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Detection of tick-borne pathogens in wild birds and their ticks in Western Siberia and high level of their mismatch

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Abstract: The Tomsk region located in the south of Western Siberia is one of the most high-risk areas for tick-borne diseases due to elevated incidence of tick-borne encephalitis and Lyme disease in humans. Wild birds may be considered as one of the reservoirs for tick-borne pathogens and hosts for infected ticks. A high mobility of wild birds leads to unpredictable possibilities for the dissemination of tick-borne pathogens into new geographical regions. The primary goal of this study was to evaluate the prevalence of tick-borne pathogens in wild birds and ticks that feed on them as well as to determine the role of different species of birds in maintaining the tick-borne infectious foci. We analysed the samples of 443 wild birds (60 species) and 378 ticks belonging to the genus *Ixodes* Latraille, 1795 collected from the wild birds, for detecting occurrence of eight tick-borne pathogens, the namely tick-borne encephalitis virus (TBEV), West Nile virus (WNV), and species of *Borrelia*, *Rickettsia*, *Ehrlichia*, *Anaplasma*, *Bartonella* and *Babesia* Starcovici, 1893, using RT-PCR/or PCR and enzyme immunoassay. One or more tick-borne infection markers were detected in 43 species of birds. All markers were detected in samples collected from fieldfare *Turdus pilaris* Linnaeus, Blyth's reed warbler *Acrocephalus dumetorum* Blyth, common redstart *Phoenicurus phoenicurus* (Linnaeus), and common chaffinch *Fringilla coelebs* Linnaeus. Although all pathogens have been identified in birds and ticks, we found that in the majority of cases (75.5%), there were mismatches of pathogens in birds and ticks collected from them. Wild birds and their ticks may play an extremely important role in the dissemination of tick-borne pathogens into different geographical regions.

Keywords: birds, *Ixodes*, WNV, TBEV, *Borrelia* spp., *Rickettsia* spp., *Anaplasma* spp., *Bartonella* spp., *Ehrlichia* spp., *Babesia* spp.

The prevalence of vector-borne diseases in the world has remained a very relevant concern. Numerous studies have demonstrated an important role of wild birds in spreading parasites and pathogens. Wild birds also serve as reservoirs for viruses, bacteria and protists that are pathogenic for humans (Hubálek 2004, Tsiodras et al. 2008, Hasle 2013).

The Tomsk region, where we conducted this study, is one of the most high-risk areas for tick-borne diseases due to elevated incidence of tick-borne encephalitis and Lyme disease in humans (State Report Tomsk 2017). The major vector for these diseases in the western part of Russia is *Ixodes persulcatus* Schulze, 1930. Since the beginning of the 21st century, another tick with similar ecology, *Ixodes pavlovskyi* Pomerantsev, 1946, has been found in the same habitats (Romanenko and Chekalkina 2004) and currently predominates over *I. persulcatus* in urban areas. Although both ticks can bite humans, *I. pavlovskyi* is also known as an ornithophilic tick (Ushakova et al. 1969, Moskvitina et al. 2014). Its disjunct habitat range includes the mountain territories in the Russian Far East, Altai, and Gornaya Shoriya, and its appearance in the Tomsk region is probably caused by wild birds. The prevalence of tick-borne encephalitis virus (TBEV) and *Borrelia* spp. in questing ticks in the Tomsk region has been estimated to be up to 9.3% and 28.5%, respectively (Moskvitina et al. 2014, Pankina et al. 2015).

There are 333 species of birds in the Tomsk region and more than 250 of them have annual migration (Ryabitsev et al. 2001). The geographical location of this region in the Eurasian continent provides a wide range of directions for the migration of wild birds to the wintering grounds. According to the data of ringing (Moskvitin and Dubovik 1969, 1977, Moskvitin and Strelkov 1977, Moskvitin 1992, Ryabitsev 2001), Siberian birds spend the winter in Africa, Europe, West Asia, India, and Southeast Asia (Fig. 1). This creates preconditions for the dispersion of pathogens from

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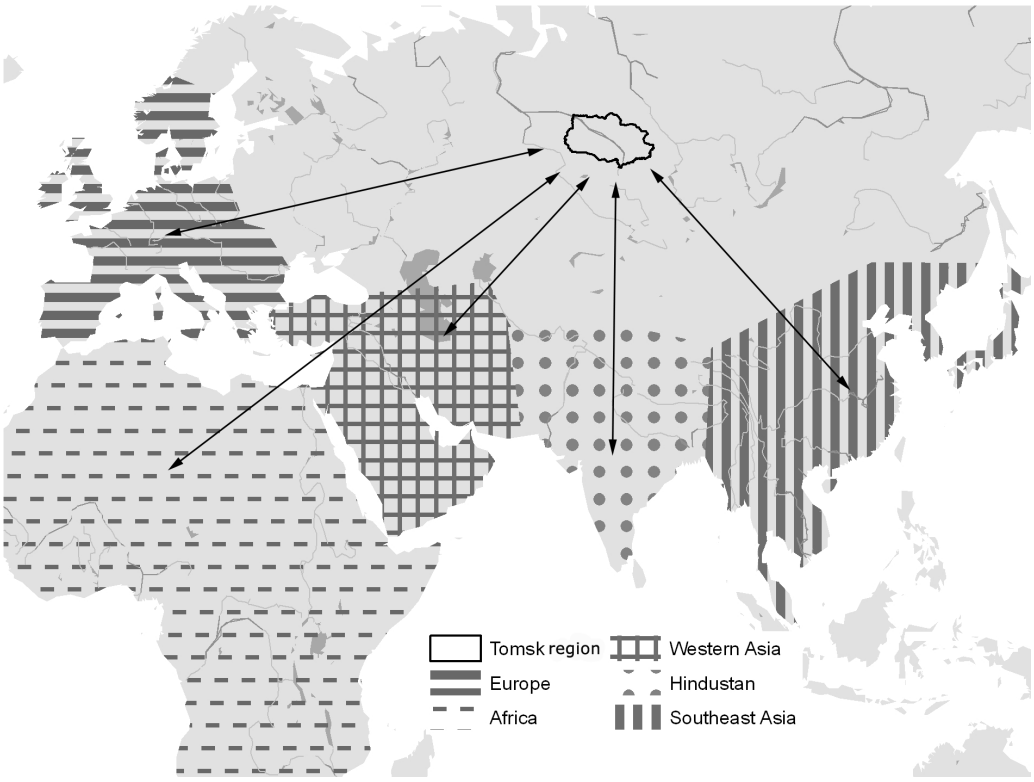

Fig. 1. Scheme of the wintering grounds of wild birds from Western Siberia.

different areas with various epidemiological settings. Numerous pathogens have been found in ticks and vertebrate hosts in the Tomsk region (Chausov et al. 2010). In addition to TBEV and *Borrelia* spp., some other pathogens such as species of *Rickettsia*, *Anaplasma*, *Babesia*, *Ehrlichia*, and *Bartonella* were also found. Surprisingly, West Nile virus (WNV) was found in ticks from the genus *Ixodes* Latraille, 1795, which attack both humans and vertebrates. We assumed that the circulation of WNV in the tick vertebral system is theoretically possible (Moskvitina et al. 2008, 2014), which has been previously demonstrated experimentally (Azarova and Mishaeva 2002). Although several studies have focused on the detection of various pathogens in birds and ticks collected from them (Hildebrandt et al. 2010, Špitalská et al. 2011, Dubska et al. 2012, Kang et al. 2013, Movila et al. 2013, Toma et al. 2014, Diakou et al. 2016), there is no clear information on the relationship between pathogens, vectors, and hosts. Therefore, this study was conducted to identify the pathogens that were detected in different species of birds and ticks parasitising on them and to evaluate their interdependence.

