The Trans-Atlantic Movement of the Spirochete *Borrelia garinii*

THE ROLE OF TICKS AND THEIR SEABIRD HOSTS

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Abstract. The spirochete *Borrelia garinii*, one of three genospecies of *B. burgdorferi* sensu lato (*B. burgdorferi* s.l.) that can cause Lyme disease in humans, has recently been isolated from seabirds from a colony in Newfoundland, Canada. Previous records of *B. garinii* in seabirds suggest that it has been endemic in seabird colonies in the greater North Atlantic since at least the early 1990s. We determined the prevalence of *B. garinii* in different seabird hosts from colonies in the northwest Atlantic. We recorded *B. garinii* from Gannet Islands, Labrador, and Gull Island, Newfoundland, Canada, in Atlantic Puffins (*Freiricia arctica*), Herring Gulls (*Larus argentatus*), Common Murres (*Uria aalge*), and Razorbills (*Alca torda*). Prevalence of infections varied between years and within and among species. Ticks from Atlantic Puffins had a prevalence ranging from 10.3 to 36.4%, although the highest prevalence was noted in Herring Gulls (37.5%) in 2005. Earlier studies from the same localities failed to find evidence of *B. garinii*, suggesting a recent arrival of the spirochete into the northwest Atlantic. *B. garinii* is closely related to European strains of the spirochete, and its likely source is from areas of endemicity in the Bothnian Gulf and the northeast Atlantic seabird colonies where seabirds, songbirds, and two different tick species come in close proximity. Phylogenetic studies suggest a gradual movement of the European strains into seabird colonies in the northeast Atlantic with subsequent spread into the North and northwest Atlantic colonies. Atlantic Puffins seem to be suitable reservoirs, although other abundant species such as Common Murres and Thick-billed Murres (*Uria lomvia*) may be involved in *B. garinii* dynamics. Further work is urgently needed to help document the ecology and spread of this spirochete of importance to human health.


El Movimiento Tras-Atlántico de la Espiroqueta *Borrelia garinii*: El Papel de las Garrapatas y las Aves Marinhas Como sus Hospederos

Resumen. La espiroqueta *Borrelia garinii*, una de las tres especies de *B. burgdorferi* sensu lato (*B. burgdorferi* s.l.) que causan la enfermedad de Lyme o borreliosis en humanos, ha sido recientemente aislada de aves marinhas de una colonia en Newfoundland, Canada. Los registros previos de *B. garinii* en aves marinhas sugieren que dicho parasito ha sido endémico en las colonias de aves marinhas en el gran Atlántico Norte desde, al menos, principios de los 1990s. Determinamos...

la prevalencia de *B. garinii* en diferentes aves marinhas en colonias del noroeste del Atlántico. Registramos *B. garinii*, en las Islas Gannet, Labrador y Gull, pertenecientes a Newfoundland, Canada, infectando frailecillos comunes (*Fratrica arctica*), gaviotas argénteas (*Larus argentatus*), araos comunes (*Uria aalge*) y alacas comunes (*Alca torda*). La prevalencia de infección varió entre años, entre especies y dentro de cada especie. Las Garrapatas que parasitaron a los frailecillos comunes tuvieron una prevalencia de 10.3–36.4%, aunque la prevalencia más alta fue registrada en gaviotas argénteas (37.5%) en 2005. Estudios previos realizados en las mismas localidades no encontraron evidencia de *B. garinii*, lo que sugiere una llegada reciente de la espiroqueta en el Atlántico Noroeste. *B. garinii* está cercanamente relacionada con cepas Europeas de la espiroqueta y su fuente de procedencia es posiblemente las áreas del Golfo de Bothnian y las colonias de aves marinhas del Atlántico Noreste, en donde las aves marinhas, las aves canorahs y dos especies de garrapatas están muy cercanas unas a otras. Los estudios filogenéticos sugieren un movimiento gradual de las cepas Europeas hacia las colonias de aves marinhas en el Atlántico Noreste, con una expansión subsecuente hacia las colonias del Atlántico Norte y Noroeste. Los frailecillos comunes parecen ser reservorios efectivos de la enfermedad, aunque otras especies abundantes, tales como el Arao común y el Arao de Brunnich o pico ancho (*Uria lomvia*), pueden estar involucradas en la dinámica de *B. garinii*. Se necesitan estudios urgentes que ayuden a documentar la ecología y la expansión de esta espiroqueta que tiene importancia para la salud humana.

