

**INFLUENCE OF THE TAIGA TICK *IXODES PERSULCATUS* SCHULZE, 1930 (ACARI: IXODIDAE) ON HUMORAL IMMUNE RESPONSIVENESS OF RED VOLES *CLETHRIONOMYS RUTILUS* PALLAS, 1779 AND FIELD MICE *APODEMUS AGRARIUS* PALLAS 1771 (RODENTIA: CRICETIDAE AND MURIDAE) IN NATURAL POPULATIONS**

**ВЛИЯНИЕ ПАРАЗИТИРОВАНИЯ ТАЕЖНЫХ КЛЕЩЕЙ *IXODES PERSULCATUS* SCHULZE, 1930 (ACARI: IXODIDAE) НА ГУМОРАЛЬНЫЙ ИММУННЫЙ ОТВЕТ КРАСНЫХ ПОЛЕВОК *CLETHRIONOMYS RUTILUS* PALLAS, 1779 И ПОЛЕВЫХ МЫШЕЙ *APODEMUS AGRARIUS* PALLAS 1771 (RODENTIA: CRICETIDAE AND MURIDAE) В ПРИРОДНЫХ ПОПУЛЯЦИЯХ**

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Key words: ticks, *Ixodes persulcatus*, red voles, field mice, immune responsiveness, natural populations  
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### ABSTRACT

Based on the five-year population study of red voles *Clethrionomys rutilus* Pallas and field mice *Apodemus agrarius* Pallas in southern West Siberia, we analysed the distribution of immature stages of ticks *Ixodes persulcatus* on different demographic groups of the hosts, and seasonal changes of their incidence in the populations. We assessed primary humoral immune response of the voles and mice (splenic plaque-forming cells) to antigenic challenge (injection of sheep erythrocytes) in respect to occurrence of these parasites. Immune responses in immature and mature voles, which were parasitized by *I. persulcatus* at capture, were significantly higher as compared to non-infested hosts. For field mice similar effect of tick infestation was observed only in immature summer-born rodents. We discuss possible mechanisms of influence of ticks on variability of immune reactions in the populations.

### РЕЗЮМЕ

На основании пятилетнего изучения популяций красных полевок *Clethrionomys rutilus* Pallas и полевых мышей *Apodemus agrarius* Pallas на юге Западной Сибири проанализировано распределение преимагинальных фаз *Ixodes persulcatus* по поло-возрастным группам хозяев и сезонные изменения зараженности популяций зверьков клещами. У мышей и полевок оценивали гуморальный иммунный ответ (количество антителообразующих клеток) на введение антигена (эритроциты барана). Иммунный ответ половозрелых и неполовозрелых красных полевок, на которых в момент отлова было отмечено

паразитирование клещей, был достоверно выше, чем у зверьков, свободных от клещей. У полевых мышей аналогичный эффект был обнаружен лишь у неполовозрелых сеголеток. Обсуждаются возможные механизмы влияния паразитирования клещей на изменчивость иммунореактивности в природных популяциях этих хозяев.

### INTRODUCTION

Immune reactions play an important role in interrelations between ixodid ticks and their vertebrate hosts [see reviews by Balashov, 1982; Ribero, 1989a; Kaufman, 1989; Rechav, 1992]. Immunity of the hosts might be one of the principal factors in determining numbers and pattern of distribution of parasites in different animal populations [Berding et al., 1987; Anderson, 1994]. For example, sexual and age variations in parasite burden of animals in natural populations are frequently a consequence of differential resistance to within demographic groups [Folstad et al., 1989; Haukisalme et al., 1995; Zuk et al., 1996]. The changes of immunity also may govern seasonal and long-term fluctuations in parasite and infectious agents in animal populations [Cook and Beer, 1958; Andrews et al., 1972; Geller and Christian, 1982; Bradley et al., 1988]. At the same time, the assumptions about the role of immune reactions in regulating parasite burden are based primarily on results of laboratory experiments or from indirect estimations of immunity in wild animals. The defensive reactions have been rarely assessed in population studies of tick-host relationships [McGowan et al., 1980].

