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Prevalence of *Campylobacter jejuni*, *Campylobacter lari*, and *Campylobacter coli* in Different Ecological Guilds and Taxa of Migrating Birds†

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A total of 1,794 migrating birds trapped at a coastal site in southern Sweden were sampled for detection of *Campylobacter* spp. All isolates phenotypically identified as *Campylobacter jejuni* and a subset of those identified as non-*C. jejuni* were identified to the species level by PCR-based techniques. *C. jejuni* was found in 5.0% of the birds, *Campylobacter lari* was found in 5.6%, and *Campylobacter coli* was found in 0.9%. An additional 10.7% of the tested birds were infected with hippurate hydrolysis-negative *Campylobacter* spp. that were not identified to the species level. The prevalence of *Campylobacter* spp. differed significantly between ecological guilds of birds. Shoreline-foraging birds feeding on invertebrates and opportunistic feeders were most commonly infected (76.8 and 50.0%, respectively). High prevalence was also shown in other ground-foraging guilds, i.e., ground-foraging invertebrate feeders (11.0%), ground-foraging insectivores (20.3%), and plant-eating species (18.8%). Almost no *Campylobacter* spp. were found in ground-foraging granivores (2.3%), arboreal insectivores (0.6%), aerial insectivores (0%), or reed- and herbaceous plant-foraging insectivores (3.5%). During the autumn migration, a high proportion of samples from juveniles were positive (7.1% in passerines, 55.0% in shorebirds), indicating transmission on the breeding grounds or during the early part of migration. Prevalence of *Campylobacter* spp. was associated with increasing body mass among passerine bird species. Furthermore, prevalence was higher in short-distance migrants wintering in Europe than in long-distance migrants wintering in Africa, the Middle East, or Asia. Among ground-foraging birds of the Muscicapidae, those of the subfamily Turdinae (i.e., *Turdus* spp.) showed a high prevalence of *Campylobacter* spp., while the organism was not isolated in any member of the subfamily Muscicapinae (i.e., *Erithacus* and *Luscinia*). The prevalence of *Campylobacter* infection in wild birds thus seems to be linked to various ecological and phylogenetic factors, with great variations in carriership between different taxa and guilds.

For decades, wild birds have been considered natural vertebrate reservoirs of *Campylobacter* spp. (23, 25) and are frequently mentioned as possible vectors for transmission to poultry (2, 15, 40), cattle (22), and humans (35, 38, 44). *Campylobacter jejuni*, the main human pathogen of the genus, is now recognized as a leading cause of acute bacterial gastroenteritis in many parts of the world (3, 18). Understanding the epidemiology of *Campylobacter* spp. in wild birds appears to be an essential part of the puzzle. However, although the prevalence of *Campylobacter* spp. in humans and poultry has been well studied (2, 3), little is known about the prevalence of this organism in wild birds. Published works on wild birds in the context of *Campylobacter* epidemiology have focused either on single taxonomic groups of birds, e.g., wildfowl (27, 29), shorebirds (19), gulls (26, 45), and corvids (38), or on birds inhabiting different habitats, e.g., rural and urban areas (20, 24, 25). The few studies examining a broad spectrum of species (25, 30, 46) lack systematic sampling procedures, possibly resulting in biased interpretation of the data.

To overcome these problems, we conducted standardized sampling of a large number of individuals and species of wild birds at a single migration locality over an entire season (March to November). Our goals were to determine in which groups of wild birds the different *Campylobacter* spp. were present and to reveal which ecological parameters influenced the prevalence of infection. The present study offers the largest survey to date of the prevalence of *Campylobacter* spp. in migratory birds (1,794 individuals from 107 species), providing a unique data set for giving new insights into the ecology and epidemiology of this host-parasite interaction.

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MATERIALS AND METHODS

Sampling procedures and measurements. Fieldwork was conducted at Ottenby Bird Observatory (56°12′N, 16°24′E), on the southernmost point of the island Öland in southeastern Sweden. Passerines were trapped with mist nets and

TABLE 1. Birds tested for presence of *Campylobacter* spp.