_**Palabras Clave:** Acari, aves marinhas, *Borrelia burgdorferi*, *Borrelia garinii*, expansión, garrapatas, islas océánicas, *Ixodes uriae*, roedores introducidos._

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*Borrelia burgdorferi* sensu lato (s.l.) is a spirochete (*Spirochaetes, Spirochaetaceae*) that causes Lyme borreliosis in North America and Eurasia (Burgdorfer et al. 1982, Peisman and Gern 2004). At least 12 genospecies are recognized within *B. burgdorferi* s.l. The transmission cycle of *B. burgdorferi* s.l. involves ticks of the genus *Ixodes* (Acarí: Ixodidae) and various mammalian or avian hosts. *Borrelia afzelii*, *B. garinii*, and *B. burgdorferi* sensu stricto are the only genotypes known to cause Lyme disease in humans, and the extent of the disease varies when caused by different strains within each genospecies (Kurtenbach et al. 2002, Lagal et al. 2003, Peisman and Gern 2004). *Borrelia garinii* strains usually circulate in cycles involving birds and rodents.

The dominant genospecies in North America is *B. burgdorferi* sensu stricto (s.s.), and although it primarily circulates in ticks and mammals (Rand et al. 2003, Peisman and Gern 2004), the spirochete is also abundant in a range of passerine songbirds (Anderson et al. 1986, Weisbrod and Johnson 1989, Magnarelli et al. 1992, McLean et al. 1993, Smith et al. 1996, Durden et al. 1997). The prevalence of *B. burgdorferi* s.s. and the ability of passerines to disperse infected larval and nymphal *Ixodes scapularis* ticks suggests that migratory passerines serve as reservoirs and are involved in the movement and expansion of Lyme disease spirochetes in North America (Lane 1991, Smith et al. 1996, Durden et al. 1997, Rand et al. 1998).

Seabirds spend most of their life in the open ocean, generally nesting in coastal cliffs or offshore islands without mammalian predators to breed over periods of 2–6 mo. After chicks are reared, they return to a pelagic existence until the next breeding season. Seabird colonies in tropical latitudes may be infested by many species of soft ticks (e.g., *Ornithodoros capensis*) as well as hard ticks (e.g., *Ixodes spp.*) (Clifford 1979, Duffy 1991). In northern temperate latitudes in both hemispheres, seabird colonies are infested by *Ixodes uriae*, a widespread and abundant tick species (Zumpt 1952, Eveleigh and Threlfall 1974, Clifford 1979).

Olsen et al. (1993) documented the presence of *B. garinii* from *I. uriae* ticks feeding on Razorbills (*Alca torda*) on the island of Bonden, Sweden. Additionally, the authors found infections from skin biopsies from the Razorbill, providing some of the first evidence of a Lyme disease cycle involving seabirds and *I. uriae* ticks. Since the island was rodent-free, these data also showed that seabirds could serve as competent reservoir hosts without the involvement of mammalian reservoirs. Subsequently, *I. uriae* ticks feeding on Atlantic Puffins (*Fratrica arctica*) on the Faeroe Islands, Black Guillemots (*Cepphus grylle*) in Iceland, and Fork-tailed Storm Petrels (*Oceanodroma*
furcata) in Alaska tested positive for *B. garinii* (Olsen et al. 1995, Gylfe et al. 1999). The presence of *B. garinii* in the Southern Hemisphere in King Penguins (*Aptenodytes patagonicus*) and Black-browed Albatrosses (*Diomedea melanophris*) from Campbell Island off New Zealand as well as the Falkland Islands testified to its widespread occurrence in both the hemispheres (Olsen et al. 1995, Gauthier-Clerc et al. 1999).