MATERIALS AND METHODS

Bird capture and tick collection

Fieldwork was conducted from April to August during 2006–2011. The study material was collected in Tomsk (56.4826N, 84.9950E) and their nearest suburbs within 15 km zone. Altogether, 736 wild birds were examined for the presence of feeding ticks, of which 293 birds were captured using mist nets and subsequently released and 443 were shot during the hunt and subsequently analysed for the presence of pathogens. A total of 804 larvae, nymphs and adults from the genus *Ixodes* were collected from the birds. Feeding ticks were analysed for the presence of pathogens. We have previously reported the prevalence and intensity of tick infection in birds (Moskvitina et al. 2014). Ticks from each bird were collected separately in Eppendorf tubes and after their species identification using a taxonomic guide (Filippova 1977), they were stored alive at 4°C or frozen at −20°C until the detection of pathogens. The identification of bird species was performed according to a field guide (Ryabitsev 2001). All procedures involving wild birds were conducted according to permits 70 No. 024401 and 70 No. 024399 from the local government and regulations for working with wild animals.

Detection of selected pathogens

A total of 443 specimens of 60 species of birds (spleen, liver, and brain) and 378 ticks (all stages) were examined for the presence of eight pathogens (TBEV, WNV, spp. of *Borrelia*, *Rickettsia*, *Ehrlichia*, *Anaplasma*, *Bartonella*, and *Babesia*).

Enzyme immunoassay

TBEV antigens were detected via enzyme immunoassay analysis as described previously (Ternovoi et al. 2007). Briefly, the viral antigen was captured on the surface of 96-well polystyrene plates from 100 µl of the homogenates of ticks and internal organs (spleen, liver and brain from individual bird) using monoclonal antibodies 10H10 against protein E of TBEV that was preliminarily immobilised on the plates. Immune complexes were detected using EB1 monoclonal antibody against protein E of TBEV labeled with biotin, which was identified by avidin-peroxidase. WNV antigens were detected using a previously described

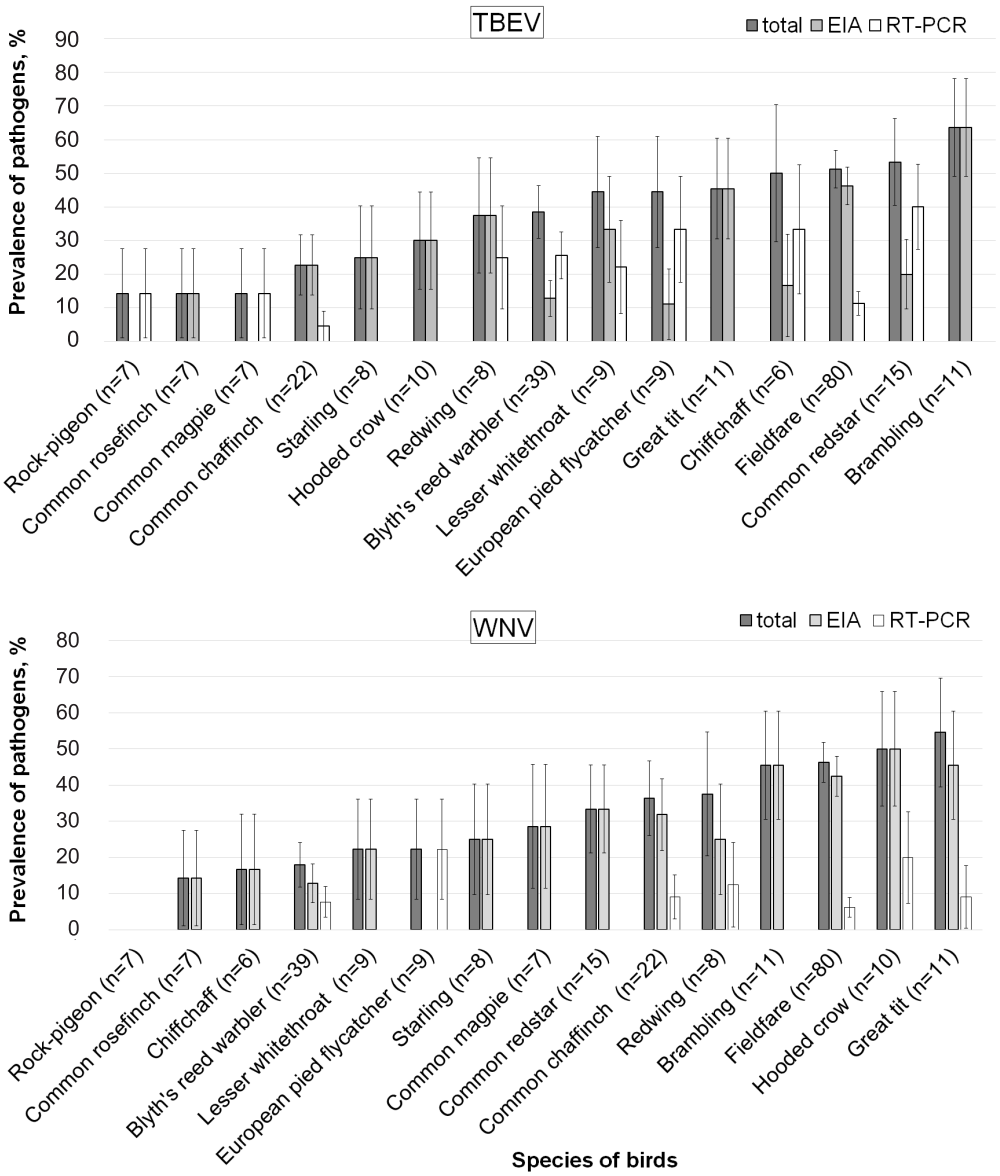

Fig. 2. Prevalence of TBEV and WNV markers (total, viral antigen, and RNA) in wild birds.

technique (Ternovoi et al. 2004). WNV antigens were captured on the surface of 96-well plates from 10% homogenates of samples of animals (ticks and birds) by the enzyme immunoassay analysis using a mixture of three purified murine monoclonal antibodies, 3A6, 6H4, and 2B9, against WNV. The immune complex was detected using murine polyclonal antiviral IgG labeled with biotin and streptavidin peroxidase. Samples were considered as positive if the signal exceeded the negative control by two or more times.

