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Blackbirds and Song Thrushes Constitute a Key Reservoir of *Borrelia garinii*, the Causative Agent of Borreliosis in Central Europe▽†

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Blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*) were found to carry 95% of all spirochete-infected tick larvae among 40 bird species captured in Central Europe. More than 90% of the infections were typed as *Borrelia garinii* and *Borrelia valaisiana*. We conclude that thrushes are key players in the maintenance of these spirochete species in this region of Central Europe.

Lyme borreliosis is a tick-transmitted zoonosis caused by spirochete bacteria from the genus *Borrelia*. This genus comprises 13 named species, and at least 4 of these cause disease in humans, namely, *Borrelia burgdorferi*, *Borrelia spielmanii*, *Borrelia afzelii*, and *Borrelia garinii* (1, 14). All known strains of Lyme borreliosis spirochetes are maintained in nature by vertebrate hosts and ixodid ticks, with humans being ecological dead-end hosts.

For Europe, pheasants (*Phasianus colchicus*), a few seabird species, and some passerine bird species have been shown to be reservoir competent for *B. garinii* and *B. valaisiana* but not for *B. afzelii*, a rodent specialist (4, 5, 6, 7, 13). However, little is known about the roles of the numerous European woodland bird species in the ecology of Lyme borreliosis spirochetes (2, 13). Therefore, we captured birds of a wide range of species, many of which are migratory, and determined their importance as hosts to ticks and as reservoirs for Lyme borreliosis spirochetes in selected sites of Central Europe.

Ticks were collected from birds captured in four woodlands in Slovakia (16) during 2001 and 2002 and, in 2003, at one woodland in the southeastern Czech Republic. Questing adult and nymphal *Ixodes ricinus* ticks were collected from Slovak sites. Extracted DNA (3) was subjected to nested PCR targeting the 5S-23S intergenic spacer and also, in some cases, the *flaB* gene of Lyme borreliosis spirochetes (8, 15). Spirochete infections determined in ticks were assigned to species by the reverse line blot assay (5, 8, 15) or by DNA sequencing.

Risk factors for tick infestation and infection with *B. burgdorferi* genospecies were investigated in negative binomial and logistic regression models, respectively. Explanatory variables were month, year, site, and bird species. Data from the Czech Republic were excluded because of differences in collection year and bird species range. The level of significance was set at a P value of <0.05. Because of the poor fit of Poisson regression models, the negative binomial models were used. For detailed statistical methods and results, see the supplemental material.

Tick infestations of birds. Of 529 birds captured (345 and 184 at sites in Slovakia and the Czech Republic, respectively, comprising 40 species of 17 families), 187 (145 in Slovakia and 42 in the Czech Republic) carried *I. ricinus* (463 and 157 larvae and 375 and 495 nymphs in Slovakia and the Czech Republic, respectively) (Table 1). In Slovakia, blackbirds (*Turdus merula*), song thrushes (*Turdus philomelos*), and European robins (*Erithacus rubecula*) carried 55.6% of all collected *I. ricinus* ticks. In the Czech Republic, European robins were less common and blackbirds and song thrushes carried 78.8% of *I. ricinus* ticks. When significant differences in infestation levels among months were accounted for, interspecies differences in tick infestations were found to be highly significant in Slovakia (Table 2). Five species/species groups carried significantly more larvae than all other bird species, being, in descending order, song thrushes, blackbirds, wheatears, finches and weaver finches, and tits (Table 2). Three species/species groups carried significantly more nymphs than other species, being, in descending order, blackbirds, song thrushes, and finches and weaver finches combined (Table 2).