Many important seabird colonies sustaining globally significant populations occur in the northwest Atlantic (Lock et al. 1994, Gaston and Jones 1998). Recently, the presence of *B. garinii* was recorded from *I. uriae* ticks on Gull Island, Newfoundland, Canada, constituting the first record of this spirochete from a colony in the northwest Atlantic (Smith et al. 2006). Since dispersal and wintering movements of immature and adult seabirds from the North Atlantic (Lock et al. 1994, Gaston and Jones 1998, Huettmann and Diamond 2000) overlap with some of the seabird colonies with recorded *B. garinii* infestations (Olsen et al. 1995, Bunikis et al. 1996), we hypothesized that infections of *B. garinii* were more widespread and present in more seabird species. Additionally, since *B. garinii* is widespread and identical strains occur in both hemispheres, we reviewed the evidence on the phylogeny and ecology of *B. garinii* strains from seabirds to attempt to explain the current distribution of this spirochete among seabirds.

The objectives of this study were (1) to determine the prevalence of *B. garinii* in selected seabird colonies of Newfoundland and Labrador and (2) to review the potential of seabirds and the associated tick species *Ixodes uriae* in the dispersal of *B. garinii* over short and long distances.

**MATERIALS AND METHODS**

**Study Area**

Ticks were collected alive from the Gannet Islands, Labrador, in 2005 and 2006; Cape St. Mary’s Seabird Sanctuary in 2006; and Gull Island, Newfoundland in 2004, 2005, and 2006. The Gannet Islands Ecological Reserve consists of a group of small islands about 29 km off the coast of Cartwright, southern Labrador (54°00’N, 56°30’W). A cluster of six islands is referred to individually as Gannet Clusters 1 through 6 (GC1–6) (Lock et al. 1994). Five islands (GC1–5) are located within 500 m of one another, with GC6, the largest of the cluster, located 1.5 km west of the GC1. Highest seabird densities occur during the summer breeding season on GC1–4 and Outer Gannet. The Gannet Islands collectively host over 39,300 breeding pairs of Atlantic Puffins, 10,000 breeding pairs of Razorbills, over 1,270 breeding pairs of Thick-billed Murres (*Uria lomvia*), and over 47,000 breeding pairs of Common Murres (*U. aalge*). The deer mouse (*Peromyscus maniculatus*) is abundant on most of the Gannet Islands. Cape St. Mary’s Ecological Reserve is one of six ecological reserves of Newfoundland and Labrador. It is located about 200 km southwest of St. John’s on the southwestern tip of the Avalon Peninsula (46°50’N, 54°12’W). About 24,000 Northern Gannets (*Morus bassanus*), 20,000 Black-legged Kittiwakes (*Rissa tridactyla*), 20,000 Common Murres, and 2,000 Thick-billed Murres live within the reserve during the breeding season. Land mammals such as the short-tailed weasel (*Mustela erminea*) and the meadow vole (*Microtus pennsylvanicus*) have access to the colony, which is partly on the mainland.

Gull Island (47°15’N, 52°46’W) is located in southeastern Newfoundland, Canada. It is one of four islands in the Witless Bay Ecological Reserve and is about 5 km southeast of the town of Witless Bay (Robertson et al. 2004). Gull Island hosts diverse seabird breeding colonies including 350,000 breeding pairs of Leach’s Storm-Petrels (*Oceanodroma leucorhoa*), 1,600 pairs of Common Murres, 285 breeding pairs of Razorbills, and 4,300 breeding pairs of Black-legged Kittiwakes (Robertson et al. 2004), over 2,600 breeding pairs of Herring Gulls (*Larus argentatus*), and 88 breeding pairs of Great Black-backed Gulls (*L. marinus*; Robertson et al. 2004). Gull Island has the largest North American colony of Atlantic Puffins, estimated at about 140,000 breeding pairs (Robertson et al. 2004). Land mammals are absent from the colony, although there have been periodic reports of one or two minks (*Mustela vison*) that did not survive the winter.

