

THE ROLE OF MIGRATORY PASSERINE BIRDS IN PATHOGEN EXCHANGE BETWEEN COFEEDING *IXODES RICINUS* TICKS (ACARINA, IXODIDAE)

РОЛЬ ПРОЛЕТНЫХ ПТИЦ В ОБМЕНЕ ПАТОГЕНАМИ МЕЖДУ ПИТАЮЩИМИСЯ НА НИХ ОСОБЯМИ *IXODES RICINUS* (ACARINA, IXODIDAE)

H.V. Dubinina, A.N. Alekseev
Е.В. Дубинина, А.Н. Алексеев

Zoological Institute, Russian Academy of Sciences, 199034 St. Petersburg, Russia
Зоологический институт Российской академии наук, 199034 Санкт-Петербург, Россия

Key words: passerine birds, ticks, pathogen exchange, transmission
Ключевые слова: воробьиные птицы, клещи, обмен возбудителями, передача

ABSTRACT

Prevalence of tick-borne pathogens was compared in immature stages of *Ixodes ricinus* ticks collected from vegetation and from migratory passerine birds on the Curonian Spit, Kalinigrad Region, Russia. Great similarity of pathogen prevalence was noted in both cases in all ticks tested as singletons. No pathogens were detected among the tick larvae captured from vegetation, whereas in the larvae taken from birds a dual (*Borrelia afzelii* and *Borrelia garinii*) infection was detected. In one nymph, even a triple infection (*B. afzelii*, *B. garinii* and *Ehrlichia muris*) was revealed. In contrast, this never occurred in tick immatures taken from vegetation. Apparently, bird blood may serve not only a source of tick-borne pathogens (e.g. *B. garinii*, according to Kurtenbach et al. [2002]), but also as an amplifier for their reproduction. A statistically significant prevalence of the pathogens among ticks collected from birds in pools even as small as 2–3 specimens over singletons allows to emphasize the roles the migratory birds play in pathogen exchange between cofeeding immature ixodid ticks.

РЕЗЮМЕ

Произведено сравнение экстенсивности заражения преимагинальных фаз *Ixodes ricinus*, собранных с растительности на флаг и снятых с пролетных птиц на Куршской косе Калининградской области. Обнаружено значительное сходство состава патогенов у той и другой группы клещей. В личинках, собранных на флаг и исследованных индивидуально, патогены обнаружены не были, тогда как в единичных личинках, снятых с пролетных птиц, даже двойное заражение (*Borrelia afzelii* и *B. garinii*) не было исключением. В одной нимфе, снятой с птицы, были обнаружены одновременно 3 патогена: *B. afzelii*, *B. garinii* и *Ehrlichia muris*. Такой факт

ни разу не был констатирован ни для личинок, ни для нимф, собранных с растительности. Таким образом, кровь птиц — не только источник некоторых клещевых патогенов, например *B. garinii* [Kurtenbach et al., 2002], но и амплификатор репродукции других. Статистически значимые различия экстенсивности заражения в группах клещей, собранных с одной птицы (даже если в группе было всего 2–3 личинки или нимфы), с единичными особями (как с растительности, так и с птиц) — свидетельство роли перелетных птиц в обмене возбудителями при совместном питании на них личинок и нимф иксодовых клещей.

INTRODUCTION

Birds as hosts of different mites were investigated by Professor Vsevolod B. Dubinin (1913–1958), a famous Russian zoologist. He studied the role birds play as a source of food, as a habitat and as a “transport” means for a very wide range of families, genera and species of Acarina [Dubinin, 1948a, 1951, 1953]. Among the parasites he described, there were consumers of skin, feathers, body liquid and blood. Among the latter consumers, there were immatures and very rarely adults of ixodid ticks. In the 1940's and early 1950's, ixodid ticks parasitizing birds were known only as a vector and a reservoir of tick-borne encephalitis viruses. Over the last half of the 20th century, the role of some species of the genus *Ixodes* as vectors of other human pathogens were revealed. The importance of birds as a source of blood was emphasized since the discovery of their capacity to serve by themselves as reservoirs and sources of pathogens [Ilyichev, Lvov, 1979].