PCR analysis

RNA extraction, reverse transcription, and detection of TBEV and WNV cDNA using RT-PCR, as well as the detection of other bacterial and protozoan pathogens using PCR, were performed as described earlier (Chausov et al. 2010). Briefly, a combined RNA/DNA mixture was extracted from 100 µl of the homogenate of ticks and organs of birds using a RIBOSorb (AmpliSens, Moscow, Russia) set and a DNA/RNA Extraction Kit (NPF Litekh, Moscow, Russia), according to the manufacturers' instructions. Synthesis of cDNA was performed using a REVERTA-L kit (AmpliSens, Moscow, Russia) according the manufacturer's protocol. We calculated and synthesised the oligonucleotide primers for detecting the RNA and DNA of TBEV, WNV, and species of *Borrelia*, *Rickettsia*, *Ehrlichia*, *Babesia*, and *Bartonella* based on the comparison of the nucleotide sequences of their different strains deposited in GenBank. Table 1 shows the primer pairs for the amplification of the sequences of viral, bacterial, and protozoan agent markers.

Comparison of pathogens in birds and ticks

In 45 cases, we conducted pairwise comparisons of the pathogens in birds and ticks that feed on them. All analysed ticks were engorged with blood. Among all the cases of pairwise comparisons of pathogens between birds and ticks feeding on them, we made the following statement: If the infected birds were carriers of uninfected ticks (irrespective of how many uninfected ticks were on the bird and what development stages and species they were), these cases were considered as one event of comparison. The same situation was considered if ticks on one bird were in-

Table 1. Oligonucleotide primers used in the study

Name	Pathogen, target gene	Sequence	Length of PCR, bp
TBElf TBE2r	TBEV, 5'-end	AGATTTTCTTGCACGTGCRTGCGTTTG CCCAKCATGCGCATCAAC	240
WNlf WN2r	WNV, protein E	CCTTGGWATGAGCAACAGAGACTTC GTGTCAATRCTTCCTTTGCCAAATA	336
Borrlf Borr2r	*Borrelia* spp., flagellin gene	TTAGCAGTTCAATCAGGTTAACG CAACCTCATCTGTCATTGTAGC	636
Ricklf Rick2r	*Rickettsia* spp., citrate synthase gene	TCTCATCCTATGGCTATTATGCTTGC ATAAATATYTTATTAAGAGCATTTTTTTT	286
Bab1f Bab2r	*Babesia* spp., 18S RNA	GTAGGACTTTGGTTCTATTTTG GTCAATCCTACCGTTTGTCTGG	442
Bart1f Bart2r	*Bartonella* spp., hemin binding protein gene	ACTTCTGTTATCGCTTTRRTTTC TCACCACCAGCAACATAAGGCATAAT	525
Ehrl1f Ehrllr	*Ehrlichia* spp., disulphide oxidoreductase gene	TTGCAAAATGATGTCTGAAGATATGAAACA GCTGCTCCACCAATAAATGTATCYCCTA	377
HS1-f HS6-r	*Anaplasma* ssp., groESL operon (Sumner et al. 1997)	CGYCAGTGGGCTGGTAATGAA CCWCCWGGTACWACACCTTC	1320–1360

Note: The usability of the primers for detection of tick-borne infection markers has been confirmed by sequencing as described by us for: TBEV (Ponomareva et al. 2021); West Nile virus, genotype I (MN149538 isolated from *Acrocephalus dumetorum* Blyth); *Borrelia* spp. (EU919255, MN193533 for *B. garinii* and MN986989 for *B. miyamotoi*); *Rickettsia* spp. (MK304547 for *R. raoultii* and KP866150 for *R. helvetica*); *Ehrlichia* spp. (EU919250 for *E.muris* and Kartashov et al. 2020); *Anaplasma* spp. (Kartashov et al. 2019); *Bartonella* spp. and *Babesia* spp. (MH424325 for *B. caballi* and Rar et al. 2005).

fected with a pathogen common for all ticks that fed on this bird. If the infected or uninfected bird was a carrier of several ticks each of which was infected with a different set of pathogens, every case of comparison of the pathogens in this bird and each tick was considered as an independent event. By the term "event" we mean one pairwise comparison of pathogens in a bird and in a tick (or ticks) feeding on it. We excluded from the analysis those cases when both the bird and the tick were free of pathogens.

Statistical analysis

Statistica 6.0 and Microsoft Office Excel 2007 were used to perform statistical analysis. The F-test was used to confirm the differences in the rates of infected animals. The Spearman method was used to evaluate the correlations of some parameters.

RESULTS

Pathogens detected in wild birds

A total of 60 species of wild birds were examined for the presence of the above-mentioned tick-borne pathogens. We found that 43 species (71.7%) were the carriers of some pathogens (Table 2). Some species among individually analysed birds had one to eight infection agents, which were detected in their samples. The number of pathogens in some species of birds did not always depend on the number of analysed samples of that species of birds. Sometimes, the number of pathogen markers was higher in species with a small sample (the common willow (n = 2) had four pathogens and the Eurasian nuthatch (n = 3) had five pathogens; scientific names of birds are in Table 2) than in species with a larger sample (the great tit (n = 11) had only three pathogens and the garden warbler (n = 5) had only one pathogen).

We assumed that some species of birds were more or less susceptible to pathogens and, consequently, played a different role as reservoirs. To illustrate this assumption, we estimated the percentage of birds of different species infected by TBEV and WNV (Fig. 2). We confirmed that the species had a different percentage of prevalence of viral infections. For some species, but not all, the percentage of birds infected with viruses was associated with the frequency of their contact with ticks. For instance, the fieldfare, whose mean abundance of parasites was 5.7 ticks per bird, had one of the highest percentages of viral infection markers of approximately 50% (Fig. 2). In contrast, birds rarely attacked by ticks, such as the rock pigeon, the common rosefinch, and the magpie, whose mean abundance were 0, 0.3, and 0.5 ticks per bird, respectively, had a low prevalence of viruses. However, there were also such species (the hooded crow, the great tit and the brambling) that were not in close contact with ticks but showed a high prevalence of infections, probably due to their susceptibility.

Regarding the methods of detecting viral infections, the viral antigen, compared with the viral RNA, was detected more often for TBEV markers by 1.6 times and for WNV markers by 4.6 times. In some species, RNA could be detected more often than the antigen. Simultaneously, both methods confirmed the presence of TBEV markers in birds in 7.3% of cases and WNV markers in 6.3% of cases.

The number of pathogens was almost similar in the groups of sedentary and migratory birds. There were also no significant differences in the percentage of birds infected with certain pathogens in both groups, except that of species *Borrelia* and *Bartonella* (Table 3). The mass departure of Siberian birds from nest sites to the wintering areas after tick parasitisation can result in the distribution and exchange of pathogens between the territories.