Infection of *I. ricinus* ticks collected from birds. A total of 1,461 *I. ricinus* ticks (607 larvae and 854 nymphs) derived from 189 birds were tested for infection with Lyme borreliosis spirochetes. One-third of these birds, belonging to nine species, carried infected ticks (Table 3). The overall prevalences of infection in bird-derived larvae and nymphs with spirochetes

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TABLE 1. List of birds captured in Slovakia and the Czech Republic and prevalence of their infestation with *I. ricinus* ticks

Bird species[a]	No. of birds infested/no. captured	No. of larvae	No. of nymphs
Aegithalos caudatus (Linnaeus, 1758) (long-tailed tit)	0/8		
Certhia familiaris (Linnaeus, 1758) (Eurasian treecreeper)	0/6		
Prunella modularis (Linnaeus, 1758) (dunnock)[b,c]	5/6	16	64
Garrulus glandarius (Linnaeus, 1758) (Eurasian jay)[b,d]	2/2	1	27
Emberiza cia (Linnaeus, 1758) (rock bunting)	1/3	1	0
Emberiza citrinella (Linnaeus, 1758) (yellowhammer)[d]	2/6	3	10
Carduelis carduelis (Linnaeus, 1758) (European goldfinch)	0/1		
Carduelis chloris (Linnaeus, 1758) (European greenfinch)	0/3		
Coccothraustes coccothraustes (Linnaeus, 1758) (hawfinch)[b]	15/23	33	45
Fringilla coelebs (Linnaeus, 1758) (chaffinch)[b]	8/20	72	21
Serinus serinus (Linnaeus, 1758) (serin)	1/1	0	1
Hirundo rustica (Linnaeus, 1758) (barn swallow)	0/6		
Lanius collurio (Linnaeus, 1758) (red-backed shrike)	2/9	0	3
Anthus trivialis (Linnaeus, 1758) (tree pipit)	1/1	1	0
Ficedula albicollis (Temminck, 1815) (collared flycatcher)	0/2		
Muscicapa striata (Pallas, 1764) (spotted flycatcher)	1/6	0	1
Parus caeruleus (Linnaeus, 1758) (blue tit)	4/16	0	8
Parus major (Linnaeus, 1758) (great tit)[b,d]	29/147	41	37
Parus montanus (Baldenstein, 1824) (willow tit)	1/5	3	4
Parus palustris (Linnaeus, 1758) (marsh tit)	8/22	4	6
Parus ater (Linnaeus, 1758) (coal tit)[c]	3/14	5	1
Passer domesticus (Linnaeus, 1758) (house sparrow)	1/1	0	1
Passer montanus (Linnaeus, 1758) (Eurasian tree sparrow)	0/2		
Dendrocopos major (Linnaeus, 1758) (great spotted woodpecker)	0/5		
Picus canus (Gmelin, 1788) (gray-headed woodpecker)	0/1		
Sitta europaea (Linnaeus, 1758) (nuthatch)[d]	8/19	14	6
Acrocephalus palustris (Bechstein, 1798) (marsh warbler)	1/6	0	2
Phylloscopus collybita (Vieillost, 1817) (chiffchaff)[d]	3/8	2	2
Phylloscopus sibilatrix (Bechstein, 1793) (wood warbler)	0/1		
Regulus regulus (Linnaeus, 1758) (goldcrest)	0/1		
Sylvia atricapilla (Linnaeus, 1758) (blackcap)[b,d]	16/60	18	19
Sylvia borin (Boddaert, 1783) (garden warbler)	0/1		
Sylvia communis (Latham, 1787) (common whitethroat)	0/1		
Sylvia curruca (Linnaeus, 1758) (lesser whitethroat)	3/3	2	2
Sylvia nisoria (Bechstein, 1795) (barred warbler)	1/2	0	1
Troglodytes troglodytes (Linnaeus, 1758) (winter wren)	0/1		
Erithacus rubecula (Linnaeus, 1758) (European robin)[b,d]	24/45	118	25
Luscinia megarhynchos (Brehm, 1831) (nightingale)	6/7	8	9
Turdus merula (Linnaeus, 1758) (blackbird)[b,d]	26/31	148	390
Turdus philomelos (Brehm, 1831) (song thrush)[b,d]	22/27	130	185
Total	194/529	620	870

[a] Bird species with no mark were captured in Slovakia only.

[b] Bird species with *Borrelia*-infected ticks.

[c] Bird species captured in the Czech Republic only.