The phoresy so well described by professor V.B. Dubinin of mites and other parasites, includ-

ing ixodids, has since been shown to concern not only parasites being transferred by migratory birds but their pathogens as well. Recent data [Alekseev et al., 2001a] that *Ixodes ricinus* (L.) ticks cofeeding on migratory birds are capable of containing two and even three pathogens at once emphasize the role of bird — tick cooperation. At the same time, ticks cofeeding on one and the same bird and supporting different pathogens are capable of the pathogen exchange when feeding on the host blood. Thus the bird parasite (=mite or tick) coexistence reveals another aspect of importance from epizootological and epidemiological points of view.

At present, pathogen exchange between ticks cofeeding on an aviremic or even viremic vertebrate host is well-known, being described not only in special but even in popular science literature [Randolf et al., 1996]. This was first discovered in the couple Thogoto virus—*Rhipicephalus appendiculatus* Neumann tick [Jones et al., 1987] and confirmed later for the tick-borne encephalitis virus (TBEV) and *Ixodes persulcatus* Schulze tick pair [Alekseev, Chunikhin, 1991]. More recently, another specific tick-borne pathogen, *Borrelia burgdorferi* sensu lato, was revealed as being involved [Gern, Rais, 1996]. Transmission of the latter pathogen was further proved for non-laboratory animals, e.g. *I. ricinus* ticks cofeeding on sheep [Ogden et al., 1997] also transmitted *Borrelia* from one to another. Decisive role of larvae and nymphs cofeeding on the same animal for the tick-borne encephalitis foci existence was emphasized in the series of data summarized by Randolph et al. [1999, 2000].

In 1935, still before the discovery that *I. persulcatus* ticks could transfer TBEV [Zilber, 1939; Pavlovsky, Soloviev, 1940], the feeding periods of *I. persulcatus* larvae and nymphs coinciding on small animals and birds were described by Khodakovsky [1947]. This was also confirmed in 1943 by Dubinin, who checked *I. persulcatus* immature stages on passerine birds [Dubinin, 1948b]. Both Khodakovsky and Dubinin were apparently the first to have described the frequency of occurrence of this phenomenon in passerine birds, migratory ones included. Transcontinental transfers of ticks on migratory birds were revealed later [Hoogstraal, Kaiser, 1961; Hoogstraal et al., 1961, 1963]. Transhemispheric transfer of *B. burgdorferi* s.l. and the role of *Ixodes uriae* White in this process were described much later [Olsén et al., 1993, 1995a].

The importance of birds, and of the ticks they carry about, as a source of *Borrelia* dissemination

has been studied in the U.S.A. [Anderson et al., 1986; Weisbrod, Johnson, 1989; Magnarelli et al., 1992], Japan [Miyamoto et al., 1993; Nakao et al., 1994] and Europe [Olsén et al., 1995b]. The European team has revealed borreliae in both immature stages of *I. ricinus* ticks, i.e. larvae as well as nymphs. Alekseev et al. [2001a] has recorded not only *Borrelia* but also *Ehrlichia* in the immatures of *I. ricinus* collected from migratory passerines on the Curonian Spit, Baltic region of Russia. Blackbirds, *Turdus iliacus* L., stopping over on the spit during their migration for some 3–4 days appear to represent not only a reservoir [Alekseev et al., 2001a] but also a source of *Borrelia* for *I. ricinus* nymphs in Switzerland [Humair et al., 1998]. According to our data, just a singleton nymph discovered on *T. iliacus* on the Curonian Spit was infected by *Borrelia afzelii* [Alekseev et al., 2001a].

Kurtenbach et al. [1998a] demonstrated the competence of pheasants as reservoirs for *Borrelia garinii*. Using pheasants, Kurtenbach et al. [1998a, b] proved that *I. ricinus* fed on these birds and getting *B. garinii* from the host lost their capability to support *B. afzelii* obtained from mice at the previous stage of their development. Summarizing the abundant material collected mainly in Western Europe, Kurtenbach et al. [2002] conclude that birds can serve as a source of *B. garinii* (20047 type), *B. valaisiana* and *B. burgdorferi* sensu stricto only, whereas small mammals are capable of infecting *I. ricinus* by *B. garinii* (NT29), *B. afzelii*, *B. bissettii*, *B. japonica* and *B. burgdorferi* s.s. These authors mention, however, the presence of neither HGE nor HME *Ehrlichia*-agents in ticks taken from birds or on vegetation.

The present study attempts to prove, yet without discussing the prevalence of this or that *Borrelia* species as a source of infection of *I. ricinus* larvae and nymphs from bird blood during the period of cofeeding, that these immature stages are capable of transmitting to one another the different species of tick-borne agents pathogenic to man. For this purpose, the occurrences of tick-borne pathogens determined in ticks taken not only from migratory birds but also from vegetation near the places of bird catch are compared. Thus the roles the migratory passerine birds possibly play in bacterial pathogen (*Borrelia* and *Ehrlichia*) exchange would be documented.