Number of pathogens in birds against number of ticks

We attempted to verify whether the number of pathogens in birds that play the major role in sustaining the tick population (the tree pipit, the fieldfare and the redwing) was in fact higher than that in birds that have less contact with ticks (the European pied flycatcher and the lesser whiteth-

Table 2. Species of wild birds with infections markers in Western Siberia and places of their wintering ground

Species of birds[a]	Number of infected/examined birds								
	TBEV Total infected (antigen/RNA)/ examined	**WNV** Total infected (antigen/RNA)/ examined	***Borrelia* spp.**	***Rickettsia* spp.**	***Bartonella* spp.**	***Babesia* spp.**	***Ehrlichia* spp.**	***Anaplasma* spp.**	Migratory (M) / sedentary (S) status of birds and geographic location of wintering grounds
Fieldfare *Turdus pilaris* Linnaeus	41(37/9)/80	37(34/5)/80	8/80	7/80	5/22	3/22	2/22	2/22	M, Europe
Blyth's reed warbler *Acrocephalus dumetorum* Blyth	15(5/0)/39	7(5/3)/39	4/39	8/39	1/13	1/13	1/13	3/13	M, India
Common redstart *Phoenicurus phoenicurus* (Linnaeus)	8(3/6)/15	5(5/0)/15	2/15	3/15	1/4	2/4	1/4	1/4	M, Africa
Common chaffinch *Fringilla coelebs* Linnaeus	5(5/1)/22	8(7/2)/22	2/22	1/22	2/12	2/12	2/12	1/12	M, Kaspian and Near East
European pied flycatcher *Ficedula hypoleuca* (Pallas)	4(1/3)/9	2(0/2)/9	1/9	1/9	2/4	1/4	0/4	0/4	M, Africa
Brambling *Fringilla montifringilla* Linnaeus	7(7/0)/11	5(5/0)/11	0/11	2/11	0/3	1/3	0/3	1/3	M, Europe and India
Eurasian nuthatch *Sitta europaea* Linnaeus	1(1/0)/3	2(2/0)/3	0/3	1/3	0/1	1/1	0/1	1/1	S
Lesser whitethroat *Sylvia curruca* (Linnaeus)	4(3/2)/9	2(2/0)/9	1/9	0/9	1/4	0/4	0/4	1/4	M, Africa and India
Sand martin *Riparia riparia* [b] (Linnaeus)	10(3/7)/48	4(4/0)/48	9/21	3/21	0/21	0/21	0/21	2/21	M, Africa and India
Hooded crow *Corvus cornix* Linnaeus	3(3/0)/10	5(5/2)/10	1/10	1/10	n.a.[c]	n.a.	n.a.	n.a.	S
Willow warbler *Phylloscopus trochilus* (Linnaeus)	2(2/1)/2	2(2/0)/2	1/2	1/2	0/1	0/1	0/1	0/1	M, Arfica
Common rosefinch *Carpodacus erythrinus* (Pallas)	1(1/0)/7	1(1/0)/7	1/7	1/7	0/2	0/2	0/2	0/2	M, India and South-East Asia
Rock-pigeon *Columba livia* Gmelin	1(0/1)/7	0/7	0/7	4/7	0/7	1/7	0/7	3/7	S
Redwing *Turdus illiacus* Linnaeus	3(3/2)/8	3(2/1)/8	0/8	1/8	2/4	0/4	0/4	0/4	M, Europe
Common woodcock *Scolopax rusticola* Linnaeus	0/5	1(1/0)/5	0/5	1/5	1/4	1/4	0/4	0/4	M, Europe
Chiffchaff *Phylloscopus collybita* (Vieillot)	3(1/2)/6	1(1/0)/6	0/6	1/6	0/4	0/4	0/4	0/4	M, Europe and Africa
Tree pipit *Anthus trivialis* (Linnaeus)	3(0/3)/3	0/3	2/3	1/3	0/1	0/1	0/1	0/1	M, Africa and India
European greenfinch *Chloris chloris* (Linnaeus)	1(1/0)/2	2(1/1)/2	0/2	1/2	n.a.	n.a.	n.a.	n.a.	M, Europe and Kaspian
Great tit *Parus major* Linnaeus	5(5/0)/11	6(5/1)/11	0/11	2/11	0/3	0/3	0/3	0/3	S
Common bullfinch *Phyrrhula phyrhula* (Linnaeus)	2(2/0)/4	1(1/0)/4	0/4	1/4	0/2	0/2	0/2	0/2	S
Starling *Sturnus vulgaris* Linnaeus	2(2/0)/8	2(2/0)/8	0/8	1/8	n.a.	n.a.	n.a.	n.a.	M, Africa, Europe and India
Eurasian tree sparrow *Passer montanus* (Linnaeus)	3(3/0)/3	3(3/0)/3	0/3	0/3	n.a.	n.a.	n.a.	n.a.	S
Yellow hammer *Emberiza citronella* Linnaeus	2(2/0)/4	2(2/0)/4	0/4	0/4	n.a.	n.a.	n.a.	n.a.	M, Middle Asia, partially sedentary
Jackdaw *Corvus monedula* Linnaeus	1(1/0)/4	3(3/1)/4	0/4	0/4	n.a.	n.a.	n.a.	n.a.	M, Middle Asia
Lapwing *Vanellus vanellus* (Linnaeus)	2(0/2)/8	2(0/2)/8	0/8	0/8	n.a.	n.a.	n.a.	n.a.	M, Europe and Kaspian
Mallard *Anas platyrhynchos* Linnaeus	4(0/4)/35	0/35	1/35	0/35	n.a.	n.a.	n.a.	n.a.	M, Kaspian and India
Pallas' warbler *Phylloscopus proregulus* (Pallas)	1(0/1)/1	0/1	0/1	0/1	1/1	0/1	0/1	0/1	M, South-East Asia
Siberian rubythroat *Luscinia calliope* (Pallas)	2(1/2)/3	0/3	1/3	0/3	0/1	0/1	0/1	0/1	M, South-East Asia
Goldfinch *Carduelis carduelis* (Linnaeus)	2(0/2)/4	0/4	0/4	1/4	0/2	0/2	0/2	0/2	S
Willow tit *Parus montanus* Baldenstein	2(2/0)/4	2(2/0)/4	0/4	0/4	n.a.	n.a.	n.a.	n.a.	S
Common magpie *Pica pica* (Linnaeus)	1(0/1)/7	2(2/0)/7	0/7	0/7	n.a.	n.a.	n.a.	n.a.	S
Hazelhen *Tetrastes bonasia* (Linnaeus)	1(0/1)/5	0/5	0/5	0/5	n.a.	n.a.	n.a.	n.a.	S
Thrush nightingale *Luscinia luscinia* (Linnaeus)	1(0/1)/1	0/1	0/1	0/1	n.a.	n.a.	n.a.	n.a.	M, Africa
Eurasian siskin *Spinus spinus* (Linnaeus)	1(1/0)/3	0/3	0/3	0/3	0/1	0/1	0/1	0/1	S or M, Middle Asia
Greater spotted woodpecker *Dendrocopos major* (Linnaeus)	1(0/1)/2	0/2	0/2	0/2	0/1	0/1	0/1	0/1	S
Garden warbler *Sylvia borin* (Boddaert)	0/5	0/5	0/5	0/5	0/3	0/3	1/3	0/3	M, Africa
Bluestart *Tarsiger cyanurus* (Pallas)	0/2	1(0/1)/2	0/2	0/2	0/2	0/2	0/2	0/2	M, South-East Asia
European wigeon *Anas penelope* Linnaeus	0/5	0/5	1/5	0/5	n.a.	n.a.	n.a.	n.a.	M, Europe, Kaspian and India
Green-winged teal *Anas crecca* Linnaeus	1(0/1)/3	0/3	0/3	0/3	n.a.	n.a.	n.a.	n.a.	M, India, Kaspian and Near East
Common merganser *Mergus merganser* Linnaeus	1(0/1)/3	0/3	0/3	0/3	n.a.	n.a.	n.a.	n.a.	M, Europe
Waxwing *Bombycilla garrulous* (Linnaeus)	1(1/0)/1	0/1	0/1	0/1	n.a.	n.a.	n.a.	n.a.	S or M, India
Coal tit *Parus ater* Linnaeus	1(1/0)/1	0/1	0/1	0/1	n.a.	n.a.	n.a.	n.a.	S
Spoonbill *Anas clypeata* Linnaeus	1(1/0)/3	0/3	0/3	0/3	n.a.	n.a.	n.a.	n.a.	M, India, Europe and Kaspian