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On the other hand, to facilitate successful continuation of life cycle, parasites also may modify immune reactions of infested animals. The suppression of immune reactions of hosts has been demonstrated in certain species of ixodid ticks [Chinery and Ayitey-Smith, 1977; Wikel and Whelen, 1986; Fivas, 1989; Ribero, 1989a, b; Wikel and Ramachandra, 1992; Schorderet and Brossard, 1993; Dusbabek et al., 1995].

Influence of parasites on structure and population dynamics of the hosts is widely discussed in the ecological literature [Anderson, 1979; Dobson and Hudson, 1986; Gregory and Keymer, 1987; Scott and Dobson, 1989]. For small mammals, however, the data on influence of parasites on fitness and survival of their hosts are few and also contradictory. Some investigations have revealed that tick infestation affects certain morphological and/or physiological parameters of their natural rodent hosts, primarily due to the action of toxic components of tick's saliva [Okulova and Aristova, 1973; Lebedeva, 1980]. In addition, level of ectoparasite infestation may be related to mortality in small mammals [Lechmann, 1992].

In our previous studies of West-Siberian population of voles of the genus *Clethrionomys*, the humoral immune reactions changed relative to reproductive state, season and phase of population cycle [Moshkin et al., 1995; Moshkin et al., in press]. We now ask if ticks can influence variations in immunity of small rodents in natural populations.

The red vole *Clethrionomys rutilus* Pallas, 1779 (Rodentia: Cricetidae) and the field mouse *Apodemus agrarius* Pallas, 1771 (Rodentia: Muridae) are the common hosts of immature taiga ticks *Ixodes persulcatus* Schulze, 1930 (Acari: Ixodidae) within almost all its range in Asia and Europe. In the present study, we estimated the influence of larval and nymphal taiga ticks on variability in immune responses to heterologous antigenic challenge in natural populations of red voles and field mice.

## STUDY AREA

We conducted our work in a 900 ha area located 30 km S from Novosibirsk, Russia (54° N, 80° E) from 1990 to 1996. The landscape was represented by pine (*Pinus sylvestris* L.) and birch (*Betula verrucosa* L.) forests alternated with agricultural lands. The vegetation cover of the study area has been described in detail by Taran and Spiridonov [1977], and the fauna of small mammals was reviewed recently by Shubin [1991].

## MATERIAL AND METHODS

Red voles and field mice were trapped in live-traps (May–Sep) and pitfalls (Jun–Aug). Captured rodents were placed individually into cotton fabric bags and brought to laboratory. Immediately after the capture, approximately 40 % of the animals were sacrificed by cervical dislocation and then

examined for the occurrence of larval and nymphal taiga ticks [Zhmaeva, Zemskaya and Shluger, 1964].

We counted attached ticks on the remaining rodents before placing the animals into a vivarium. The voles were kept in a plastic mouse cages (22×35×8 cm) under ambient temperature and natural photoperiod. After 3 to 5 days the rodents were injected intraperitoneally by 0.5 ml of 2 % suspension ( $2 \times 10^8$  cells) of sheep red blood cells (SRBC). In five days after immunisation the voles were sacrificed by cervical dislocation and we estimated numbers of splenic plaque-forming cells (PFC) using the Cunningham technique [Cunningham, 1965; Cunningham and Szenberg, 1968; Moshkin et al., in press].

We recorded mass of the spleen and reproductive status for each animal. The reproductive status of males was determined by testes weight (spermatogenesis occurs in mature male red voles with testes  $\geq 100$  mg; threshold weight for male field mice was 500 mg). Females of both species with embryos or placental scars in utero were considered reproductively active. We distinguished overwintered from summer-born individuals by examination of skull ossification and tooth development [Koshkina, 1955; Adamczewka-Andrejewska, 1973].