MATERIAL AND METHODS

Ticks. In the Kalinigrad Region, *I. ricinus* nymphs and adults were collected by flagging in

the spring (early May) and in the fall (early September) of 1995–1998 on the Curonian Spit (Kurische Nehrung) near Lesnoye and Rybachiy. Ticks were captured also from the migratory birds trapped, banded and then released by staff members of the Ornithological Station, i.e. “Rybachiy” Biological Station and “Fringilla” Field Station, of the Zoological Institute of the Russian Academy of Sciences in 2000. The passerines were caught using Rybachiy-type nets [Dolnik, Paevsky, 1976] and mist nets at the ground level. All ticks taken from one and the same bird were placed in a vial containing 70% ethanol.

Ticks collected by flagging were also fixed. The total number of trapped birds amounted to 1606, of which 110 supported tick pools, singletons included. The total number of *I. ricinus* captured on vegetation during the 1995–1998 seasons exceeded 3,000.

Pathogen detection. All ticks collected were screened for pathogens. Total DNA was extracted from the ticks and subjected to DNA amplification [Alekseev et al., 1998]. Both generic and species identities of *Borrelia* and *Ehrlichia* pathogenic to

man were detected by PCR using specific primers of *B. afzelii*, *B. garinii*, human granulocytic ehrlichiosis (HGE), and human monocytic ehrlichiosis (HME) agents [Alekseev et al., 2001a]. Ticks taken during 1995–1996 were screened for *Borrelia* species only. The data of pathogen prevalence were compared using Yates’ corrected chi-square test.

RESULTS

To precisely compare the rates of larval and nymphal infection, the immatures were analyzed in two groups. The first contained singletons taken from vegetation only, whereas the second the pools of ticks captured from one bird only. Each group was subdivided into two subgroups. One included monoinfected, the other multiinfected specimens. The prevalence of bacterial agents appears to be very similar regardless of the origins of the monoinfected ticks either from vegetation or from birds (Table 1).

Dually infected larvae were revealed on birds only (Table 2), whereas among the larvae taken from vegetation neither mono- nor dually infected specimens ever occurred.

Table 1. Prevalence of bacterial pathogens in monoinfected immature stages of *Ixodes ricinus* ticks collected in singletons on vegetation or from migratory passerine birds

Таблица 1. Встречаемость бактериальных патогенов у единичных моноинфицированных личинок и нимф *Ixodes ricinus*, собранных с растительности или с пролетных воробьиных птиц

Ticks			Pathogens							
Collected from	Season of collection	No.	<i>B. afzelii</i>		<i>B. garinii</i>		<i>B. valaisiana</i>		<i>Ehrlichia</i> sp.*	
			abs.	%	abs.	%	abs.	%	abs.	%
Vegetation	1995–1998	64	45	70.30	7	10.95	8	12.50	4	6.25
Birds	2000	29	21	72.40	4	13.80	1	3.50	3	10.30
Chi-square values**			0.04		0.15		1.87		0.48	

* *Ehrlichia* sp. — either HME-agent, *Ehrlichia muris*, or HGE-agent, *Anaplasma phagocytophila*.

** None of the differences checked, according to chi-square tests, was statistically significant.

Table 2. Types of *Ixodes ricinus* larval infection from migratory passerine birds

Таблица 2. Типы зараженности личинок *Ixodes ricinus*, собранных с пролетных воробьиных птиц

Type of collection	No. of cases	No. of cases with pathogens						
		<i>E</i>	<i>Ba</i>	<i>Bg</i>	<i>Ba+Bg</i>	<i>Ba+Bbss</i>	<i>Ba+E</i>	
In singletons	3	0	2	0	1	0	0	
In pools	only larvae	3	0	1	1	1	0	0
	larvae and nymphs	8	1	1	1	3	1	1

E — *Ehrlichia* sp. (either HME-agent, *Ehrlichia muris*, or HGE-agent, *Anaplasma phagocytophila*); *Ba* — *B. afzelii*; *Bg* — *B. garinii*; *Bbss* — *B. burgdorferi* sensu stricto.