[a] Species are listed according to the number of revealed pathogens; [b] This species belongs to specific parasitic system including tick *Ixodes lividus* Koch, 1844, inhabiting sand martins caves; [c] not analyzed

root). Comparison of the index of the abundance of ticks per bird among the different species of birds with the number of pathogens found in these species revealed that there were no statistically significant differences ($r = -0.05$, $P < 0.05$). Moreover, considering the fieldfare as a basic feeder for ticks, we examined whether the number of pathogens was higher in individuals with several ticks. Our analysis within one species of birds revealed the same result, i.e., no relationship between the number of pathogens and the number of ticks per bird ($r = 0.05$, $P < 0.05$). However, the ticks collected from the birds that were in close contact with ticks were more often considered to be carriers of the pathogens than the ticks collected from the birds that served as secondary feeders, for example, the family Sylviidae.

Comparison of infection markers in birds and ticks

We revealed the tendency of simultaneous infections (coinfections) in birds and ticks. Coinfections (two to seven pathogens simultaneously in one bird) were highly common. Some individuals were positive for the markers from

Table 3. Prevalence of pathogens (%) in sedentary and migratory birds

Group of birds	TBEV	WNV	*Borrelia* spp.	*Rickettsia* spp.	*Bartonella* spp.	*Babesia* spp.	*Ehrlichia* spp.	*Anaplasma* spp.
Sedentary	37.7; n = 61	34.4 n = 61	1.63 n = 61	16.4 n = 61	0.0 n = 16	12.5 n = 16	0 n = 16	25.0 n = 16
Migrants	35.8 n = 355	25.4 n = 355	10.4 n = 355	10.1 n = 355	14.9 n = 107	10.3 n = 107	6.5 n = 107	11.2 n = 107
F – test	F = 0.28	F = 1.43	F = 2.89*	F = 1.34	F = 2.96*	F = 0.261	F = 1.93	F = 1.35
p-value	P > 0.05	P > 0.05	P < 0.01	P > 0.05	P < 0.01	P > 0.05	P > 0.05	P > 0.05

*Differences are statistically significant

four to seven infections. For instance, the fieldfare had four pathogens (WNV, *Rickettsia* spp., *Babesia* spp. and *Ehrlichia* spp.) and six pathogens (TBEV, *Borrelia* spp., *Bartonella* spp., *Babesia* spp., *Ehrlichia* spp. and *Anaplasma* spp.), the common chaffinch had four pathogens (TBEV, WNV, *Borrelia* spp. and *Rickettsia* spp.) and five pathogens (*Borrelia* spp., *Batronella* spp., *Babesia* spp., *Ehrlichia* spp. and *Anaplasma* spp.), and the common redstart had seven pathogens (all except WNV). We also found up to four infection markers in individual ticks.

In the present study, we focused on the comparison of pathogens in individual birds and the ticks that fed strictly on them.

As we had data on the pairwise comparison of infected birds and ticks captured from these individuals, we compared the number and composition of pathogens in these pairs (n = 45). Consequently, we identified several variants of pairwise combinations (Table 4) as follows:

- Birds had one or more markers of infections, but the ticks collected from these birds were free of pathogens (53.3 %).
- Infections in birds were not found, but the ticks collected from them had one infection agent (11.1 %).
- Complete match by the type of pathogens was observed in the infected birds and the ticks collected from them (8.9 % of cases).
- Both birds and ticks were infected by one to four pathogens, one or more of them being the same. In general, a partial match was detected in 15.6 % of cases.
- Birds and ticks contain different infections, and their mismatch was observed in 11.1 % of cases.

DISCUSSION

Of the 43 species of birds examined in the Tomsk region in which the pathogens were identified, the proportions of birds associated with wintering in different regions were as follows: 23.3 % in Europe, 25.6 % in India, 18.6 % in Africa, 16.3 % in the Caspian and the Middle East, 9.3 % in Southeast Asia, and 6.9 % in Central Asia, and 32.6 % of birds were sedentary. It is certain that the emergence of the Far Eastern strain of TBEV, as well as WNV and the tick *Ixodes pavlovskyi*, in our region was directly caused by birds (Ternovoi et al. 2004, Mikryukova et al. 2014, Moskvitina et al. 2014). Similarly, owing to birds, the tick *Hyalomma marginatum* Koch, 1844 has extended its habitat range in Europe, potentially spreading the pathogens associated with it (Poupon et al. 2006, Molin et al. 2011, Diakou et al. 2016, Klaus et al. 2016). This tick was found on the migrating birds *Phoenicurus phoenicurus* (Linnaeus) and *Anthus trivialis* (Linnaeus) in the westernmost region of Russia, i.e., the Kaliningrad region, where one of the ticks was found to have an exotic species, *Rickettsia aeshlimannii* (see Movila et al. 2013). We can expect the discovery of the same species of pathogens that have been identified in the wintering areas of our birds (Cazorla et al. 2008, Tonetti et al. 2009, Ghosh and Nagar 2014, Sparagano et al. 2015, Yang et al. 2015, Kuo et al. 2017).

It is obvious that birds often attacked by ticks, primarily those from the family Turdidae, play an important role in maintaining the foci of natural infections. This was confirmed by the number of infected ticks that were more common on ground-foraging birds, which are the major tick hosts. A correlational analysis between the number of pathogens detected in birds and the number of ticks parasitising on them revealed that the number of pathogens was equal in birds with frequent and rare contact with ticks. On the one hand, it was logical to assume that the more often the ticks attack, the more infections the birds have. In contrast, we may expect the result indicating that more frequent attacks by ticks lead to fewer pathogens. The latter result may be associated with the formation of immune mechanisms of pathogen suppression during prolonged and/or multiple parasitisation of ticks, as demonstrated in several studies (Wakelin 1996, Wikel et al. 1997, Kislenko and Korotkov 1998, Heylen et al. 2010).