The level of infestation by immature ticks in various demographic groups of hosts was determined using the data pooled for all years of the study. The analysed variables were not normally distributed and required non-parametric statistical tests [Plokhinskii, 1970; Sokal and Rohlf, 1981]. The significance of variations with age of hosts and season were tested by Kruskal-Wallis one-way analysis of variance. The comparison of mean ranks was performed using Mann-Whitney U-test.

To estimate the influence of ticks on variability of immune response in voles, we carried out 2-way ANOVA [Sokal and Rohlf, 1981] for log-transformed numbers of SRBC per 1 mg of row spleen weight. Reproductive status is one of principal factors affecting immune responsiveness to heterologous erythrocytes in voles of the genus *Clethrionomys* [Moshkin et al., 1995; Moshkin et al., in press]. In the analysis of variations for immune responses in voles and mice in relation with tick parasitism we took this factor into consideration. To minimise variations of immune response between different months and years we subtracted each monthly mean value from respective data set.

Relations between tick abundance and immune response of hosts were assessed by Spearman rank correlation analysis [Spearman, 1904]. To estimate whether variations in immune responsiveness are density-dependent, pooled larvae and nymphs into one sample [Okulova and Aristova, 1973] based on the assumption that the degree of physiological alteration is proportional to the volume of blood absorbed by certain stages during engorgement. According to Balashov [1964], these volumes differs in 6 times for the taiga tick. Based

on this we added the number of nymphs with this coefficient to the number of larvae. The calculations were made using a standard program STATISTICA CSS4. Statistical significance was indicated at  $p < 0.05$ .

We captured and examined 743 red voles and 496 field mice for ticks, and assessed humoral immune response to SRBC in 278 voles and 201 mice. Totally we have recorded 1949 larval and 549 nymphal taiga ticks on red voles, the numbers of immature ticks on field mice were 549 and 250, respectively.

## RESULTS

**Abundance of ticks.** On the whole, red voles were more heavily infested with larval taiga ticks (Table 1). The difference of mean ranks estimated by Mann-Whitney U-test was significant at  $p < 0.001$ . Field mice tended to be more heavily infested with tick nymphs as compared to red voles, but the difference was not significant. Abundance of all immature stages of ticks on red voles varied significantly with year of sampling (Kruskal-Wallis test;

$p < 0.01$  for larvae and  $p < 0.05$  for nymphs). The variations were also significant for tick larvae on field mice ( $p < 0.001$ ).

The patterns of changes in abundance with age and sex of rodents were similar in both voles and field mice (Fig. 1). The abundance of larvae and nymphs was significantly less immature compared to breeding summer-born and overwintered animals ( $p < 0.001$  for red voles and field mice). In reproductively active rodents the abundance of larval and nymphal ticks was higher in males than in females. The sex difference in mean level of infestation was significant for larvae on breeding red voles ( $p < 0.001$ ) and for both larvae and nymphs on overwintered field mice ( $p < 0.05$ ).

**Seasonal variations.** The abundance of all immature stages of the taiga tick varied significantly among months in both species of hosts (Kruskal-Wallis test;  $p < 0.001$ ). Maximum infestation with larvae was recorded on June (Fig. 2). The abundance of nymphs on red voles was maximal on May and June, that on field mice was on June.

Table 1. Prevalence and abundance of immature taiga ticks *Ixodes persulcatus* on red voles and field mice

Таблица 1. Встречаемость и обилие преимаго таежного клеща *Ixodes persulcatus* на красных полевках и полевых мышках