Family and species[a]	Guild[b]	No. of birds tested (spring/autumn)	No. of birds positive (spring/autumn)			
			C. jejuni	*C. lari*	*C. coli*	*Campylobacter* spp.
Phalacrocoracidae						
Phalacrocorax carbo	K	0/1				
Anatidae						
Anas acuta	J	0/1				0/1
Anas crecca	J	0/2				0/1
Anas penelope	J	0/1				
Aythya fuligula	I	0/2				
Branta bernicla	J	0/4				0/1
Somateria mollissima	I	0/1				0/1
Accipitridae						
Accipiter gentilis	A	0/1				
Accipiter nisus	A	0/32	0/1			0/1
Phasianidae						
Perdix perdix	J	3/0				
Rallidae						
Rallus aquaticus	H	0/1				
Charadriidae						
Charadrius dubius	H	0/2				
Charadrius hiaticula	H	0/6		0/1		0/1
Pluvialis squatarola	H	0/1				0/1
Scolopacidae						
Actitis hypoleucos	H	0/8		0/3		0/5
Arenaria interpres	H	0/4		0/3		
Calidris alba	H	0/1				
Calidris alpina	H	0/313	0/29	0/70	0/6	0/145
Calidris canutus	H	0/3		0/2		
Calidris ferruginea	H	0/9	0/1	0/6		0/2
Calidris minuta	H	0/8	0/2			0/5
Calidris temminckii	H	0/4		0/2		
Gallinago gallinago	H	0/1				0/1
Limicola falcinellus	H	0/11	0/4	0/5	0/3	
Lymnocryptes minimus	H	0/1				0/1
Philomachus pugnax	H	0/1	0/1		0/1	
Scolopax rusticola	H	0/1				0/1
Tringa glareola	H	0/6	0/1			0/1
Tringa nebularia	H	0/1				0/1
Tringa ochropus	H	0/1				
Laridae						
Larus canus	L	0/1				
Larus ridibundus	L	0/3				
Columbidae						
Columba palumbus	J	1/4				
Cuculidae						
Cuculus canorus	E	0/2				
Strigidae						
Aegolius funereus	A	1/0				
Asio flammeus	A	0/2				
Asio otus	A	3/46	2/8			
Caprimulgidae						
Caprimulgus europaeus	F	0/1				
Picidae						
Dendrocopos major	E	1/0				
Picus viridis	E	2/3				
Alaudidae						
Alauda arvensis	C	0/2				
Hirundinidae						
Delichon urbica	F	12/1				
Hirundo rustica	F	1/3				
Muscicapidae						
Ficedula albicollis	F	2/1				
Ficedula hypoleuca	F	3/2				
Ficedula parva	F	4/1				
Muscicapa striata	F	5/6				
Erithacus rubecula	B	86/213				
Luscinia luscinia	B	7/4				
Luscinia svecica	B	14/5				
Oenanthe oenanthe	D	1/1				