[d] Bird species captured in Slovakia and the Czech Republic also.

were 22.4% and 25.3%, respectively. Blackbirds and song thrushes were significantly more likely to carry spirochete-infected larvae (43.8% and 51.9%, respectively) (Table 2). There was no significant difference among bird species in the prevalence of infection in nymphs.

B. garinii and *B. valaisiana* were the most frequent genospecies (infecting 50.3% and 43.8%, respectively). No larvae were infected with *B. afzelii* and *B. burgdorferi*, but 3.7% and 0.3% of nymphs, respectively, were infected with these species. Mixed infections were detected in 33 ticks, with the most frequent combination being *B. garinii* and *B. valaisiana* (87.8%) (Table 3).

Most *B. garinii*-infected larvae (96.5%) and nymphs (86.7%) were collected from song thrushes and blackbirds, which was highly significant at the Slovak sites (Table 2). All *B. valaisiana*-infected larvae and nearly all *B. valaisiana*-infected nymphs from birds in Slovakia came from song thrushes and blackbirds. There were no significant differences among years, sites, months, or bird species in the prevalence of *B. afzelii* infection in nymphs collected from the birds. Most of the sequenced untypeable samples (80%) clustered with *B. garinii*, except for two infections in nymphs from birds that clustered with *B. afzelii* and one sample with *B. valaisiana*.

Four species of the Lyme borreliosis group were identified in 914 questing *I. ricinus* ticks, of which 40.5% were assigned to *B. valaisiana*, 33% to *B. garinii*, 23% to *B. afzelii*, and 2.2% to *B. burgdorferi* (Table 4).

Here, we show that among 40 bird species captured in woodlands of Slovakia and the Czech Republic, 2 species of thrushes (i.e., blackbird and song thrush) constitute the core reservoir of *B. garinii* and *B. valaisiana*. The comparison of the genospecies richness in tick larvae derived from the birds with that determined for questing nymphs and adults collected at the same sites confirms previous observations that birds are not involved in the maintenance of *B. afzelii* (6, 8, 9, 10).

TABLE 2. Variables significantly associated with infestation of birds with larval and nymphal *Ixodes ricinus* ticks (in the most parsimonious negative binomial regression models) and with infection with *B. burgdorferi* sensu lato and its genospecies in larvae and nymphs collected from the birds (in the most parsimonious logistic regression models)[a]

Outcome, explanatory variable, and factor	Coefficient SE	OR (95% CI)	Wald *z*	*P*
Infestation with nymphal *I. ricinus*				
Mo				
July	−1.60 (0.46)		−3.48	<0.001
October	−1.90 (0.50)		−3.79	<0.001
Other[b]				
Bird species/species group				
Blackbird	2.80 (0.43)		6.57	<0.001
Song thrush	2.56 (0.43)		5.90	<0.001
Finches and weaver finches	0.99 (0.27)		3.64	<0.001
Other[b]				
Constant	−0.08 (0.37)		−0.21	
Infestation with larval *I. ricinus*				
Mo				
May	1.97 (0.84)		2.34	<0.05
June	2.37 (0.97)		2.44	<0.05
July	1.91 (0.84)		2.28	<0.05
September	3.74 (1.14)		3.26	<0.05
Bird species/species group				
Song thrush	3.32 (0.68)		4.88	<0.001
Blackbird	3.17 (0.71)		4.46	<0.001
Wheatears (robin and nightingale)	2.33 (0.46)		5.00	<0.001
Finches and weaver finches	2.14 (0.43)		4.92	<0.001
Tits	1.20 (0.45)		2.68	<0.01
Other[b]				
Constant	−3.26 (0.86)		−3.79	
Infection of larvae with *B. burgdorferi* sensu lato				
Bird species/species group				
Blackbird and song thrush		1.495 (81–27 × 10^3)	4.93	<0.001
Other[b]				
Constant		0.002 (0–0.01)	−5.96	
Infection of nymphs with *B. burgdorferi* sensu lato				
Mo				
May to July		32.46 (3.03–343.77)	2.88	<0.01
Other[b]				
Constant		0.004 (0–0.05)	−4.34	
Infection of larvae with *B. garinii*				
Yr				
2001		22.42 (1.16–103.01)	−2.06	<0.05
2002[b]				
Bird species/species group				
Blackbird and song thrush		4.817 (44–44 × 10^4)	3.54	<0.001
Other[b]				
Constant		0.004 (0–0.15)	−3.02	
Infection of nymphs with *B. garinii*				
Bird species/species group				
Blackbird and song thrush		28.79 (4.35–190.57)	3.49	<0.001
Other[b]				
Constant		0 (0–0.01)	−4.56	
Infection of nymphs with *B. valaisiana*				
Bird species/species group				
Blackbird and song thrush		7.48 (2.08–26.84)	3.09	<0.01
Other[b]				
Constant		0.03 (0.01–0.08)	−6.55	

