).

The aim of this work is to study the features of the life cycle of spinturnicid mites of the boreal zone of the Palearctic.

MATERIALS AND METHODS

Material for this work was collected in 2010–2016 (year-round) in locations of the boreal zone and territories close to it according to climatic conditions (northwestern Altai). In the winter, combing out was performed in the caves of Leningrad oblast, the Urals, and western and eastern Siberia; in the summer, it was performed in the areas of northern Poland, the Urals, western and eastern Siberia, and the Far East (Fig. 1). Data from the collection of parasitic arthropods of the Zoological Institute, Russian Academy of Sciences (St. Petersburg), taken in Crimea (for comparison) and Central Siberia (quantitatively included in the

study) were also used. The total volume of collected and analyzed material is \sim 2500 individuals.

The periodization of the life cycle of bats corresponds to that given earlier (Lučan, 2006). During the course of the year, six periods can be distinguished in the activity of bats: hibernation (from October 10 to April 30); spring transmigration to summer shelters (from May 1 to May 15); prelactation period (from May 16 to June 20); lactation period (from June 21 to July 15); postlactation period (from July 16 to August 15); and autumn transmigration to winter shelters (from August 16 to October 9).

In our material, the most widespread species of the genus *Spinturnix* in the taiga zone are represented (*S. myoti* (Kolenati, 1856): *S. mystacina* (Kolenati, 1857), *S. kolenatii* Oudemans, 1910, *S. plecotinus* (Koch, 1839), *S. maedai* Uchikawa, Wada, 1979), as is one species with a narrower range (*S. uchikawai* Orlova, Zhigalin, Zhigalina, 2015). The hosts of all the parasites studied were sedentary species of bats; ectoparasite of migratory bat species *S. acuminatus* (C.L. Koch, 1836) was not included in this study.

When studying the infestation, only findings of parasites on their main hosts were taken into account. To characterize the number of ticks, indices MI (mean intensity, the average number of parasites on one infected host) and P (prevalence, the proportion of infected individuals) were used. The length of the forearm (spoke-bone, the longest tubular bone in bats) was used as a comparison parameter in the study of the influence of the size of the host's body on its infestation, since this indicator characterizes the size of wing, i.e., the part of the body on which *Spinturnix*

mites predominantly parasitize, and, in our opinion, is more adequate for studying this dependence.

To investigate the relationship between the variables, the Pearson correlation index (r) was used.

RESULTS

The life cycle of gamasid mites is composed of the following phases of development: egg–larva–nymph I (protonymph)–nymph II (deuteronymph)–imago. However, the parasitic way of life causes a significant transformation of this model: the egg and larva in Spinturnicidae are embryonated, and an active blood-sucking protonymph is born. The deuteronymph, which actively parasitizes in spinturnicid mites, is similar to an adult mite in size and appearance. Thus, the life cycle of spinturnicid mites is extremely shortened, which contributes to preservation of the offspring (Bregetova, 1956).

The study of the sex-age structure of gamasid mites of fam. Spinturnicidae in winter and summer shelters shows that all our finds of species of the genus *Spinturnix* during the wintering of the hosts are represented only by adult mites, while individuals of the preimaginal stages, as well as females with intrauterine protonymphs, are abundantly represented only in summer colonies (Fig. 2). Sexually mature individuals prevail throughout the year.

The largest number of ticks collected (~1500) belongs to the species *S. myoti*, which allows us to use it as a model.

Spinturnix myoti (Kolenati, 1856). The main hosts of S. myoti are many species of common bats (predominantly large ones): the greater mouse-eared bat Myotis myotis, the lesser mouse-eared bat M. blythii, Natterer's bat M. nattereri (Kuhl, 1817), the pond bat M. dasycneme (Boie, 1825), Daubenton's bat M. daubentonii, the eastern water bat M. petax (Hollister, 1912), and others.