Year	Number of rodents	Larvae		Nymphs	
		Prevalence (%)	Abundance (A ±S.D.)	Prevalence (%)	Abundance (A ±S.D.)
<b>Red vole</b>					
1991	140	60.7	3.4 ±5.4	11.4	0.2± 0.5
1992	127	53.5	2.7± 5.8	15.7	0.3± 0.9
1993	115	36.5	2.7± 7.9	13.0	0.2± 0.8
1994	120	45.0	2.7± 5.8	9.2	0.1± 0.4
1995	115	40.0	1.7± 3.4	13.9	0.2± 0.5
1996	126	50.8	2.3 ±4.3	12.7	0.2± 0.6
<b>Total</b>	<b>743</b>	<b>48.3</b>	<b>2.6± 5.6</b>	<b>12.6</b>	<b>0.2± 0.6</b>
<b>Field mouse</b>					
1991	49	49.0	2.3± 5.4	24.5	0.6 ±1.7
1992	66	34.8	1.6±4.2	19.7	1.1 ±4.0
1993	124	39.5	1.0 ±1.8	20.2	0.5±1.4
1994	89	4.04	1.0± 1.7	9.0	0.2± 0.6
1995	106	17.9	0.4± 1.2	7.5	0.3±1.3
1996	62	32.3	1.1± 2.8	19.4	0.6±2.2
<b>Total</b>	<b>496</b>	<b>34.5</b>	<b>1.0± 2.8</b>	<b>15.7</b>	<b>0.5± 2.0</b>

Table 2.  
Analysis of variance for immune response in relation to breeding status and the taiga tick parasitism  
Таблица 2.  
Результаты дисперсионного анализа иммунного ответа в зависимости от репродуктивного  
состояния зверьков и их зараженности клещами

Source of variation	d.f.	Sum of squares	F	P
<b>Red vole</b>				
Reproductive status (R)	1	0.98	8.24	<0.01
Infestation with ticks (I)	1	1.34	11.38	<0.001
Interaction (R×I)	1	0.01	0.07	0.79
Residual	247	0.12	-	-
Total	247	34.57	-	-
<b>Field mouse</b>				
Reproductive status (R)	1	0.64	4.01	<0.05
Infestation with ticks (I)	1	0.05	0.31	0.58
Interaction (R×I)	1	0.58	3.64	0.06
Residual	197	0.16	-	-
Total	197	32.30	-	-

