

ACTIVITY PERIODS AND QUESTING BEHAVIOR OF THE SEABIRD TICK *IXODES URIAE* (ACARI: IXODIDAE) ON GULL ISLAND, NEWFOUNDLAND: THE ROLE OF PUFFIN CHICKS

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ABSTRACT: Questing behavior of *Ixodes uriae* and their associated seasonal, host-feeding patterns are crucial to our understanding of tick life history strategies and the ecology of diseases that they transmit. Consequently, we quantified questing behavior of nymphs and adult female *I. uriae* ticks at Gull Island, a seabird colony in Newfoundland, Canada, to examine seasonal variation of off-host and on-host tick activity. We sampled a total of 133 adult Atlantic puffins (*Fratercula arctica*), 152 puffin chicks, and 145 herring gull (*Larus argentatus*) chicks for ticks during the breeding seasons of 2004 and 2005. Questing ticks were sampled by dragging a white flannel cloth across the grassy breeding areas during the mo of May, June, July, and August. Nymph questing activity reached a peak during mid-July (79 and 110 individuals/hr in 2004 and 2005, respectively). The prevalence of nymphs and adult female ticks on different seabird hosts varied between years and during the seasons. Puffin chicks had the highest prevalence (above 70% in July) of nymphs in both years and this was correlated with questing activity. Female ticks rarely fed on puffin chicks, but were prevalent on adult puffins and gulls, although prevalence and questing of ticks were not correlated in these hosts. These patterns of off-host and on-host tick activity suggests that *I. uriae* ticks likely use a combination of questing and passive waiting, e.g., in puffin burrows, to detect hosts, depending on the tick stage and the host species.

Ticks are ubiquitous parasites of seabirds in most breeding colonies (Clifford, 1979). Parasite infestations and related disease transmission are regarded as important costs of colonial living (Alexander, 1974); however, evidence for a role for parasites in modulating seabird reproductive success remains scarce (Coulson, 2001). A few studies have documented costs such as retarded chick growth rates, nest desertion, and reproductive failure in some seabird species (Feare et al., 1967; Duffy, 1991; Morbey, 1996; Gauthier-Clerc et al., 1998; Bergstrom et al., 1999; Mangin et al., 2003). However, some studies were unable to find any relationship between tick infestations and reproductive success or survival (e.g., Barton, 1996; Gauthier-Clerc et al., 2003). *Ixodes uriae* (Acari: Ixodidae) is perhaps the most widespread seabird tick, with a circumpolar distribution on both hemispheres (Clifford, 1979). The length of its life cycle ranges from 2 yr in the southern hemisphere (Murray and Vestjens, 1967) to 8 yr in the northern hemisphere (Eveleigh and Threlfall, 1974; Steele et al., 1990; Barton et al., 1996). The species is a generalist, feeding on more than 50 seabird species, apparently having a preference for common murres (*Uria aalge*) in the northern hemisphere (Eveleigh and Threlfall, 1974). A similarly high prevalence on black-legged kittiwakes (*Rissa tridactyla*), which are ecologically and behaviorally different from murres, illustrates the flexibility of *I. uriae* in host preference and a dependence on host availability (e.g., Mehl and Traavik, 1983; Danchin, 1992; Barton, 1996; McCoy and Tirard, 2002). *Ixodes uriae* may even 'specialize' on kittiwakes within a colony, giving rise to genetically distinct local races (McCoy et al., 1999). The prevalence and abundance of *I. uriae* on seabirds varies with species and geographic locality, and interest has risen in recent years because of its involvement in the maintenance of *Borrelia garinii*, 1 of the 3 genospecies of the spirochete recognized as the causative agent of Lyme disease (Olsen et al., 1993, 1995; Muzaffar and Jones, 2004; Smith et al., 2006). Several viruses (such as orbiviruses, flaviviruses, and bunyaviruses) have been isolated from *I. uriae* (Main et al., 1973; Oprandy et al., 1988; reviewed by Muzaffar

and Jones, 2004) and the ticks play an important role in the persistence of these microbes in nature (Oprandy et al., 1988; Nunn et al. 2006a, 2006b).

Ixodes uriae has 3 active life stages, namely the larva, the nymph, and the sexually dimorphic adult stage (Eveleigh and Threlfall, 1974). There is a great deal of variation in the feeding preferences and timing of activity of the larvae, nymphs, and adults of *I. uriae* (Eveleigh and Threlfall, 1974; Barton et al., 1996). Each stage requires a blood meal from a suitable host, which it acquires over a period of 5–8 days to transform into the subsequent stage (Eveleigh and Threlfall, 1974; Finney et al., 1999). Adult males do not feed, but the females require a blood meal to successfully lay eggs. In the northern temperate latitudes, each life stage is believed to feed only once a year, because the short duration of summer and availability of seabird hosts restrict the tick activity periods to about 2 mo and the slow development rates prevent molting into the subsequent stages. Seasonal variation in the activity periods of different life stages and the availability of suitable seabird hosts together determine the successful completion of the life cycle. Questing behavior (the active search by ticks for a host) of ixodid ticks is crucial to locating a host and acquiring a blood meal. Because *I. uriae* is regarded as a nidicolous species, living in cracks in the rocks near nesting areas or in and around burrows of seabirds, questing behavior has not been quantified in most previous studies (e.g., Eveleigh and Threlfall, 1974; Steele et al., 1990; Barton, 1996; Barton et al., 1996) although it has been observed and reported in some studies (e.g., Mehl and Traavik, 1983). Questing behavior of different tick stages is integral to understanding and modeling population dynamics of ticks. Questing behavior has been quantified in many nonnidicolous species (Rand et al., 2003; Ogden et al., 2005), but in relatively few nidicolous species (Sonenshine, 1991). Comparisons of on-host and off-host abundance of ticks are also paramount to determining the risk of tick-borne diseases (LoGiudice et al., 2003; Ogden et al., 2005). To this end, we initiated a study of behavior of *I. uriae* ticks at this major seabird colony in Newfoundland. The primary objectives of our study were to (1) quantify seasonal patterns of questing behavior of nymphs and adults, (2) quantify the infestation levels of nymphs and adults