The percentage of infected S. myoti individuals during the wintering period in Smolinskaya and Barsukovskaya caves is about 50%, and the average number of mites per infected individual in this period ranges from two (for pond bats) to four (for eastern water bats). In June–July, when female bats give birth and feed the pups, the proportion of infected individuals in some brood colonies reaches 100%, and the average number of mites per infected host is 8-10. The maximum number of ectoparasites of this species on one host in our collections is 34 (colony of M. dasvcneme at the Beryozka recreation center). We do not go into the sexual and age aspects of host infestation because they have been studied sufficiently (Zahn and Rupp, 2004; Christe et al., 2007; Lourenço and Palmeirim, 2008; Sharifi et al., 2008; Piksa et al., 2011; Encarnação et al., 2012); however, we note that, as a whole, our material confirms the pattern noted earlier by foreign authors, according to which infesta-

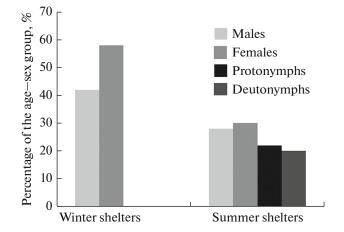


Fig. 2. General sex-age structure of species of the genus *Spinturnix* (n = 2454) in winter and summer shelters.

tion in summer shelters of females (primarily pregnant and lactating) and juvenile individuals is higher than in males (5, 12.2, 3.7, respectively).

Individuals of the preimaginal stages (proto- and deutonymphs) can be found only in May-October, their share in the total material volume increases steadily from the period of spring migration of bats to lactation (as the proportion of females with intrauterine protonymph decreases), reaching a maximum (48%), and then it also decreases evenly to hibernation. Immature individuals were not found throughout the wintering period, and during the prelactation, lactation, and postlactation periods, the share of protoand deutonymphs in the population was quite high (on average, 44%). As the undervearling bats begin to fly and mature, the number of females with intrauterine protonymphs and proto- and deutonymphs in collections decreases (September), and by October they almost completely disappear.

It should be noted that, while generally preserving the tendency toward intensification of the process of parasite reproduction during pregnancy and lactation of hosts, the most important difference between the life cycles of spinturnicid mites in the boreal zone is, apparently, the complete cessation of the breeding process in winter shelters (Figs. 3-5) for a sufficiently long period (not less than three months). However, in the subboreal belt, parasite reproduction occurs in winter shelters (Estrada-Pena et al., 1991), as is indicated by constant findings of preimaginal stages of the tick (5-15% of the population) in different periods of hibernation. This is confirmed by the data from the collection of the Zoological Museum, Russian Academy of Sciences, composed of finds of S. myoti in the Crimea: in material that includes 44 parasite specimens collected from hibernating individuals in the middle of November (15 specimens of the lesser mouse-eared bat, MI = 2.9, P = 100%), there are two females with intrauterine protonymphs and a proto-

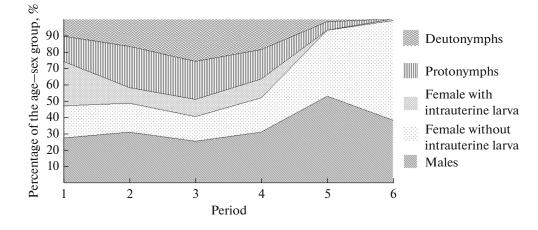


Fig. 3. The sex-age structure of *Spinturnix myoti* infrapopulations throughout the year (n = 1448). 1, Spring transmigration; 2, prelactation; 3, lactation; 4, postlactation; 5, autumn transmigration; 6, hibernation.

nymph. In all the material collected by us for *S. myoti*, only two random findings of females with an intrauterine protonymph (in late October and in the second half of March, i.e., at the beginning and the end of wintering) were discovered in caves. Among the specimens collected from hibernating areas, females predominated (62% of the total number of imaginal individuals (n = 199)).