Continued on following page

TABLE 1—*Continued*

Family and species[a]	Guild[b]	No. of birds tested (spring/autumn)	No. of birds positive (spring/autumn)			
			C. jejuni	*C. lari*	*C. coli*	*Campylobacter* spp.
Phoenicurus ochruros	D	9/2				
Phoenicurus phoenicurus	E	17/27				
Saxicola rubetra	G	1/2				
Turdus iliacus	B	2/8	0/5			
Turdus merula	B	32/12	3/4	4/0	7/0	0/2
Turdus philomelos	B	6/19	1/6			0/1
Turdus pilaris	B	11/3	0/2			
Turdus torquatus	B	1/0				
Turdus viscivorus	B	1/0	1/0			
Sylviidae						
Acrocephalus palustris	G	2/2				
Acrocephalus schoenobaenus	G	0/14				
Acrocephalus scirpaceus	G	3/4	0/1			
Hippolais icterina	E	4/4				
Locustella naevia	G	0/1				
Phylloscopus collybita	E	5/3				
Phylloscopus fuscatus	E	0/1				
Phylloscopus proregulus	E	0/2				
Phylloscopus sibilatrix	E	0/2				
Phylloscopus trochilus	E	47/60				
Sylvia atricapilla	E	2/8				
Sylvia borin	E	1/3				
Sylvia communis	G	10/10				
Sylvia curruca	E	16/19				
Sylvia nisoria	E	1/0				
Regulidae						
Regulus regulus	E	14/186				0/2
Aegithalidae						
Aegithalos caudatus	E	0/8				
Paridae						
Parus ater	E	0/2				
Parus caeruleus	E	1/6				
Parus major	E	2/8				0/1
Certhiidae						
Certhia familiaris	E	0/7				
Troglodytes troglodytes	G	19/18	0/1	0/1		
Laniidae						
Lanius collurio	A	2/7				
Lanius excubitor	A	0/1				
Corvidae						
Corvus monedula	L	4/0	4/0			
Sturnidae						
Sturnus vulgaris	B	7/24	1/9	0/2		0/2
Passeridae						
Passer domesticus	C	1/3				
Passer montanus	C	1/10				
Anthus pratensis	D	0/9		0/1		0/2
Anthus trivialis	D	4/8				
Motacilla alba	D	0/32	0/2		0/8	
Motacilla flava	D	0/3			0/1	
Prunella modularis	C	4/9	0/1			
Fringillidae						
Carduelis cannabina	C	2/0				
Carduelis carduelis	C	2/3				
Carduelis chloris	C	5/24			0/1	
Carduelis flammea	C	1/5				
Carduelis flavirostris	C	0/15				
Carpodacus erythrinus	C	4/2				
Coccothraustes coccothraustes	C	3/0				
Fringilla coelebs	C	12/14				
Fringilla montifringilla	C	3/6				
Loxia curvirostra	C	1/0				
Serinus serinus	C	7/0				
Emberiza citrinella	C	4/15	0/1			
Emberiza hortulana	C	5/1			0/1	
Emberiza schoeniclus	C	0/8				

[a] Taxonomy according to Sibley and Ahlquist (36) and Sibley and Monroe (37).

[b] Guilds: A, raptors; B, ground-foraging invertebrate feeders; C, ground-foraging granivores; D, ground-foraging insectivores; E, arboreal insectivores; F, aerial insectivores; G, reed- and herbaceous plant-foraging insectivores; H, shoreline-foraging invertebrate feeders; I, aquatic invertebrate feeders; J, plant-eating species; K, fish-eating species; L, opportunistic feeders.

Helgoland traps (6) in the bird observatory garden, and shorebirds were trapped with Ottenby funnel traps (6) on the shoreline surrounding the point. Captured birds were banded, weighed, and measured and their ages were determined according to differences in feather shape and wear (4, 33, 41), enabling separation of juvenile and adult birds in autumn and yearling and adult birds in spring.

Birds migrating through Ottenby breed mostly in Sweden, Finland, and Russia (1). All trapped birds except jackdaws (*Corvus monedula*) were regarded as migrants, since the observatory garden offers only limited breeding possibilities. Every 10th bird banded during the studied migration periods, 25 March to 15 June 2000 (spring migration) and 1 July to 15 November 2000 (autumn migration), was sampled for the prevalence of *Campylobacter* spp. During days on which more than 500 birds were trapped (>500 birds, $n = 5$), the sampling was less intense. Species normally trapped only in small numbers at Ottenby (<10 individuals per year) were sampled in higher proportions.

Two different approaches were used to obtain fecal samples, depending on the size of the trapped bird. Smaller birds were put in a dark box one by one with a clean sheet of paper at the bottom. After the bird had defecated (normally after 5 to 10 min), the fecal sample was placed in charcoal transport medium (Transwab; BioDisc, Solna, Sweden) and stored at refrigerator temperature until cultivation. Large birds, i.e., those with a body mass exceeding 250 g, were sampled by insertion of a sterile swab 1 to 2 cm into the cloaca.