The finding that the number of pathogens in birds did not directly depend on the number of parasitic ticks can be explained by the fact that the birds get infected over a long period, and thus the number of pathogens does not necessarily depend on the number of ticks found on them at the time of capture.

Quite unexpectedly, we found a significant number of birds (32.9 %) with WNV markers far from the territories endemic for this infection. Furthermore, the obtained indicator of prevalence significantly exceeded that in several other regions (Balança et al. 2009, Jourdain et al. 2011, López et al. 2011, Murata et al. 2011, Czank et al. 2016). The prevalence of infections in different species of ticks by WNV markers also confirmed to be quite high at 3.4–5.1 %. In contrast, in Italy and Greece, which are located closer to the areas of WNV distribution, this virus was not detected in ticks parasitising on migratory birds (Hagman et al. 2014).

The suggestion that tropical arboviruses can be disseminated and settled in temperate latitudes in ticks was made more than 30 years ago (Nekipelov 1978). Despite the fact that WNV is traditionally considered as a mosquito infection, it is known that argasid and ixodid ticks can be involved in the circulation of this pathogen (Mumcuoglu 2005, Reiter 2010). In some cases, in the absence of mosquitoes, circu-

Table 4. Comparison of infection markers in wild birds and attached ticks

Variants of combinations	Pathogens in birds		Pathogens in ticks	
	Species of birds	Pathogens	Species, number and developmental stages of ticks (F–Adult female; N–Nymph; L– Larvae)	Pathogens
1. Birds are infected with one or more pathogens, but ticks collected from them are not infected	Fieldfare	TBEV (antigen)	2 N. *I. persulcatus*	Not found
	Fieldfare	TBEV (antigen)	1 N. *I. persulcatus*, 4 L. *I. persulcatus*., 3 L. *I. pavlovskyi*	Not found
	Redwing	TBEV (antigen+RNA)	2 N. *I. pavlovskyi*	Not found
	Lesser whitethroat	TBEV (antigen)	1 N. *I. pavlovskyi*	Not found
	Common redstart	TBEV (RNA)	2 N. *I. pavlovskyi*, 1 L. *I. pavlovskyi*, 1 L. *I. persulcatus*	Not found
	Fieldfare	WNV (antigen)	1 F *I. persulcatus*, 1 F *I. pavlovskyi*	Not found
	Redwing	WNV (RNA)	2 F. *I. pavlovskyi*, 4 N. and 8 L. *I. pavlovskyi*	Not found
	Common redstart	WNV (antigen)	1 N. *I. persulcatus*, 6 N. *I. pavlovskyi*, 2 L. *I. pavlovskyi*	Not found
	Hooded crow	WNV (antigen+RNA)	6 F. *I. persulcatus*, 3 F. *I. pavlovskyi*	Not found
	Blyth's reed warbler	*Borrelia* spp.	2 L. *I. persulcatus*, 1 L. *I. pavlovskyi*	Not found
	Blyth's reed warbler	*Rickettsia* spp.	1 L. *I. persulcatus*	Not found
	Common chaffinch	*Babesia* spp.	2 L. *I. pavlovskyi*	Not found
	Fieldfare	*Batronella* spp.	1 N. *I. pavlovskyi*	Not found
	Fieldfare	TBEV+WNV (both antigen)	1 N. *I. pavlovskyi*	Not found
	Fieldfare	TBEV+WNV (both antigen)	1 F. *I. persulcatus*, 2 F. *I. pavlovskyi*	Not found
	Eurasian tree sparrow	TBEV+WNV (both antigen)	1 N. *I. pavlovskyi*	Not found
	Eurasian tree sparrow	TBEV+WNV (both antigen)	1 L. *I. pavlovskyi*	Not found
	Eurasian tree sparrow	TBEV+WNV (both antigen)	1 N. *I. persulcatus*, 1 L. *I. pavlovskyi*	Not found
	Common redstart	TBEV (antigen+RNA) + +WNV (antigen)	4 N. *I. pavlovskyi*, 4 L. *I. pavlovskyi*	Not found
	Fieldfare	TBEV (antigen)+*Rickettsia* spp.	1 F. *I. pavlovskyi*	Not found
	Common redstart	*Borrelia* spp.+*Rickettsia* spp.	1 N. and 10 L. *I. pavlovskyi*	Not found
	Fieldfare	TBEV (antigen) +WNV (antigen) +*Rickettsia* spp.	2 N. *I. pavlovskyi*	Not found
	Eurasian nuthatch	*Rickettsia* spp.+*Babesia* spp. +*Anaplasma* spp.	1 N. *I. persulcatus*	Not found
	Fieldfare	WNV (antigen+RNA) +*Erhlichia* spp. + *Babesia* spp.+*Rickettsia* spp.	1 F. *I. pavlovskyi*	Not found
2. Birds are free of pathogens, but ticks feeding on them are infected with one infection	Brambling	Not found	1 N. *I. persulcatus*	*Borrelia* spp.
	Fieldfare	Not found	3 N. *I. pavlovskyi*	*Borrelia* spp.
	Fieldfare	Not found	6 N. *I. pavlovskyi*	TBEV (RNA)
	Fieldfare	Not found	1 F. *I. persulcatus*	*Anaplasma* spp.
	Common chaffinch	Not found	3 N. *I. persulcatus*	*Anaplasma* spp.
3. Exact matching of pathogens	Fieldfare	TBEV (antigen+RNA) +WNV (antigen)	3 N. *I. pavlovskyi*	TBEV (RNA)+WNV (antigen+RNA)
	Fieldfare	TBEV (antigen+RNA) +WNV (antigen)	1 N. *I. pavlovskyi*	TBEV+WNV (both antigen)
	Common redstart	TBEV+WNV (both antigen)	2 L. *I. persulcatus*	TBEV+WNV (both RNA)
	Tree pipit[3]	TBEV (RNA) +*Borrelia* spp.	2 L. *I. persulcatus*	TBEV (RNA)+*Borrelia* spp.
4. Birds are infected with from 1 to several infections and ticks taken from them have overlapping infection	Fieldfare	TBEV +WNV (both antigen)	1 F. *I. persulcatus*	WNV (antigen)
	Fieldfare	TBEV+WNV (both antigen)	1 F. *I. persulcatus*	TBEV (antigen)
	Fieldfare[1]	TBEV+WNV (both antigen)	1 F. *I. pavlovskyi*	WNV (antigen+RNA) +*Borrelia* spp.
	Fieldfare[2]	TBEV (antigen+RNA) +WNV (antigen)	1 N. *I. pavlovskyi*	TBEV (antigen) +WNV (antigen) +*Borrelia* spp.
	Fieldfare[2]	TBEV (antigen+RNA) +WNV (antigen)	2 F. *I. pavlovskyi*	WNV (antigen)+*Borrelia* spp.+*Ricketsia* spp.
	Tree pipit[3]	TBEV (RNA) +*Borrelia* spp.	1 N. *I. persulcatus*	TBEV (RNA)
	Redwing[4]	*Bartonella* spp.	1 N. *I. pavlovskyi*	*Bartonella* spp. + WNV (RNA) + *Anaplasma* spp. + *Babesia* spp.
	Fieldfare	TBEV (antigen+RNA)	2 F. *I. pavlovskyi*	WNV (RNA)
5. Complete mismatch of pathogens in birds and ticks	Fieldfare	TBEV (antigen)	2 F., 2 N., 3 L. *I. persulcatus*	*Rickettsia* spp.
	Fieldfare	*Borrelia* spp.	3 F. *I. pavlovskyi*	TBEV (RNA)
	Redwing[4]	*Bartonella* spp.	1 N. *I. pavlovskyi*	*Babesia* spp.
	Fieldfare[1]	TBEV+WNV (both antigen)	1 F. *I. pavlovskyi*	*Borrelia* spp.