[a] For both negative binomial and logistic regression models, the most parsimonious models were those in which no explanatory variables could be removed without significantly ($P < 0.05$) affecting model deviance. OR, odds ratio; 95% CI, 95% confidence interval.

[b] Reference factor.

TABLE 3. Prevalence of *Borrelia* genospecies in *I. ricinus* ticks feeding on birds[a]

Bird species	Stage	No. of infected ticks[c]/no. tested (%)	No. of birds yielding infected ticks/no. tested (%)	No. of ticks infected with indicated *Borrelia* genospecies[b] (no. infested with infected ticks)								
				BGA	BVA	BAF	BBSS	BGA + BVA	BGA + BAF	BVA + BAF	BGA + BVA + BAF	ND
Prunella modularis (dunnock)	L	2/16 (12.5)	1/5 (20)		2 (1)							
	N	20/63 (31.7)	4/5 (80)	7 (4)	8 (2)	3 (1)						2 (2)
Garrulus glandarius (Eurasian jay)	L	0/1 (0)	0/2 (0)									
	N	3/27 (11.1)	2/2 (100)	1 (1)	2 (2)							
Coccothraustes coccothraustes (hawfinch)	L	1/33 (3)	1/15 (6.7)	1 (1)								
	N	8/44 (18.2)	6/15 (40)	2 (2)	4 (4)							2 (2)
Fringilla coelebs (chaffinch)	L	1/71 (1.4)	1/8 (12.5)									1 (1)
	N	1/21 (4.8)	1/8 (12.5)	1 (1)								
Parus major (great tit)	L	1/40 (2.5)	1/24 (4.2)	1 (1)								
	N	5/37 (13.5)	4/24 (16.7)	2 (2)	2 (2)							1 (1)
Sylvia atricapilla (blackcap)	L	0/16 (0)	0/16 (0)									
	N	1/18 (5.6)	1/16 (6.3)			1 (1)						
Erithacus rubecula (European robin)	L	0/114 (0)	0/23 (0)									
	N	1/24 (4.2)	1/23 (4.3)					1 (1)				
Turdus merula (blackbird)	L	64/146 (43.8)	13/26 (50)	29 (6)	23 (6)			6 (5)				6 (2)
	N	126/383	20/26 (76.9)	53 (8)	38 (15)	6 (5)	1 (1)	16 (3)	1 (1)	1 (1)	1 (1)	9 (6)
Turdus philomelos (song thrush)	L	67/129 (51.9)	11/22 (50)	27 (8)	36 (6)			1 (1)				3 (3)
	N	51/181 (28.2)	14/22 (63.6)	31 (13)	8 (2)	1 (1)		5 (3)		1 (1)		5 (4)
Total	L	136/566 (24)	28/141 (19.9)	58 (16)	61 (13)	0 (0)	0 (0)	7 (6)	0 (0)	0 (0)	0 (0)	10 (6)
	N	216/798 (27.1)	53/141 (37.6)	97 (31)	62 (27)	11 (8)	1 (1)	22 (7)	1 (1)	2 (2)	1 (1)	19 (15)

[a] BGA, *B. garinii*; BVA, *B. valaisiana*; BAF, *B. afzelii*; BBSS, *B. burgdorferi* sensu stricto; ND, not determined; L, larvae; N, nymphs.
[b] In some cases, the sum of *Borrelia* species infections was greater than the number of infected ticks because of mixed infections.
[c] Number of ticks that tested positive for *Borrelia* species.