Table 3. Infection rates of mono- and multiinfected *Ixodes ricinus* immature stages in relation to the place and type of collection
 Таблица 3. Соотношение моно- и полиинфицированных личинок и нимф *Ixodes ricinus*, собранных с растительности и группами и поодиночке с пролетных воробьиных птиц

Collection			Ticks					
Type	Sources	Symbols	No. of infected to No. of collected		No. of monoinfected to No. of infected		No. of multiinfected to No. of infected	
			abs.	%	abs.	%	abs.	%
In singletons	vegetation	A	82/260	31.5	64/82	78.0	8/82	9.8
	bird	B	38/73	52.1	31/38	81.6	7/38	18.4
In pools	bird	C	19/37	38.7	11/19	67.9	8/19	42.1
Chi-square, <i>p</i> values		A – B	10.41; <0.1		0.2; >0.1		0.17; >0.1	
		B – C	0.005; >0.1		3.66; <0.1		3.64; <0.1	
		A – C	5.666; <0.05		3.3; <0.1		12.11; <0.001	

The data pool is too modest to be analyzed statistically but it is of interest to emphasize that all three infected larvae contained *B. afzelii* either as a dual or a mono-infection agent. The groups of larvae supported *B. afzelii* in two out of three cases. *Ehrlichia* sp. as a mono- or a dual infection agent was solely reported in pools where not only tick larvae but nymphs were present as well. Dual infections of nymphs were common while one nymph contained even three pathogens at once: *B. afzelii*, *B. garinii*, and HME-agent (*E. muris*). It is noteworthy that, among eight pools of larvae and nymphs, in five cases (62.5%) more than one pathogen were found. This fact suggests that multi-infections in tick pools, and even in singletons, is rather a rule than an exception. Table 3 shows this in further detail.

Not only in pools but also in singletons the number and ratios of multiinfected ticks were 2–4 times higher than among the immature ticks taken from vegetation. The difference is statistically significant.

DISCUSSION

The results of this study appear to disagree with the data presented by Kurtenbach et al. [2002]. The prevalence of *B. garinii* among the ticks taken from birds was not significantly different from that in singletons collected on vegetation: 9.7 versus 12.1%, respectively (Table 1). Likewise, the *B. afzelii* prevalence in the nymphs occurring on vegetation was not significantly smaller than that in the ticks coming from birds: 70.3 versus 72.4%, respectively. Furthermore, the *B. afzelii* prevalence in *I. ricinus* adults was nearly equal to that in the nymphs, 71.2% [Alekseev et al., 1998, 2001b].

This shows that larval and nymphal parasitization means no decrease in *B. afzelii* prevalence in tick adults coming from an area where passerine birds may be one of the main sources of host blood. The rate of prevalence of *B. garinii* in adult ticks was also almost the same as in the immatures collected on vegetation or from birds: 10 versus 9.7 and 12.1%, respectively.

Somewhat strangely, the number of mono-infected ticks was significantly smaller among the specimens collected from birds in pools than that of the ticks taken as singletons. In both cases ticks might have got a pathogen at a previous stage of development, e.g. from the egg (for larvae) or from the larva (for nymphs). Yet their rate of infection was less than that of the ticks coming from vegetation or from birds in singletons: 67.9 versus 78.0 and 81.6%, respectively. It is noteworthy that, among singletons of immature stages taken both on vegetation and from birds, the rate of multiinfected specimens was high enough: 9.8 and 18.4%, respectively (Table 3).

Much more important seems the fact that multi-infections in pools occurred 2–4 times more frequently than among singletons (Table 3). This difference was quite significant statistically (chi-square 12.11). Among the ticks in pools there were even only pairs of specimens [Alekseev et al., 2001a]. All this seems to provide a sound basis for concluding that co-feeding larvae and nymphs exchange the pathogens while in pools. This is especially plausible because, as it is well-known, groups of *I. ricinus* larvae and nymphs tend to feed on birds only in such restricted, presumably safe places like under the beak and around the eyes (Fig. 1).



Fig. 1. A pool of *Ixodes ricinus* immatures on a Song thrush (courtesy of Dr. Kazimir Bolshakov).
Рис. 1. Напитавшиеся личинки *Ixodes ricinus* на голове певчего дрозда (фото Казимира Большакова).