[1-4] Birds under the same number represent the same individual

lation occurs exclusively owing to ticks (Lvov and Il'ichev 1979). In Russia, several WNV strains were isolated from ticks (Platonov 2001), although these strains were less dangerous for vertebrates (Lvov et al. 2004).

On the basis of the above-described data, WNV can persist and winter in ticks, thereby hypothetically supporting its circulation in nature. This scenario is probably in action in our research area. Earlier, WNV was found here in

questing adult ticks that were sampled using a flag. Moreover, it was found in small mammals and birds and the subadult ticks that fed on them (Moskvitina et al. 2008). The transmission of this infection by ticks was confirmed by WNV markers (antigens and RT-PCR detection) in sedentary birds (great tit, hooded crow, Eurasian nuthatch, common bullfinch, and willow tit) and in ticks collected from them. WNV was found in sedentary birds as frequently as in migratory birds. WNV was also detected in the nestlings of migratory birds that had never migrated yet. Furthermore, the highest rate of infection by WNV was exhibited by the great tit, the sedentary or vagrant bird, which does not migrate to WNV-endemic areas (Fig. 2). The second most infected bird was the hooded crow, the bird belonging to the family Corvidae and well-known as a WNV reservoir (Eidson et al. 2001).

Notwithstanding that several facts indicate that ticks are involved in the transmission of WNV, the level of viremia in birds after a tick bite remains unknown. Attempts to isolate WNV from ticks and bird organs have been unsuccessful, although this was possible for TBEV (Mikryukova et al. 2014). According to experimental data (Ciota et al. 2015), WNV in the tick cell line culture underwent genetic modification and actually became unable to infect vertebrates. However, there are contrasting data that have been obtained experimentally (Azarova and Mishaeva 2002). The authors confirmed in the laboratory the transmission of WNV from infected mice to uninfected ticks (*Ixodes ricinus*) and from infected ticks to uninfected mice through the developmental stages of ticks and the transovarial transfer of pathogen with titres sufficient for circulation.

Therefore, laboratory experiments confirm the possibility of the participation of ticks of the genus *Ixodes* in the circulation of the virus. However, the question of the participation of ticks in the transmission of WNV in nature remains open. We cannot deny that some birds could be infected in wintering areas and through mosquito bites, especially considering the duration of WNV viremia in birds (Wheeler 2012).

The data obtained in the present study on the infection of birds and ticks by various pathogens have similarities with both different territories and their regional specificities. Hence, the presence of Borrelia spp. in ticks collected from birds in Western Siberia (Moskvitina et al. 2014) confirmed to be quite similar to that found in some countries of Europe such as Germany (Franke et al. 2010), Czech Republic (Dubska et al. 2011), Latvia (Capligina et al. 2014), Switzerland (Lommano et al. 2014), but it was lower than that in Italy (Toma et al. 2014), Great Britain (Kurtenbach et al. 1998), the USA (Hamer et al. 2012), and the western part of Russia (Alekseev et al. 2001).

The prevalence of tick infection with *Rickettsia* spp. was lower than that in the majority of studies (Špitalská et al. 2011, Hornok et al. 2014, Toma et al. 2014, Diakou et al. 2016), and that of *Ehrlichia* spp. was also lower (Alekseev et al. 2001, Toma et al. 2014). At the same time, the level of infection was higher than that reported in several studies on *Bartonella* spp. (Molin et al. 2011, Movila et al. 2014) and on *Anaplasma* spp. (Dubska et al. 2012, Palomar et al. 2012, Geller et al. 2013, Lommano et al. 2014).

Most of the studies conducted in recent years were aimed primarily at identifying pathogens in ticks collected from birds, with the results being considered *a priori* as facts confirming the circulation of certain infections in ticks and birds (Dubska et al. 2012, Capligina et al. 2014, Lommano et al. 2014, Michelet et al. 2016). In our opinion, the detection of pathogens only in ticks found on some species of birds, without identifying the pathogens in the bird itself, cannot be unequivocal evidence of the role of birds in the circulation of pathogens.

For instance, in several studies, the great tit was reported as a carrier of ticks infected with *Borrelia* spp. (Comstedt et al. 2006, Dubska et al. 2009, Geller et al. 2013, Heylen et al 2013, Hornok et al. 2013), as well as with *Anaplasma* spp. (Špitalská et al. 2011) and *Babesia* spp. (Hildebrandt et al. 2010). However, none of the birds of this species we analysed exhibited markers of these pathogens. On the one hand, this may be a random coincidence or regional specificity, because the great tit in our biotopes is not often infected with ticks. At the same time, as mentioned earlier, the great tit ranked the topmost in terms of the level of infection with WNV and TBEV and was also a carrier of *Rickettsia* spp. The latter finding corresponds to the fact that ticks in the great tit were infected by this species of pathogen as reported in several studies (Hildebrandt et al. 2010, Movila et al. 2011, Špitalská et al. 2011, Hornok et al. 2013).

A similar situation was observed with the redwing, one of the important tick hosts. Like the great tit, several authors have mentioned it as a carrier of ticks infected with *Anaplasma* spp., *Babesia* spp., and *Borrelia* spp. (Olsén 1995, Comstedt et al. 2006, Geller et al. 2013, Capligina et al. 2014). Our studies did not identify infection by these pathogens in the birds themselves. At the same time, this species was again a carrier of WNV, TBEV, *Rickettsia* spp., and *Bartonella* spp. The absence of *Borrelia* spp. is perhaps accidental, because a species similar to the redwing, the fieldfare, was infected with all pathogens. These results illustrate the need to evaluate the infection of not only the ticks that feed on birds but also the birds themselves, as the role of the latter may not coincide with their role assumed solely on the basis of the presence of infected ticks.

In recent years, several studies have analysed the infection of the birds themselves (de la Fuente et al. 2005, Stańczak et al. 2009, Yang et al. 2015, Ebani et al. 2016), including the infection of birds and their ectoparasites (Norte et al. 2013, Hornok et al. 2014, Sándor et al. 2016).