Spinturnix mystacina (Kolenati, 1857). This species parasitizes small common bats: Brandt's bat *M. brandtii* (Eversmann, 1845), the whiskered bat *M. mystacinus* (Kuhl, 1817), the Siberian bat *M. sibiricus* (Kastschenko, 1905), Ikonnikov's bat *M. ikonnikovi* (Ognev, 1912), David's myotis *M. davidii* (Peters, 1869), etc. In our material, *S. mystacina* is present only

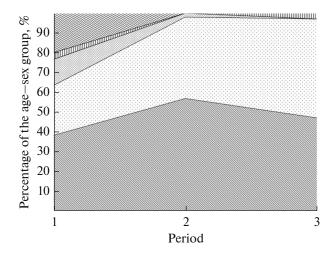


Fig. 4. The sex-age structure of *Spinturnix kolenatii* infrapopulations throughout the year (n = 276). The designations of sex-age groups are the same as in Fig. 3. 1, Lactation and postlactation; 2, hibernation (October-December); 3, hibernation (January-March) and spring transmigration.

in collections made during the wintering period, from two species of hosts: Brandt's bat in the Bolshaya Konovalovskaya Cave and the Siberian bat in the caves of the southern part of Krasnoyarsk region (materials of the collection of the Zoological Institute (St. Petersburg)) and Khakassia. For *S. mystacina* in the winter shelters, females with an intrauterine protonymph and nymph were also not noted (with the exception of two findings of females with intrauterine protonymphs made in different years in Arkheologicheskaya Cave, the temperature of which is 5°C, which is slightly higher than in the other shelters surveyed). As in the case of *S. myoti*, females predominate in winter shelters (65% of the total number of imaginal individuals).

Spinturnix uchikawai (Orlova, Zhigalin, Zhigalina, 2015). This mite parasitizes the eastern long-fingered bat *M. macrodactylus* (Temminck, 1840). We collected 347 specimens of this species at the turn of July–

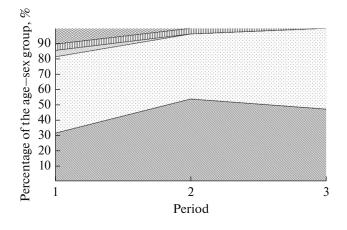


Fig. 5. The sex-age structure of *Spinturnix plecotinus* infrapopulations throughout the year (n = 138). The designations of the sex-age groups are the same as in Fig. 3. 1, Colony in summer shelters (prelactation-postlactation); 2, autumn transmigration; 3, hibernation.

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August (lactation period, since the birth of pups in the eastern long-fingered bats occurs in the middle of July). Infestation of the host with the parasite is abnormally high. The surveyed population of the eastern long-fingered bat is insular, which may be the cause of its extreme infestation. In general, the sex-age structure of the superpopulation (the totality of parasite individuals living in one shelter (Balashov, 2009)) practically does not differ from that described for *S. myoti* in the same period: adult individuals predominate (64%), among them females (61%), of which almost one-third (29%) bear an intrauterine protonymph.

Spinturnix kolenatii (Oudemans, 1910). The main hosts of this species are the serotine bat *Eptesicus serotinus* (Schreber, 1774) and the northern bat *E. nilssonii* (Keyserling and Blasius, 1839). In total 276 specimens of the species were collected. Signs of reproduction and metamorphosis (females with intrauterine protonymphs, preimaginal individuals) were not found in winter shelters (an exception is one female with an intrauterine protonymph collected in October). Infrapopulations of the parasite in brood colonies (July) are represented by all phases of development, and during the wintering period, only by adult individuals. The sex ratio in both summer and winter shelters, given the small sample size, does not significantly differ from 50/50 (Fig. 4).