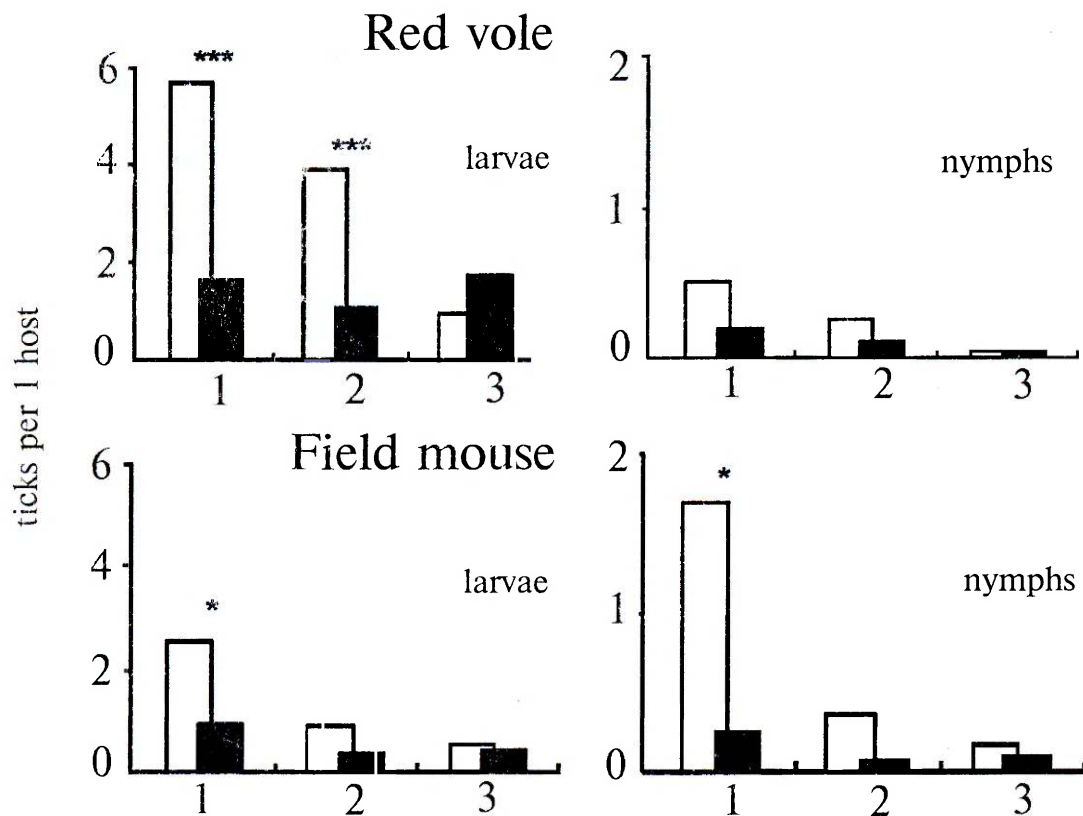


Fig. 1. Abundance of immature ticks *I.persulcatus* on various demographic groups of hosts. Males are indicated by blank bars; females are indicated by colored bars. Demographic groups: overwintered (1), breeding summer-born (2), immature summer-born (3). Significant difference of mean ranks by Mann-Whitney U-test indicated by asterisks: \* –  $p < 0.05$ ; \*\*\* –  $p < 0.001$ .

Рис. 1. Обилие преимаго таежного клеща *I.persulcatus* на различных поло-возрастных группах хозяев. Самцы — незакрашенные столбики, самки — закрашенные столбики. Демографические группы: перезимовавшие (1), размножающиеся сеголетки (2), неполовозрелые сеголетки (3). Звездочками обозначены достоверные различия средних рангов по критерию Манн-Уитни: \* –  $p < 0.05$ ; \*\*\* –  $p < 0.001$ .