These studies show both cases of coincidence and mismatch of pathogens between birds and ticks parasitising on them, which confirms the need to analyse the infection with pathogens in the bird–tick system, because this allows us to better understand the mechanism of pathogen circulation in ecosystems.

Our pairwise comparisons of pathogens in birds and ticks showed that in 75.5 % of cases, there were discrepancies in the identified pathogens. One of the reasons was that the exchange of pathogens between birds and ticks had

not occurred yet. On the other hand, there is a possibility of some barriers in the tick–bird system that prevents the transmission of pathogens. Therefore, some researchers (Alekseev and Dubinina 2007) have put forward an idea of the antagonistic relationship between pathogens, which prevents their coexistence in the same tick or vertebrate. However, from these viewpoints, it is impossible to explain the presence of mixed infections in birds if, for example, four to seven pathogens in one bird or four pathogens in one tick are detected.

Hence, the redstart had seven pathogens, except for WNV; one nymph of *I. pavlovskyi* collected from a redwing had WNV, *Babesia* spp., *Bartonella* spp., and *Anaplasma* spp., whereas the redwing itself was infected with *Bartonella* spp. The latter fact indicates the possible involvement of birds in the circulation of *Bartonella* spp.

Borrelia spp. can also be used to illustrate a different spectrum of variants of infection with this pathogen in the bird–tick system with the participation of various bird species (Table 4). Therefore, the garden warbler was infected with *Borrelia* spp., whereas the ticks on it were free of pathogens. The common redstart was infected with *Borrelia* spp. and *Rickettsia* spp., whereas the ticks were uninfected. In contrast, two cases, a brambling and a fieldfare that were free of pathogens, were carriers of nymphs infected with *Borrelia* spp. There was a case of a fieldfare infected with *Borrelia* spp., and three adult ticks (females) on it were infected with TBEV. In two fieldfares infected with TBEV + WNV, the ticks were infected with, apart from viruses, *Borrelia* spp.; in one of these birds, the tick was infected only with *Borrelia* spp. This finding may indicate either the trans-stadial transmission of *Borrelia* spp. by these ticks or that cofeeding with bacteremia has not yet begun in these birds.

Finally, a case was observed when in a tree pipit infected with TBEV + WNV + *Borrelia* spp., one nymph with TBEV and two larvae infected with TBEV + *Borrelia* spp. were found, which confirmed the transmission of this pathogen in the bird–tick system.

Of all cases of pairwise-compared infections in the bird–tick system, we detected a coincidence indicating the possibility of transmission for four pathogens, the above-mentioned *Bartonella* spp. and *Borrelia* spp. as well as TBEV and WNV. The coincidence of infections in the bird–tick system was not detected for *Ehrlichia* spp., *Babesia* spp., *Anaplasma* spp., and *Rickettsia* spp., although all these pathogens were found in birds and ticks separately.

Although a study by Sándor et al. (2016) provides evidence of infection in birds and ticks with *Anaplasma* spp. and *Rickettsia* spp., it is not clear whether the infected ticks were found on the infected birds. The study conducted by Hornok et al. (2014) reported examples of synchronous infection with *Rickettsia* spp. of birds and ticks collected from them, which confirms the transmission of this bacterium, and there is also evidence of mismatch in birds and ticks infected with *Anaplasma* spp. However, it is believed that birds play an important role in maintaining *Anaplasma* spp. (de la Fuente et al. 2005, Ioannou et al. 2009, Franke et al. 2010).

Regarding *Babesia* spp., no consensus exists on the role of birds in the circulation of these pathogens. We detected markers of this infection in 13 % (13/109) of birds, as well as in two ticks collected from an uninfected bird, which may indicate a possible transmission through the cofeeding mechanism. The same possibility has been suggested previously (Kuo et al. 2017). However, in another study (Yabsley et al. 2013), it was observed that birds are an unlikely reservoir of *Babesia* spp.

On the basis of the data of the synchronous infection of birds and ticks, we attempted to understand the relationship in the tick–bird–pathogen system. The presence of the pathogen in birds and ticks may indirectly indicate a possible transmission of infection, but the level of bacteremia and viremia in birds and ticks may not be sufficient to transmit the infection. Considering the facts we have disclosed about a high proportion of mismatches in pathogen species between birds and ticks parasitising on them, it can be assumed that the relationships between the components of the parasitic bird–tick–pathogen system are not so straightforward, depend on the multiplicity of manifestations of these connections, and require more in-depth research.

On the basis of our study results, the following conclusions can be made:

1. In 43 species of birds, one to eight infection agents transmitted through tick bites were detected. Comparison of the number of infected birds among migratory and sedentary species did not reveal significant differences between them in the prevalence of pathogens. This finding may indicate that most of the pathogens could have been transmitted through tick bites at our research sites, rather than being introduced from outside.
2. Different species of birds exhibited differences in the prevalence of pathogens, in particular viral infections (TBEV and WNV). For example, the highest prevalence of WNV infection was found in the sedentary hooded crow *Corvus cornix* and the great tit *Parus major*. Although the former species is known as a typical natural reservoir of WNV, the great tit probably proved to be nonspecific, but susceptible, to the pathogen species of birds.
3. The number of detected pathogens in birds on which ticks frequently feed did not differ from that in birds that have rare contact with ticks. In addition, the number of pathogens in individual birds did not correlate with the number of ticks parasitising on them.
4. Despite the significant prevalence of infection markers in birds and ticks, the pairwise infection comparison analysis in birds and ticks showed that complete or partial coincidence of infection markers was observed in only 24.5 % of cases. It was observed for TBEV, WNV, *Borrelia* spp. and *Bartonella* spp. We are forced to admit and emphasise that this are only preliminary data because the most of pathogens were identified only up to genus level. Viruses (TBEV and WNV), as well as the combination of TBEV and *Borrelia* spp., were the most frequently co-occurring pathogens.

Authors' contribution. Igor G. Korobitsyn wrote the manuscript, supervised ornithological work, data analysis. Nina S. Moskvitina initiated and supervised the study, critically revised the manuscript. Oleg Yu. Tyutenkov mist-netted birds and collected ticks, data analysis. Sergey I. Gashkov mist-netted birds and collected ticks. Yulia V. Kononova detected pathogens in ticks and birds by IEA, data analysis. Sergey S. Moskvitin mist-netted birds and collected ticks. Vladimir N. Romanenko identified ticks based on morphology. Tamara P. Mikryukova performed the molecular analyses. Elena V. Protopopova performed the molecular analyses. Mikhail Yu. Kartashov detected pathogens in ticks. Evgeny V. Chausov detected pathogens in ticks. Svetlana N. Konovalova detected pathogens in ticks. Natalia L. Tupota detected pathogens in ticks. Alexandra O. Sementsova detected pathogens in ticks. Vladimir A. Ternovoi performed the molecular analyses. Valery B. Loktev supervised parasitological and microbiological work

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