Spinturnix plecotinus (Koch. 1839). Parasite feeders in the area studied are species of the genus *Plecotus* (long-eared bats: the brown long-eared bat *Plecotus* auritus (Linnaeus, 1758) and Ognev's long-eared bat P. ognevi (Kishida, 1927)) (Radovsky, 1967; Stanyukovich, 1997); in our material there are 138 specimens of the parasite. This small volume does not allow for unambiguous conclusions, but the small (compared to S. myoti and S. kolenatii) share of proto- and deutonymphs in summer shelters (15% in total) is notable, which agrees with the extremely small proportion of females with intrauterine protonymphs (4% of the total number of individuals, 8% of the total number of females). During the autumn and spring transmigration (in the caves of Okhotnichya and Argaley-3, respectively), the proportion of infected individuals was 69%, MI = 2.3; females with intrauterine protonymphs and preimaginal individuals were absent (Fig. 5).

Spinturnix maedai (Uchikawa, Wada, 1979). This is a specific parasite of the genus Murina (tube-nose bats); in our collections there are 28 individuals (10 males and 18 females), most of which were collected during the wintering period; the material contains only adult individuals.

DISCUSSION

Comparison of the data obtained by us and the literature data shows several interesting regular occurrences (Tables 1, 2). First of all, the high infestation of

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bats of the subboreal zone in the summer (MI > 10 for all) attracts attention, while in most boreal species the values of this indicator are 3.2-8.6. The eastern long-fingered bat, the very high infestation of which (MI > 30) has not yet been explained (island effect?), is excluded from further analysis.

It should also be noted that in terms of infestation, different species of bats differ more significantly in summer than in winter, when in the vast majority of species MI = 1.8-4.4, and the *P* value rarely reaches 60%. Below are analyzed the most likely predictors, the influence of which can determine the trends observed.

Host body size. This factor largely explains the data obtained, since the growth of infestation of species clearly occurs in the series of body size growth and its mass (Tables 1, 2). The largest values of infestation parameters in the summer and winter alike show the largest species (in summer, MI = 19, 15.9, and 11 for the greater mouse-eared bat, the lesser mouse-eared bat, and also the common bent-wing bat, respectively; in winter, MI = 7.2 and 4 for the lesser mouse-eared bat and the greater mouse-eared bat, respectively). The largest boreal species (the pond bat) is also characterized by the highest summer values of MI and *P* among the species of its natural zone.

The medium-sized (comparable in size to boreal species) Asian barbastelle and Geoffroy's bat are characterized by a very low infestation index. Table 1 shows only the data on the infestation of the Asian barbastelle by Spinturnix punctata (Sundevall, 1833) in the winter shelters (Rybin, 1983-the Latin name of the host is not given in the source; it is now known that two species of *Barbastella* bats inhabit the territory studied by the author: Barbastella caspica (Satunin, 1908) and *B. darjelingensis* (Hodgson, 1855)). The available data on the infestation with the same parasite species of a slightly smaller western barbastelle Barbastella barbastellus Schreber, 1774 (length of the forearm is 35-42 mm, weight is 6-15 g) are not presented in the table, since Haitlinger, in his article (Haitlinger, 1978), does not indicate the period during which the collection was conducted, but the values given by him also characterize this bat species as slightly infected (P = 14%), the number of mites on one infected host does not exceed two). In summer shelters, r = 0.88; i.e., it demonstrates a significant (p < 0.05) correlation between the length of the forearm and the infestation of bats with spinturnicid mites. Particularly notable is the strict dependence of the infestation with species of the genus Spinturnix on the body size of a number of mouse-eared bats (r = 0.99).

The size of the colonies formed by the host species. Parthenogenesis is not typical for species of the genus *Spinturnix*, which is expressed in the sex ratio tending to 1 : 1. Thus, parasite infestation depends directly on the host populations, as the probability of encountering male and female mites increases in large colonies,