TABLE 4. Prevalence of *Borrelia* genospecies in questing *I. ricinus* ticks[a]

Locality (yr)	Stage	No. of infected ticks[c]/no. tested (%)	No. of ticks infected with indicated *Borrelia* genospecies[b] (%)							
			BGA	BVA	BAF	BBSS	BGA + BVA	BGA + BAF	BGA + BVA + BAF	ND
Site 1, Šúr (2001, 2002)	N	57/205 (27.8)	18 (31.6)	22 (38.6)	3 (5.3)		8 (14)	2 (3.5)	2 (3.5)	2 (3.5)
	A	78/232 (33.6)	23 (29.5)	33 (42.3)	6 (7.7)		2 (2.6)	1 (1.3)		13 (16.7)
Site 2, Malacky (2002)	N	31/215 (14.4)	1 (3.2)	4 (12.9)	24 (77.4)	1 (3.2)				1 (3.2)
	A	13/56 (23.2)	2 (15.4)	6 (46.2)	2 (15.4)	3 (23.1)				
Site 3, Drienovec (2002)	N	4/27 (14.8)			2 (50)		1 (25)	1 (25)		
	A	20/75 (26.7)	5 (25)	8 (40)			2 (10)			5 (25)
Site 4, Brzotín (2002)	N	14/70 (20.0)	3 (21.4)	1 (7.1)	8 (57.1)	1 (7.1)				1 (7.1)
	A	10/34 (29.4)	4 (40)	3 (30)	2 (20)					1 (10)
Total	N	106/517 (20.5)	22 (20.8)	27 (25.5)	37 (34.9)	2 (1.9)	9 (8.5)	3 (2.8)	2 (1.9)	4 (3.8)
	A	121/397 (30.5)	34 (28.1)	50 (41.3)	10 (8.3)	3 (2.5)	4 (3.3)	1 (0.8)		19 (15.7)

[a] BGA, *B. garinii*; BVA, *B. valaisiana*; BAF, *B. afzelii*; BBSS, *B. burgdorferi* sensu stricto; ND, not determined; N, nymphs; A, adults.

[b] In some cases, the sum of *Borrelia* species infections was greater than the number of infected ticks because of mixed infections.

[c] Number of ticks that tested positive for *Borrelia* species.

The statistical analyses show that the relative roles of song thrushes and blackbirds as hosts for ticks and reservoirs of *B. garinii* and *B. valaisiana* in Slovakia are not due to confounding factors, such as variations among sites and months for the birds captured (see the supplemental material). The data from the Czech Republic could not be included in the statistical analyses, because it differed in terms of times of collection and in the range of species of birds that were captured. However, it also showed that the roles of thrushes and blackbirds as hosts for ticks and reservoirs of *B. garinii* and *B. valaisiana* are similar in both countries. Infestation of blackbirds and song thrushes with large numbers of *Borrelia*-infected tick larvae has also been observed in Asia (11, 12).

In conclusion, blackbirds and song thrushes (both members of the thrush group) appear to constitute a core functional group among the avian reservoir host community for Lyme borreliosis spirochetes in the region. Thus, the ecology of these two avian species is likely to be key to the eco-epidemiology of *B. garinii*, the causative agent of borreliosis in Central Europe.

Nucleotide sequence accession numbers. The GenBank accession numbers of the sequences obtained in this study are DQ520861, DQ520872, DQ520863, DQ520871, DQ520870, DQ458997, DQ520865, DQ517433, DQ520862, DQ520864, DQ520869, DQ520866, DQ520868, DQ520867 (5S-23S ribosomal DNA intergenic spacer), DQ490971, DQ490973, DQ490972, DQ490977, DQ490978, DQ490967, DQ490970, DQ490976, DQ490974, DQ490968, DQ490975, and DQ490969 (*flaB* gene).

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