Laboratory analyses. Samples were cultivated at the Department of Clinical Microbiology at Kalmar County Hospital by methods routinely used for clinical samples. Each sample was plated onto a *Campylobacter*-selective, blood-free medium (45.5 g of *Campylobacter*-selective agar base LAB M/LAB 112 per liter, 2 ampoules of cefoperazone-amphotericin supplement LAB M/X 112; Lab M, Bury, England). Incubation was performed at 42°C in a microaerobic atmosphere (85% N_2, 10% CO_2, 5% O_2). Plates were examined after 48 and 72 h. Isolates with gram-negative gull-shaped cells (identified by light microscopy at a magnification of ×1,000), positive reactions in catalase and oxidase tests, and inability to grow under aerobic conditions at 37°C were regarded as *Campylobacter* spp. Cultures were frozen at −80°C in broth (75% horse serum, 75 g of glucose BDH 10117 4Y/liter, 1.25 g of Lab Lemco Oxoid L29/liter, 2 g of Bacto Peptone [Difco catalog no. 0118-15]/liter). Due to the large number of samples to be analyzed, no enrichment step was included as this would have obstructed fulfillment of the entire study. Further, the sampling scheme was in operation every day during the field season, including holidays and weekends, and therefore not all samples could be analyzed on the date of collection. The majority of samples were analyzed within 48 h after sampling, while a few were analyzed up to 4 days after collection. However, previous testing of our methods showed good recovery of *Campylobacter* spp. even 5 days after sampling (data not shown).

The isolates were subjected to a hippurate hydrolysis test, and all isolates with positive reactions were further analyzed by one of two genotypic tests for confirmation of species identification. A PCR directed at the 23S rRNA gene identified isolates as being thermotolerant *Campylobacter* spp. Subsequent endonuclease digestion of the PCR products produces species-specific fragment patterns (17). In short, the PCR mixture contained 0.25 μM (each) primers THERM1 and THERM4 (17), 50 mM KCl, 10 mM Tris-HCl, 1.5 mM $MgCl_2$, 0.1 mM each deoxynucleotide, and 0.02 U of AmpliTaq Gold (PE Applied Biosystems, Branchburg, N.J.). An initial denaturing step of 12 min at 94°C to activate the AmpliTaq enzyme started the PCR, followed by 45 cycles with a thermal profile of 94°C for 1 min, 56°C for 1 min, and 72°C for 1 min, followed by a final extension step of 72°C for 10 min. Species determination was performed through digestion of 10 μl of the PCR products with 0.5 U of *Alu*I for 1 h and subsequent separation of digestion products on agarose gels. Banding patterns were compared to those produced by type strains of *C. jejuni*, *Campylobacter coli*, and *Campylobacter lari*. The second method used for species identification is a multiplex PCR with primer pairs specific for *C. jejuni* and *C. coli* (43). We followed the protocol of Vandamme et al. (43) but performed the reaction with 25-μl volumes instead of 50-μl volumes. Boiled lysates or purified DNA (Puregene DNA isolation kit; Gentra Systems, Minneapolis, Minn.) was used as the template for both methods, and reference strains of *C. jejuni*, *C. coli*, and *C. lari* were used as controls. A subset (106 of 295 isolates) of the hippurate hydrolysis-negative isolates was genetically characterized by using a published PCR-restriction fragment length polymorphic analysis protocol (28). The template DNA used in this method was isolated as described previously (16). In short, material from one colony was mixed with 300 μl of a 20% Chelex-100 suspension in Tris-EDTA buffer and heated for 10 min at 95°C. After centrifugation, the supernatant was used as the template in the PCRs. The restriction patterns obtained in the PCR-restriction fragment length polymorphic analysis were visually compared to patterns obtained from 43 reference strains, including *C. coli* (4), *Campylobacter fetus* (2), *Campylobacter helveticus* (1), *Campylobacter hyointestinalis* (5), *C. jejuni* (5), *C. lari* (6), *Campylobacter mucosalis* (1), *Campylobacter sputorum* (3), *Campylobacter upsaliensis* (5), and *Arcobacter* (11). Reference strains were obtained from the American Type Culture Collection (*C. fetus*) and the BCCM/LMG collection (Ghent, Belgium).