		Species of the	e genus <i>Spintur</i>	nix	
Parameter	SPu*	SPs*	SK	SPl	SMa
Faranicier		The	nain hosts		
	BDC	MSh	EN	PA, PO	MH
Length of forearm, mm	41-45	44-48	38-43	34-44	36-44
Body weight, g	8-18	14–22	8-14	5-14	7-13
	Sum	mer shelters			•
Total number of surveyed host individuals, N	—	—	64	19 (45*)	-
MI	—	11-22	3.9 (3.1*)	3.3 (2.3*)	-
P, %	—	40	73 (39*)	78 (31.6*)	-
The maximum number of mites per host	_		28	8	_
Percentage of preimagoes, %	_	<50	23	12	_
Percentage of females with intrauterine larvae in the total number of individuals	_	_	12	4	_
Percentage of females with intrauterine larva in the total number of females	_	_	32	8	
Size of brood colonies	_	10000-20000	<10	<10	_
	Win	ter shelters	<u>.</u>	1	
Total number of individuals surveyed, N	38	_	47	61	57
MI	1.3	1—4	3.1	2.2	2.4
Р	29	40	51	61	16
Maximum number of mites per host	3	14	7	8	7
Size of wintering colonies (in the study area)	<100	10000-20000	1-2	1-2	<300-400

Table 1. Comparison of parameters of different species of vesper bats and their infestation with Spinturnix spp. mites

SPu, Spinturnix punctate; SPs, S. psi; SK, S. kolenatii; SPl, S. plecotinus; SMa, S. maedai; BD, Barbastella darjelingensis or B. caspica; MSh, Miniopterus schreibersii (Kuhl, 1817); EN, Eptesicus nilssoni; PA, Plecotus auritus; PO, P. ognevi; MH, Murina hilgendorfi Peters, 1880; MI, average number of parasites on one infected host, P, percentage of infected individuals, "-" means no data (for Tables 1, 2). * Tagiltsev, 1971; Rybin, 1983; Haitlinger, 1978; Deunff and Beaucournu, 1981; Estrada-Pena et al., 1991.

which stimulates reproductive activity. The process of parasite reproduction is most active in summer shelters, so it is advisable to trace the relationship of infestation to the size of summer gatherings of bats. On the whole, this regularity is confirmed, and in the main, the most infected species actually form the largest clusters (the common bent-wing bat, greater mouseeared bat, and lesser mouse-eared bat) (Tables 1, 2). Among the boreal species, the dependence described can be traced more clearly: the pond bat forms the largest summer colonies in the taiga zone, and the least infected species (long-eared bats, northern bat, small mouse-eared bats: Daubenton's bat, Siberian bat, Brandt's bat) either do not form brood colonies or unite into small clusters of several dozen individuals.

It should be emphasized that the size of the wintering colonies, apparently, has little effect on the infestation of bats. So, the Siberian bat and Brandt's bat (widely distributed in the taiga zone species) are characterized by a low infestation index. In winter shelters they form clusters up to 800–1000 individuals and are often the most massive species in winter stays. The association of reproduction processes in spinturnicid mites and their hosts determines the primary association of hatching mites to summer shelters, which, apparently, determines the weak effect of the size of winter accumulations on the infestation of bats.

Note that, despite the synchronization of reproduction processes in spinturnicid and bats, caused by immune and hormonal factors, in caves of the subboreal zone, where the temperature in winter shelters is 7°C or higher, the reproductive activity and metamorphosis of the mites do not cease during the period of hibernation of hosts, although they are substantially