**Laboratory Methods**

A total of over 1,500 ticks were shipped alive to the Vector-Borne Disease Laboratory, Maine Medical Center, during the years 2005 and 2006. The following analyses, described briefly here, were conducted at the Maine Medical Center. A subset of ticks was dissected and midguts were screened for the presence of spirochetes by fluorescent microscopy using a polyclonal anti-borrelial antibody.
DNA was extracted from positive ticks using the Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA). DNA amplification was performed in a designated room using genus-specific primers that include the partial sequence of rrs-rrlA intergenic spacer region, as described by Bunikis et al. (2004) with use of negative controls. Amplification products were visualized on a 1% agarose gel containing 0.5 µg/ml ethidium bromide. At a second laboratory, ticks positive by fluorescent antibody screen were prepared as above for DNA extraction, and PCR was performed using primers directed at the 16s ribosomal DNA. Sequences of amplicons obtained at both laboratories were confirmed to be *B. garinii*.

**RESULTS**

A total of 181 ticks (from all sites) was tested for *B. garinii*, of which a total of 23 ticks (nymphs and females) from Gull Island and the Gannet Islands tested positive (Table 2.1). Specimens from the Gannet Islands in 2005 and Gull Island in 2004 could not be tested since they were dead on arrival at the Maine Medical Center. The prevalence of *B. garinii* differed between both seabird species and years (Table 2.1). Higher prevalence was observed in female ticks than in nymphs in 2005, although

**TABLE 2.1**

*Prevalence of Borrelia garinii among Ixodes uriae ticks tested from different localities in the northwestern North Atlantic.*

<table>
<thead>
<tr>
<th>Year</th>
<th>Locality</th>
<th>Source</th>
<th>Life stage</th>
<th>Number tested</th>
<th>Number infected</th>
<th>Prevalence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>Gull Island</td>
<td>Atlantic Puffin</td>
<td>Nymph</td>
<td>6</td>
<td>1</td>
<td>16.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>11</td>
<td>4</td>
<td>36.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Herring Gull (chick)</td>
<td>Female</td>
<td>8</td>
<td>3</td>
<td>37.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Soil in puffin habitat</td>
<td>Nymph</td>
<td>18</td>
<td>1</td>
<td>5.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>6</td>
<td>1</td>
<td>16.7</td>
</tr>
<tr>
<td>2005 totals</td>
<td></td>
<td></td>
<td></td>
<td>49</td>
<td>10</td>
<td>20.4</td>
</tr>
<tr>
<td>2006</td>
<td>Gull Island</td>
<td>Atlantic Puffin</td>
<td>Larva</td>
<td>2</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Nymph</td>
<td>3</td>
<td>0</td>
<td>0.0</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>29</td>
<td>3</td>
<td>10.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Atlantic Puffin (chick)</td>
<td>Female</td>
<td>7</td>
<td>2</td>
<td>28.6</td>
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<td></td>
<td></td>
<td>Black-legged Kittiwake (chick)</td>
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<td>6</td>
<td>0</td>
<td>0.0</td>
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<tr>
<td></td>
<td></td>
<td>Soil in puffin habitat</td>
<td>Larva</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Nymph</td>
<td>34</td>
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<td></td>
<td></td>
<td>Female</td>
<td>4</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Gannet Islands</td>
<td>Common Murre</td>
<td>Female</td>
<td>11</td>
<td>2</td>
<td>18.2</td>
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<td>Common Murre</td>
<td>Female</td>
<td>14</td>
<td>2</td>
<td>14.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Razorbill (chick)</td>
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<td>12</td>
<td>3</td>
<td>25.0</td>
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<td>Soil in puffin habitat</td>
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<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>8</td>
<td>1</td>
<td>12.5</td>
</tr>
<tr>
<td>2006 totals</td>
<td></td>
<td></td>
<td></td>
<td>132</td>
<td>13</td>
<td>9.8</td>
</tr>
<tr>
<td>Grand totals</td>
<td></td>
<td></td>
<td></td>
<td>181</td>
<td>23</td>
<td>12.7</td>
</tr>
</tbody>
</table>
the difference was not significant (Fisher's exact test, \( P = 0.074 \)). All nymphs tested in 2006 were negative. In general, ticks collected from Herring Gull chicks and Atlantic Puffin adults and chicks showed the greatest prevalence of *B. garinii*. The lowest prevalence of the spirochete was recorded from ticks collected from soil or litter samples. Overall prevalence (prevalence of infection among all ticks collected from all sources) was significantly higher in 2005 than in 2006 on Gull Island (Fisher's exact test, \( P = 0.028 \)). Comparisons of sections of the genome of the *B. garinii* isolates showed greater similarity to strains collected from the Faeroe Islands, Slovenia, and western Siberia than to the North American strains (data not shown).