RESULTS

Out of 21,666 birds banded, a total of 1,794 individual birds (representing 107 species from 26 families) were tested for the presence of *Campylobacter* spp. (425 individuals in spring and 1,369 individuals in autumn) (Table 1). *C. jejuni* was isolated from 89 birds (13 in spring, 76 in autumn), *C. lari* was isolated from 100 birds (4 in spring, 96 in autumn), and *C. coli* was isolated from 17 birds (7 in spring, 10 in autumn). An additional 192 isolates from birds (all in autumn) were phenotypically assigned to the hippurate hydrolysis-negative *Campylobacter* spp. but were not identified to the species level by genotypic methods (Table 1). Ten birds had concomitant infections with *C. jejuni* and *C. coli*. Two isolates were identified as thermotolerant *Campylobacter* spp. by the 23S rRNA methods of Fermér and Engvall (17) but gave aberrant patterns after restriction enzyme digestion and were therefore regarded as nontypeable. The mean prevalence of *Campylobacter* infection was 21.6% for all tested birds but varied from 0 to 100% between species (Table 1). In total, *Campylobacter* spp. were recorded in 13 out of 26 bird families investigated. *C. jejuni* was isolated from nine families, *C. coli* was isolated from two families, and *C. lari* was isolated from six families (Table 1). These figures must be regarded as minimum values as die-off of campylobacters during transport could have occurred. Also, as no enrichment was used, low numbers of organisms may have gone undetected. Furthermore, the growth conditions used in this study preclude growth of *Campylobacter* species that require anoxic environments or the presence of H_2.

Campylobacter-positive samples were obtained from 72 juvenile birds of 24 species during the autumn migration (*C. jejuni*, 36 individuals of 14 species; *C. lari*, 7 individuals of 4 species; *C. coli*, 1 individual; hippurate hydrolysis-negative *Campylobacter* spp., 26 individuals of 18 species; nontypeable, 2 individuals of 2 species). Positive samples originated from a variety of families, namely, Sylviidae, Regulidae, Paridae, Passeridae, Fringillidae, Anatidae, Muscicapidae, Sturnidae, Accipitridae, Strigidae, Scolopacidae, and Certhidae. We compared the two most frequently sampled bird groups, passerines and shorebirds, in more detail. In passerines, 7.1% of juveniles ($n = 676$) and 6.1% of adults ($n = 115$; $\chi^{2}_{1} = 0.31$, $P = 0.58$) tested positive for *Campylobacter* spp., compared to 55.0% of juvenile ($n = 20$) and 75.8% of adult ($n = 364$; $\chi^{2}_{1} = 4.35$, $P = 0.04$) shorebirds.

The size of the bird might be related to the probability of its carrying a *Campylobacter* infection if, for example, large and small birds differ in their habits, habitat preferences, or distributions. We calculated the mean body mass for each passerine species and divided the species into two groups, infected and uninfected. We calculated the mean values for each species in each group and tested the difference between the two groups with a *t* test. The value for uninfected species was 19.3 g (standard deviation [SD] = 13.6), significantly lower than 52.2 g (SD = 56.4) for the infected species (*t* test, $t = 3.85$, $P < 0.001$, $n = 50$ uninfected species and 16 infected species). Among shorebirds, the difference in mean body mass between

TABLE 2. Prevalence of *Campylobacter* spp. in different ecological guilds

Guild	No. of species tested	% of species *Campylobacter* positive	No. of birds tested	% of birds *Campylobacter* positive
Raptors	7	28.6	95	12.6
Ground-foraging invertebrate feeders	10	70.0	455	11.0
Ground-foraging granivores	18	22.2	172	2.3
Ground-foraging insectivores	6	50.0	69	20.3
Arboreal insectivores	20	10.0	464	0.6
Aerial insectivores	7	0	42	0
Reed- and herbaceous plant-foraging insectivores	7	28.6	86	3.5
Shoreline-foraging invertebrate feeders	20	85.0	383	76.8
Aquatic invertebrate feeders	2	50.0	3	33.3
Plant-eating species	6	50.0	16	18.8
Fish-eating species	1	0	1	0
Opportunistic feeders	3	33.3	8	50.0

infected and uninfected species was lower than that for passerines, 85.4 g in infected species and 88.6 g in uninfected species. However, among shorebirds, the uninfected species group was comprised of only 3 of the 19 species (Table 1), and less than three individuals were sampled for each of these 3 uninfected species, thus precluding further statistical treatment.