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	-						•	-		
				Spe	cies of the g	Species of the genus Spinturnix	nix			
Domotor			МS			SE^*	SU		SMy	
					The ma	The main hosts				
·	MM^*	MB	MDa	П	dМ	ME	MMa	MBr	SW	ММу
Length of forearm, mm	57-66	53-63	43—49	36-42	34-39	3844	36-41		33–39	
Body weight, g	1640	630	13-25	6 - 10	69	5 - 10	6 - 10		5 - 10	
-	_		Summe	Summer shelters		_	_			
Total number of surveyed host individuals, N	Ι	404*	81	88 (15*)	141	I	12	10^{*}	9	83*
MI	19	15.9*	8.6	4.6 (3*)	3.3	2.3	30.5	2.0*	3.8	2.0*
P, %	100	86*	93	74 (60*)	56	72	100	11*	83	31.3*
The maximum number of mites per host	I	54*	34	14	17	Ι	67	Ι	7	I
Percentage of preimagoes, %	Ι	42*	40	37	46	Ι	41	Ι	16	Ι
Percentage of females with intrauterine larvae in the total number of individuals	I	Ι	15	٢	6	I	12	I	5	I
Percentage of females with intrauterine larva in the total number of females	Ι	Ι	44	33	28	I	40	I	11	I
Size of brood colonies		<1300	<500	<50	15 - 100	<300-400	>100	20-30	10-25	<40-50
_	_	_	Winter	Winter shelters	_	_	-		_	
Total number of surveyed individuals, N	Ι	15	110	13	53	Ι	I	67	66	Ι
MI	4	7.2	2.0	2.0	3.8	Ι	I	1.8	2.5	Ι
P,%	40	40	27	69	28	Ι	I	21	43	Ι
Maximum number of mites per host	Ι	17	٢	5	11	Ι	I	8	9	Ι
Size of wintering colonies (in the study area)	<4000	<200**	<1800	<1100	10—15, <150	I	I	<1000	100—150, <800	<100
		<4000***								
SM, Spintumix myoti; SU, S. uchikawai, SE, S. emarginatus; SMy, S	natus; SMy, S.		M, M. myotis	MB, M. blyth	ii; MDa, M. σ	mystacina; MM, M. myotis; MB, M. blythii; MDa, M. dasycneme; MD, M. daubentonii; MP, M. petax; ME, M. emarginatus	, M. daubenta	onii; MP, M. p	etax; ME, M.	emarginatus

. 4 ¹ Tagiltary, 1906, MMa, M. macrodactylus; MBr, M. brandtii; MS, M. sihiricus; MMy, M. mystacinus, M. "-" means no data.
^{*} Tagiltsev, 1971; Rybin, 1983; Haitlinger, 1978; Deunff and Beaucournu, 1981; Estrada-Pena et al., 1991.
** Our own data on the lesser mouse-eared bat from Western and Southern Europe.

minimized (Deunff and Beaucournu, 1981; Estrada-Pena et al., 1991). In the boreal zone, the fact of hatching and the subsequent metamorphosis of mites during the wintering season was not confirmed for any of the parasitic species studied by us. Of special interest in the study of the relationship between reproductive ability during wintering and the infestation rate are our samples of S. myoti from the lesser mouse-eared bat in northwestern Altai, where the northern boundarv of the range of this species passes. Winter stavs in the caves of the Tigirekskiy Reserve have the lowest temperature in the whole range of *M. blythii* (no higher than 4°C), and there were no signs of reproduction of spinturnicid mites during this period. However, in spite of the observed cessation of ectoparasite reproduction in the winter, the lesser mouse-eared bat shows the highest index of infestation with this parasite among species studied during its wintering period in the Altai. Consequently, the temperature of shelters cannot be considered a decisive factor in the growth of the parasite population.

CONCLUSIONS

An important feature of the life cycle of mites of the genus *Spinturnix* in the boreal zone is the complete cessation of reproduction and metamorphosis in winter shelters. Reproduction occurs only in summer shelters from the spring transmigration to the postlactation period. During the autumn transmigration to winter shelters, the proportion of females with intrauterine protonymphs sharply decreases, as does the proportion of individuals of the preimaginal stages of development.

During the entire year, in the sex-age structure of species of the genus *Spinturnix*, adults individuals predominate and the sex ratio tends to 1 : 1, but in most cases there is a slight predominance of females.

The lower infestation of boreal species in comparison with subboreal ones is explained by the habitat in the taiga zone of almost exclusively small species of bats which are characterized by a lower infestation index. Perhaps, partially, the low infestation index of a number of species is associated with the small size of brood colonies formed by many boreal species.

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