**DISCUSSION**

This study provides insight on the prevalence of the recently recorded *B. garinii* in the northwest Atlantic (Smith et al. 2006). The prevalence of *B. garinii* varied between years and between and among seabird species. Atlantic Puffins had consistently high prevalence in both years, although Herring Gull chicks yielded the highest prevalence in 2005.

On both Gull Island and the Gannet Islands, Atlantic Puffins are abundant, occurring in the tens of thousands (Lock et al. 1994, Robertson et al. 2004). Burrowing habits of the species bring them into close association with *I. uriae* ticks. Additionally, on Gull Island, Herring Gulls nest alongside puffins on grassy slopes (Robertson et al. 2004), bringing this species in close association with ticks, especially in young gulls, which often hide from predators in puffin burrows (Muzaffar and Jones 2007). The higher prevalence of *B. garinii* on Gull Island in 2005 is concomitant with the higher abundance of ticks in that year, suggesting that increased abundance of ticks could lead to increased prevalence of *B. garinii* infections in seabirds (Muzaffar and Jones 2007). Muzaffar and Jones (2007) also noted differences in the feeding preference of nymphs and adult females of *I. uriae*, with nymphs feeding preferentially on puffin chicks and adult females feeding preferentially on adult puffins. Such differences in feeding activity could be crucial in the dynamics of *B. garinii* in seabirds.

Common and Thick-billed Murres are regarded as the preferred hosts of *I. uriae* ticks and finding *B. garinii* in ticks from Common Murres is not surprising (Clifford 1979). Similarly, Razorbills sometimes share nesting habitats with murres, making them suitable tick hosts and thereby candidates for infection by *B. garinii*. Further work is needed to determine the extent to which these species that were sampled opportunistically for ticks are involved in the ecology of *B. garinii*.

The first recorded incidence of *B. garinii* in seabirds on Bonden Island (12 km from the mainland, Olsen et al. 1993) and subsequently on Malgrundet in the Bothnian Gulf of the Baltic Sea likely originated in mainland Europe (Bunikis et al. 1996) (Fig. 2.1). The Bothnian