We compared prevalence rates to distance of migration for all species not directly associated with water (i.e., shorebirds, gulls, ducks, and rails were excluded), with the birds divided into two groups. The first group was made up of short-distance migrants (birds migrating to different parts of Europe), while the second group was made up of long-distance migrants (birds migrating to Africa, the Middle East, or Asia). Among long-distance migrants, only 13 (3%) individuals representing 4 species tested positive for *Campylobacter* spp., out of 426 tested birds of 36 species. In contrast, 76 (11%) of the short-distance migrants tested positive, representing 16 species out of 716 tested birds of 43 species. These differences were significant both for number of infected species ($\chi^{2}_{1} = 7.06$, $P = 0.008$) and number of infected individuals ($\chi^{2}_{1} = 21.26$, $P < 0.001$).

The prevalence of *Campylobacter* spp. in different ecological guilds is shown in Table 2, where birds are divided into groups according to their main foraging habits (7, 8, 9, 10, 11, 12, 13, 14). Almost no *Campylobacter* spp. were found in granivores or insectivores. Most guilds that forage at ground level showed high prevalence rates; also, raptors and opportunistic feeders were often infected by *Campylobacter* spp. (Table 2). We tested for statistical association between feeding preference, i.e., feeding mainly in water or on land, and the *Campylobacter* type isolated from the bird species. Of 12 species from which *C. lari* was isolated, 8 species normally feed in water, and among 19 species from which *C. jejuni* was isolated, 13 species preferably feed on land ($\chi^{2}_{1} = 3.66$, $P = 0.06$). *C. lari* was isolated more frequently in nonpasserine individuals (30.5% of positive samples, $n = 279$) than in passerine individuals (16.3% of positive samples, $n = 49$; $\chi^{2}_{1} = 33.05$, $P < 0.001$), and there was a tendency for this to occur at the species level (passerine species, 25.0% of positive samples, $n = 16$; nonpasserine species, 50.0%, $n = 16$; $\chi^{2}_{1} = 2.13$, $P = 0.14$).

DISCUSSION

Overall, we found a high frequency of *Campylobacter* spp. in migrating birds (21.6%). However, the distribution of *Campylobacter* among bird taxa and guilds was very heterogeneous. Certain bird taxa had high prevalences, e.g., shorebirds (Scolopacidae and Charadridae, 79.6%), wagtails and pipits (Motacillinae, 25.0%), starlings (Sturnidae, 40.0%), and thrushes (Turdinae, 37.9%), while others did not (Table 1). Among the Turdinae, *Campylobacter* infection was found only in *Turdus* individuals, while *Erithacus*, *Luscinia*, *Oenanthe*, *Saxicola*, and *Phoenicurus* individuals tested negative. It is interesting to note that these results coincide with new phylogenetic classifications of the thrushes based on comparisons of genetic material. These new classifications place thrushes into two different subfamilies of the Old World flycatcher family (Muscicapidae). *Turdus* is placed in the subfamily Turdinae, while *Erithacus*, *Oenanthe*, *Luscinia*, and *Phoenicurus* are placed together with *Ficedula* and *Muscicapa* in the subfamily Muscicapinae (36, 37). Thus, in our study, all species of the Muscicapinae were free of *Campylobacter*, while almost all species of the Turdinae carried *Campylobacter* (Table 1). Why *Turdus* had such a high prevalence of *Campylobacter* while *Erithacus* had none seems to be an important question that we, unfortunately, can only ask, not answer. Although both genera forage on the ground for invertebrates, perhaps there are subtle ecological differences in microhabitat use, foraging habits, or diet that result in *Turdus* being exposed to *Campylobacter* more often than *Erithacus*. Another possible answer is that some evolutionary change in the birds of the subfamily Muscicapinae has resulted in that lineage being more resistant to *Campylobacter* than the Turdinae.

The prevalence of *Campylobacter* spp. was highly influenced by feeding habits. In some ecological guilds, e.g., most types of insectivores and granivores, *Campylobacter* spp. were rarely or never isolated. However, in other guilds, i.e., in raptors, in opportunistic feeders, and in most ground-foraging guilds, prevalence was found to be high.

The positive relationship between the prevalence of *Campylobacter* spp. and increasing body mass among the passerine bird species may have several plausible explanations. Body mass is positively correlated with longevity in passerines (5, 21), and a longer life span would increase the number of potential transmission contacts, resulting in a higher risk of contracting the bacteria. However, a large proportion of juvenile birds were already infected on their first autumn migration, at an age of 1 to 4 months, implying that transmission had already taken place on the breeding grounds, or at stopover

sites during early stages of the autumn migration, indicating that age may not be so important a factor. In shorebirds, however, *Campylobacter* isolation was more frequent in adult individuals but the number of sampled juveniles was far less than that of adults.