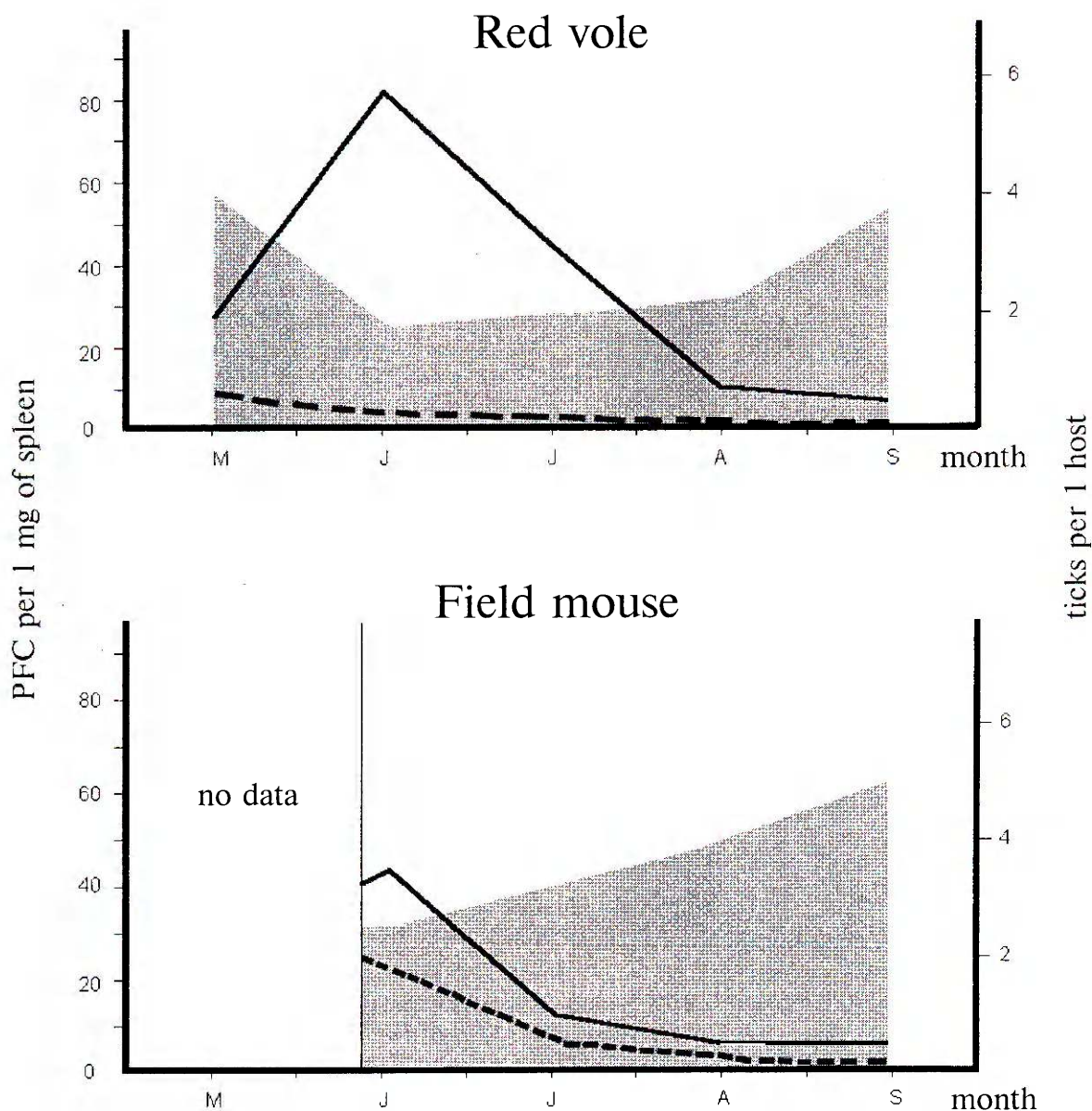


Fig. 2. Seasonal changes of infestation of hosts with larvae (solid line) and nymphs (dotted line) of tick *I.persulcatus* and of host's humoral immune response to SRBC (colored area).

Рис. 2. Сезонные изменения зараженности хозяев личинками (сплошная линия) и нимфами (пунктирная линия) таежного клеща *I.persulcatus* и изменения гуморального иммунного ответа на введение эритроцитов барана (закрашенная область).

These seasonal extremes of infestation with ticks coincided with lowest immune responsiveness to SRBC in both host species. To the end of summer season the level of infestation declined gradually in parallel with the growth of host's immune responses.

**Influence of ticks on immune responsiveness of hosts.** Tick parasitism was significantly related to immune response to SRBC in red voles (Table 2). The effect of reproductive status was also significant, but independent from the influence of tick burden. In contrast, the effect of infestation with ticks on immune responsiveness was insignificant in field mice. But the analysis indicates marginal significance of interaction between this factor and reproductive status of hosts. This gives reasons to suspect different relationships between immune responsiveness and occurrence of feeding ticks in breeding and immature mice.

In the case, this presumption was supported by the comparison of mean ranks in above mentioned groups. The immune response was significantly higher in reproductively active and immature red voles which were previously infested with ticks than in non-infested ones ( $p < 0.05$ ; Fig. 3). We observed a similar effect only in immature summer-born field mice ( $p < 0.05$ ). The immune response in adult field mice did not differ relative to tick parasitism.

The immune response of red voles was positively correlated with number of attached ticks ( $r = 0.14$ ,  $p < 0.05$ ). In field mice, no correlation between these parameters was indicated.