ACKNOWLEDGEMENTS

The authors wish to express their cordial thanks to Olga V. Voltzit (Zoological Museum of Moscow State University, Russia) for the identification of immature tick stages, and to Anatoly P. Shapoval and Nikita S. Chernetsov ("Rybachiy" Biological Station, Kaliningrad Region, Russia) for technical assistance with bird identification and tick collection. Sergei I. Golovatch (Moscow) has kindly corrected the English of an advanced draft. Both the study and publication were supported in part through grants No. 02-04-48654 and No. 02-04-63103 rendered by the Russian Foundation for Basic Research.

REFERENCES

- Alekseev A.N., Chunikhin S.P. 1991. [Virus exchange in ticks feeding on vertebrate host in the absence of viremia (Distant transmission)]. *Med. parazitol. i parasit. bolezni*, 2: 50–54. [In Russian]
- Alekseev A.N., Dubinina H.V., Antykova L.P., Dzhivanyan T.I., Rijpkema S.G.T., Verbeek-de Kruif N., Cinco M. 1998. Tick-borne borreliosis pathogen identification in *Ixodes* ticks (Acarina, Ixodidae) collected in St. Petersburg and Kaliningrad Baltic Regions of Russia. *J. Med. Entomol.*, 35 (2): 136–142.
- Alekseev A.N., Dubinina H.V., Semenov A.V., Bolshakov C.V. 2001a. Evidence of ehrlichiosis agents found in ticks (Acari: Ixodidae) collected from migratory birds. *J. Med. Entomol.*, 38 (4): 471–474.
- Alekseev A.N., Dubinina H.V., Van de Pol I., Schouls L.M. 2001b. Identification of *Ehrlichia* spp. and *Borrelia burgdorferi* in *Ixodes* ticks in the Baltic regions of Russia. *J. Clin. Microbiol.*, 39 (6): 2237–2242.
- Anderson J.F., Johnson R.C., Magnarelli L.A., Hyde F.W. 1986. Involvement of birds in the epidemiology of the Lyme disease agent *Borrelia burgdorferi*. *Infect. Immun.*, 51: 394–396.
- Dolnik V.R., Paevsky V. A. 1976. [Rybachy-type trap]. In: V.D. Ilychev (Ed.). Ringing in the study of bird migrations in the USSR, Moscow, Nauka Publ., pp. 73–81. [In Russian]
- Dubinin V.B. 1948a. [The role of animal's migration in the diseases' dissemination]. *Trudy Kazakhskoy Akademii Nauk*, 5: 13–23. [In Russian]
- Dubinin V.B. 1948b. [Ixodids ticks of the south-east Zabaykalye steppes and their epidemiological significance]. In: Epidemiologicheskie and parasitologicheskie ekspeditsii v Iran, Publisher: Moscow, Acad. Nauk SSSR, pp. 275–286. [In Russian]
- Dubinin V.B. 1951. [Feather mites (Analgesoidea). I. Introduction in the study]. Fauna SSSR. Novaya seriya, 43. Paukoobraznii, 6 (5). Publisher: Nauka, Moscow-Leningrad, 363 p. [In Russian]
- Dubinin V.B. 1953. [Feather mites (Analgesoidea). II. Epidermoptidae and Freyanidae families]. Fauna SSSR. Novaya seriya, 55. Paukoobraznii, 6, (6), Publisher: Nauka, Moscow-Leningrad, 412 p. [In Russian]
- Gern L., Rais O. 1996. Efficient transmission of *Borrelia burgdorferi* between cofeeding *Ixodes ricinus* ticks (Acari: Ixodidae). *J. Med. Entomol.*, 33: 189–192.
- Hoogstraal H., Kaiser M.N. 1961. Ticks from European-Asiatic birds migrating through Egypt into Africa. *Science*, 133: 277–278.