Based on our knowledge of *Campylobacter* survival in the environment (42), and reports of isolation of these bacteria from surface water (22, 39), it is reasonable to assume that the habitats preferred by different bird species may result in different levels of exposure to *Campylobacter*. There was a tendency for isolation rates of *C. jejuni* to differ from those of *C. lari* when the main foraging habitat of the species was considered. However, within the data set, there was a statistically significant difference in isolation of *C. lari* from nonpasserine individuals and in isolation of *C. jejuni* from passerines. At the host species level, this difference was not significant, but it probably would have been if all hippurate hydrolysis-negative *Campylobacter* spp. had been identified to the species level genetically, since nearly all of those tested proved to be *C. lari*.

Shorebirds differ in several aspects from passerines. They generally have a longer life span (11), are often gregarious, feed side by side in mixed-species flocks, and feed at water edges or in shallow waters of habitats that commonly harbor *Campylobacter* spp., e.g., at river mouths, seashores, and sewage plants. The frequent utilization of these kinds of habitats by shorebirds is a likely explanation for the high overall prevalence of *Campylobacter* spp. in this type of birds, especially since feeding activities would be the most likely route through which the birds would become exposed to the bacteria.

Are *Campylobacter* spp. a commensal of avian intestines? The growth temperature range of these bacteria, which fits the body temperature of birds rather than that of mammals (34), suggests that the answer is yes. Furthermore, in this study and in several other studies, high prevalences of *C. jejuni*, *C. coli*, and *C. lari* were found in apparently healthy birds (25, 29). High isolation rates could, in our opinion, be interpreted as evidence for a nonharmful coexistence between *Campylobacter* species and their bird hosts, indicating a long evolutionary history of host-parasite interactions. Certain strains of the bacteria might have coevolved with certain bird species, possibly protecting the host against invasion by more harmful strains. Accordingly, the finding of certain bird species with low or no prevalence of the bacteria may reflect an inability of the bacterium to maintain an infection. Alternatively, it might reflect that birds generally have a strong immune system, developed to eliminate *Campylobacter* infections or to reduce them to a level undetectable by the methods used in this study. It is not known if, or to what extent, wild birds are affected by infection with *Campylobacter* spp. nor for how long infection is maintained in a bird.

We do not know if the *Campylobacter* isolates found in this study are transmissible to humans or domesticated animals, but there might nevertheless be some epidemiological considerations. Given the occurrence of *C. jejuni*, *C. lari*, and *C. coli* in bird species capable of long-distance migration, many bird species could potentially act as vectors in long-distance transmission of these pathogens to domesticated animals or humans. For *Salmonella* spp., feeders have been regarded as likely sources for transmission of the bacteria between birds (31). This may also be the case for *Campylobacter* spp. Birds exposed to feed contaminated with *Campylobacter* spp. of human origin, or to feces contaminated with *Campylobacter* spp. of avian or human origin, could easily acquire infections. A recent study in which *C. jejuni* isolates from different sources were serotyped showed significant differences in serotype distribution between *C. jejuni* from wild birds and animals and from isolates of poultry or human origin, indicating that wildlife may be less important in the epidemiology of *C. jejuni* infections in humans (32). However, the number of wild-bird isolates included in the study was comparatively low. Given the diversity of habitats occupied by different bird species and the resulting possibility of different species being exposed to *Campylobacter* spp. from different sources, we feel that this question deserves further investigation.

The observed distribution of *Campylobacter* spp. in this study highlights the need for caution when considering wild birds as reservoirs. To correctly assess the impact of wild birds on *Campylobacter* epidemiology, it is essential to take into account the ecology of each bird species, i.e., its feeding habits, habitat preferences, migration patterns, life span, etc. Moreover, if prevalence changes along a temporal scale, that is, between different life stages like breeding, migration, molting, and wintering, comparisons of prevalence rates between studies can be misleading. Hence, it is of great importance to take ecological factors into consideration when investigating the potential role of wild birds as reservoirs and vectors of *Campylobacter* spp.

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