## DISCUSSION

Infestation of various demographic groups of hosts is determined by a wide range of factors, including territorial behaviour, activity, body size,

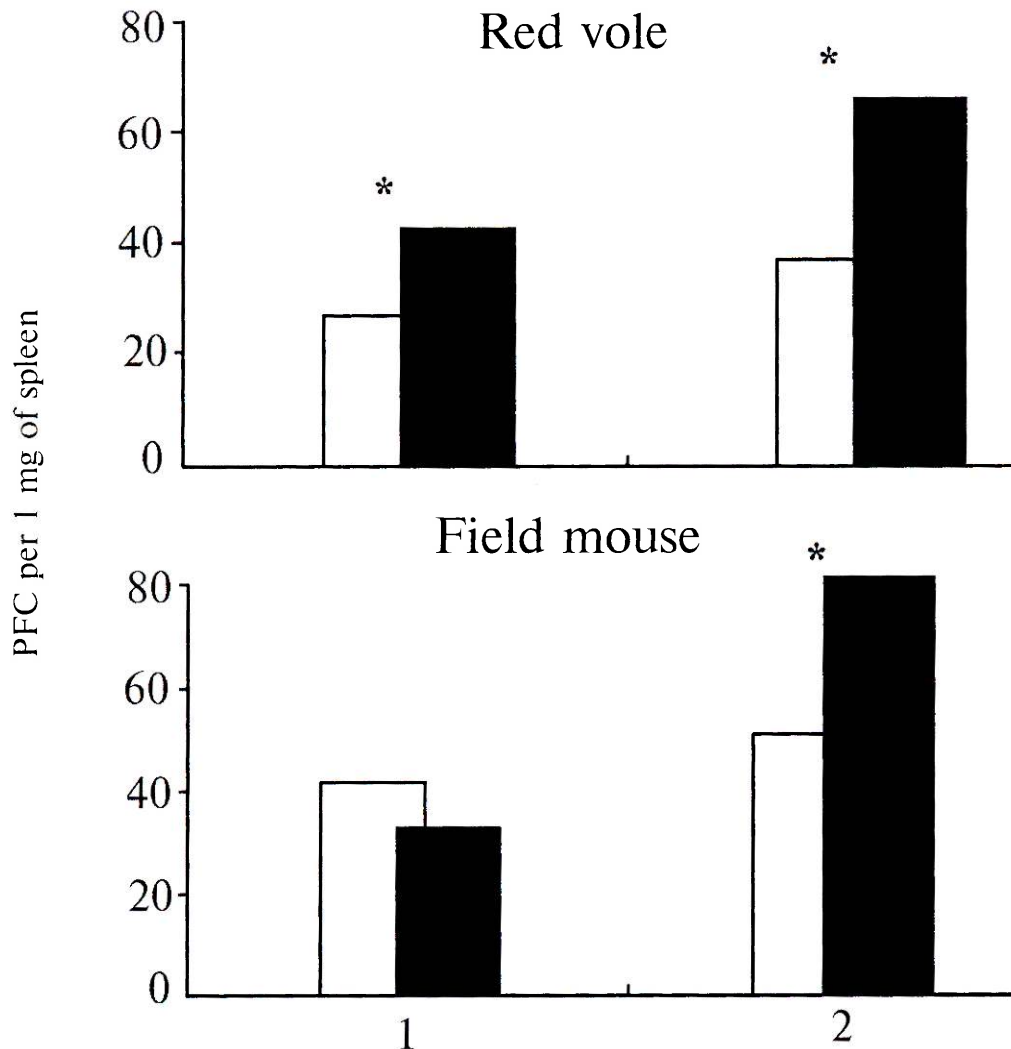


Fig. 3. Humoral immune response to SRBC of rodents, previously infested (colored bars) and non-infested (Blank bars) with ticks *I.persulcatus*. Overwintered and summer-born breeding animals (1); immature summer-born animals (2). Significant difference of mean ranks by Mann-Whitney U-test ( $p < 0.05$ ) indicated by asterisk.