- Hoogstraal H., Kaiser M.N., Traylor M.A., Gaber S., Guindy E. 1961. Ticks (Ixodoidea) on birds migrating from Africa to Europe and Asia. *Bull. WHO*, 24: 197–212.
- Hoogstraal H., Kaiser M.N., Traylor M.A., Guindy E., Gaber S. 1963. Ticks (Ixodoidea) on birds migrating from Europe and Asia to Africa, 1959–61. *Bull. WHO*, 28: 235–262.
- Humair P.F., Postic D., Wallich R., Gern L. 1998. An avian reservoir (*Turdus merula*) of the Lyme borreliosis spirochetes. *Zentralblatt Bakteriolog*, 287: 521–538.
- Ilyichev V.D., Lvov D.K. 1979. [Bird migration and pathogens transmission]. Moscow: Nauka Publ., 271 p. [In Russian]
- Jones L.D., Davies C.R., Steele G.M., Nuttall P.A. 1987. A novel mode of arbovirus transmission involving a nonviremic host. *Science*, 237 (4816): 775–777.
- Khodakovskiy A.I. 1947. [Foci of *Ixodes persulcatus* P. Sch. distribution in the taiga region of European part of the USSR]. *Parazitol. sbornik Zool. Instit. Akad. Nauk SSSR*, 9. Leningrad, Nauka Publ.: 69–82. [In Russian]
- Kurtenbach K., Carey D., Hoodless A.N., Nuttall P.A., Randolph S.E. 1998a. Competence of pheasants as reservoirs for Lyme disease spirochetes. *J. Med. Entomol.*, 35: 77–81.
- Kurtenbach K., Peacey M., Rijpkema S.G.T., Hoodless A.N., Nuttall P.A., Randolph S.E. 1998b. Differential transmission of the genospecies of *Borrelia burgdorferi* sensu lato by game birds and small rodents in England. *Appl. Environ. Microbiol.*, 64: 1169–1174.
- Kurtenbach K., De Michelis S., Sewell H.-S., Etti S., Schäfer S.M., Holmes E., Hails R., Collares-Pereira M., Santos-Reis M., Hanincová K., Labuda M., Bormane A., Donaghy M. 2002. The key roles of selection and migration in the ecology of Lyme borreliosis. *Int. J. Med. Microbiol.*, 291, Suppl. 33: 152–154.
- Magnarelli L.A., Stafford III K.C., Bladen V.C. 1992. *Borrelia burgdorferi* in *Ixodes dammini* (Acari: Ixodidae) feeding on birds in Lyme, Connecticut, U.S.A. *Can. J. Zool.*, 70: 2322–2325.
- Miyamoto K., Nakao M., Fujita H., Sato F. 1993. The ixodid ticks on migratory birds in Japan and the isolation of Lyme disease spirochetes from bird-feeding ticks. *Jap. J. Sanit. Zool.*, 44: 315–326.
- Nakao M., Miyamoto K., Fukunaga M. 1994. Lyme disease spirochetes in Japan: enzootic transmission cycles in birds, rodents, and *Ixodes persulcatus* ticks. *J. Infect. Dis.*, 170: 878–882.
- Ogden N.H., Nuttall P.A., Randolph S.E. 1997. Natural Lyme disease cycles maintained via sheep by co-feeding ticks. *Parasitology*, 115: 591–599.
- Olsén B., Duffy D.C., Jaenson T.G.T., Gylfe Å, Bonnedahl J., Bergström S. 1995a. Transhemispheric exchange of Lyme disease spirochetes by seabirds. *J. Clin. Microbiol.*, 33: 3270–3274.
- Olsén B., Jaenson T.G.T., Noppa L., Bunikis J., Bergström S. 1993. A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks. *Nature*, 362: 340–342.
- Olsén B., Jaenson T.G.T., Bergström S. 1995b. Prevalence of *Borrelia burgdorferi* sensu lato-infected ticks on migrating birds. *Appl. Environ. Microbiol.*, 61: 3082–3087.
- Pavlovskiy E.N., Soloviev V.D. 1940. [Experimental investigation of the tick-borne encephalitis virus circulation in the tick-vector body (*Ixodes persulcatus*)]. *Arkhiv Biol. Nauk*, 59: 111–117. [In Russian]
- Randolph S. E., Gern L., Nuttall P.A. 1996. Co-feeding ticks: Epidemiological significance for tick-borne pathogen transmission. *Parasitol. Today*, 12: 472–479.
- Randolph S.E., Green R.M., Peacey M.F., Rogers D.J. 2000. Seasonal synchrony: the key to tick-borne encephalitis foci identified by satellite data. *Parasitology*, 121: 15–23.
- Randolph S.E., Miklisová D., Lysy J., Rogers D.J., Labuda M. 1999. Incidence from coincidence: Patterns of tick infestations on rodents facilitate transmission of tick-borne encephalitis virus. *Parasitology*, 118: 177–186.
- Weisbrod A.R., Johnson R.C. 1989. Lyme disease and migrating birds in the Saint Croix River Valley. *Appl. Environ. Microbiol.*, 55: 1921–1924.
- Zilber L.A. 1939. [Spring (spring-summer) endemic tick-borne encephalitis]. *Arkhiv Biol. Nauk*, 56: 9–37. [In Russian]