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**Figure 2.1.** Hypothesized movement of *Borrelia garinii* from Europe into seabird colonies in the North Atlantic. (a) Co-occurrence of *Ixodes ricinus* and *I. uriae* on seabird colonies in the Bothnian Gulf and nearby areas. Movement of *B. garinii* from terrestrial to seabird cycle. (b) Establishment of *B. garinii* in seabird colonies along the Northeast Atlantic. (c) Spread of *B. garinii* from endemic focus in Northeast Atlantic to Faeroe Islands and Iceland. (d) Movement of *B. garinii* from Iceland to colonies off the coast of Greenland and Newfoundland. (e) Low-level movement of *B. garinii* infections with birds moving across the Atlantic.
Gulf ecosystem hosts a number of seabird colonies that are close to the mainland and have overlapping populations of *I. uriae* and *I. ricinus* (Clifford 1979, Bunikis et al. 1996). Coastal sites within the Bothnian Gulf off Sweden and Finland, as well as Norway, Denmark, Germany, and the British Isles lining the North Sea, have similar overlapping distributions of these two tick species (Mehl and Traavik 1983, Jaenson et al. 1994). Sympatric distributions present a unique opportunity for *B. garinii* strains from passerines to come in close proximity with *I. uriae*, the vector of *B. garinii* strains in seabirds (Jaenson et al. 1994, Bunikis et al. 1996). Although the two tick species have different ecological niches, their overlapping distributions sometimes permit co-occurrence in similar habitats (Jaenson et al. 1994). Genetically related strains of *B. garinii* have been collected from both these tick species, suggesting a route for the transition from an *I. ricinus-* *B. garinii* cycle in terrestrial birds and mammals to an *I. uriae*-*B. garinii* cycle involving seabirds. Co-occurrence also suggests that strains of *B. garinii* in the Bothnian Gulf and in the North Atlantic colonies represent a northwestward range expansion of the mainland strains of *B. garinii*, to which they are closely related (Bunikis et al. 1996, Lagal et al. 2003).

Once *B. garinii* had adapted to the seabird transmission cycles involving *I. uriae*, it could then have become established in seabird colonies along the northeast Atlantic colonies through dispersal movements of infected birds between colonies. Establishment could also be facilitated by dispersive movements of *I. uriae* ticks on prospecting fledglings of seabirds, which has been documented in Black-legged Kittiwakes (Danchin 1992, Boulainier and Danchin 1996, McCoy et al. 1999, Boulainier et al. 2001). Subsequently, movements over greater distances could have resulted in the spread of *B. garinii* in the Faeroes and colonies around Iceland (Gylfe et al. 1999). Thick-billed Murres banded in Spitsbergen, for instance, have been recovered from southwest Greenland and Newfoundland (Gaston and Hipfner 2000). Similarly, Razorbills banded as chicks in a colony in Scotland have been found nesting in the Gannet Islands, Labrador (Lavers 2007). With new pockets of endemicity in the eastern North Atlantic, long-dispersal movements of seabirds could then have facilitated the spread of *B. garinii* to colonies in the northwest Atlantic.

Smith et al. (2006) collected ticks from six sites in the northwest Atlantic: Machias Seal Island, Matinicus Rock, Petit Manan Island, and Seal Island in Maine; and Gannet Islands, Labrador, and Gull Island, Newfoundland, in Canada. None of these sites had yielded any evidence of *Borrelia* infections until 2005 on Gull Island (Smith et al. 2006) and 2006 from the Gannet Islands and Gull Island. Previous studies of ticks from a variety of seabirds in the northwest Atlantic colonies, including the Gannet Islands, had failed to find any evidence of *B. garinii* (Gylfe et al. 1999). Tick specimens have been collected earlier and tested for Lyme disease from colonies around Newfoundland (Cape St. Mary’s and Gull Island; Whitney 2001) but have never yielded *B. garinii* (Whitney 2001, Bennett 2005). Bennett (2005) sampled 91 *I. uriae* in 2003–2004 from Gull Island, Newfoundland, but these did not yield any evidence of the spirochete.

*Borrelia garinii* is present in seabird colonies in the North Atlantic. The likely source of infection is from areas of endemicity in the Bothnian Gulf and the northeast Atlantic seabird colonies, where seabirds, songbirds, and two different tick species are in close proximity. Phylogenetic studies suggest a gradual movement of the European strains into seabird colonies in the North Atlantic and then to the northwest Atlantic. Limited information exists on the distribution and movement of *B. garinii* in seabirds. Further studies are urgently needed to help understand patterns of spread and endemicism of this spirochete of human health significance. The Gannet Islands colony harbors populations of deer mice that could become adapted to *B. garinii*, and their involvement in the seabird-*Borrelia* cycle needs to be determined. Although *B. garinii* has not yet been documented from Cape St. Mary’s, the presence of *I. uriae* ticks and several seabird species in this colony on mainland Newfoundland warrants more detailed examination of this site for this spirochete.

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LITERATURE CITED