Рис. 3. Гуморальный иммунный ответ на введение эритроцитов барана у зверьков, зараженных (закрашенные столбики) и незараженных (незакрашенные столбики) таежными клещами *I.persulcatus* в момент отлова. Размножающиеся перезимовавшие зверьки и сеголетки (1); неполовозрелые сеголетки (2). Звездочками обозначены достоверные различия средних рангов по критерию Манн-Уитни ( $p < 0.05$ ).

and resistance. The number and the hierarchy of the factors is specific for each particular parasite species. For various parasites associated with small rodents parasite burden is accounted primarily by reproductively active hosts [Cook and Beer, 1958; Haukisalmi, Henttonen and Batzli, 1995]. In the case of red voles and field mice, more intensive infestation of breeding individuals also could be caused by lowered immune resistance characteristic to these groups of hosts [Moshkin et al., 1995; Moshkin et al., in press]. On the other hand, immune responsiveness is higher in non-breeding young, and infestation with ticks is lower. It seems that predominating infestation of reproductively active voles allows parasites to reduce the negative influence of their host's immunity and creates conditions for successful infestation of their population in the following season. Even if a significant portion of breeding rodents develops a high resistance to repeated infestation, this group will be eliminated almost completely by the end of sum-

mer. Young of late generations have much less contact with ticks in autumn and will be susceptible to infestation when they begin to breed in following spring. Our assumption was supported by seasonal dynamics of ticks on both voles and field mice. The abundance of ticks was maximal in June, when overwintered and breeding summer-born rodents of first generations prevail in their populations and immune responsiveness was lowest. The level of infestation with ticks declined to the end of summer together with the growth of host's immune responsiveness.

Immunomodulating effects of feeding ixodid ticks on host organism are well known, the immunosuppression contributes to a successful engorgement of these parasites [Ribero, 1989b]. Studies on guinea pigs have shown that many immune reactions, including formation PFC after immunisation with SRBC, are suppressed during tick feeding [Wikel and Ramachandra, 1992]. In this context, our observed differences in humoral immune re-

sponses of studied rodents in relation to tick parasitism were unexpected. In all red voles and in summer-born immature mice, on which feeding ticks were recorded, immune responses not only was not reduced, but on the contrary, was essentially greater as compared to non-infested animals.

Ticks may suppress the immune reactions for a short period; the number of PFC was restored for the fourth days after the termination of tick feeding [Wikel and Ramachandra, 1992]. On the other hand, it is known, that the antigens of a tick saliva can induce a marked resistance to repeated tick feeding in *Clethrionomys* voles [Labetskaya, 1990; Dizij and Kurtenbach, 1995].

To explain effects observed in our study, we propose at least three hypotheses:

the growth of immune responsiveness is a consequence of termination of action of tick's salivary suppressive agents (effect of "compressed spring");

immune responsiveness may be related to certain characteristics of hosts which determine tick burden (e.g. attractive odour or locomotory activity). For example, it is known that immunocompetence is associated with social rank in albino mice [Smith, Barnard and Behnke, 1995];

it is non-specific effect associated with the formation of anti-tick immunity in host's organism (immune cross-reactivity).

The last hypothesis may be more substantial because formation of resistance to certain helminth antigens can be accompanied by non-specific immunity to some other antigens, or cross-resistance [see review by Lejkina, 1978]. It is possible that the tick salivary antigens are capable of producing similar effects.

The voles of the genus *Clethrionomys* acquire greater immune resistance to ixodid ticks as compared to mice of the genus *Apodemus* [Nikitina and Aristova, 1964; Dizij and Kurtenbach, 1995]. The lack of increase of immune responses in adult field mice infested with ticks could be assigned to their poor resistance against ticks. To test above hypotheses, further experimental study is necessary.

Thus, the example of the studied populations of red voles and field mice confirms that ixodid ticks can influence the variability of immune reactions in their natural hosts. The results of our study are in accordance with the assumption that parasites are capable of regulating host populations even if their pathogenity is not pronounced.

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