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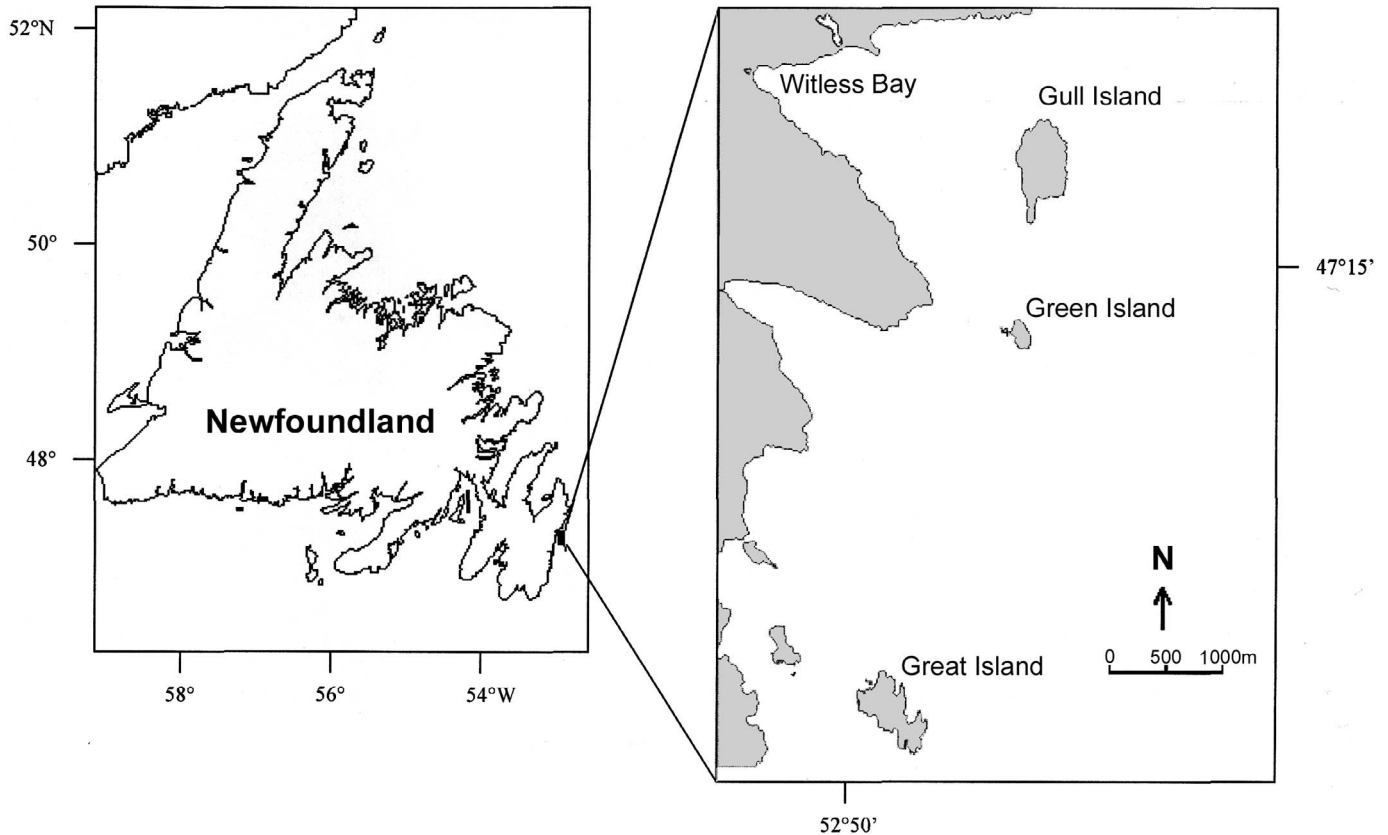


FIGURE 1. Map of Newfoundland showing the location of Gull Island.

on readily available seabird hosts, and (3) to assess the relative roles of different seabird species and ages (adults vs. chicks) in hosting different life stages of the tick.

MATERIALS AND METHODS

Study area

This study was conducted at Gull Island (47°15'N, 52°46'W) located in southeastern Newfoundland, Canada (Fig. 1). Gull Island is 1 of 4 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 is 1.6 × 0.8 km in size and is forested, with balsam fir and black spruce being the dominant tree species. The periphery of the island is either grassy or rocky slopes. Narrow ledges and vertical cliffs surround most of the island, with particularly steep cliffs (maximum 69 m) occurring along the northeastern edge of the island. Gull Island hosts diverse seabird breeding colonies including Leach's storm petrels (*Oceanodroma leucorhoa*) in most of the forested and forest-edge areas, with most recent population estimate being 350,000 breeding pairs (Stenhouse et al., 2000); about 1,600 pairs of common murre (restricted to cliff ledges); 4,300 pairs of black-legged kittiwakes (Robertson et al., 2004), more than 2,600 breeding pairs of herring gulls (*Larus argentatus*), and 88 pairs of great black-backed gulls (*Larus marinus*) (Robertson et al., 2001). Gull Island has the largest North American colony of Atlantic puffins (*Fratercula arctica*), estimated at about 140,000 breeding pairs (Robertson et al., 2004), occurring on the gently sloping grassy habitat. Small numbers of razorbills (*Alca torda*) (about 300 pairs), northern fulmars (*Fulmarus glacialis*) (about 6 pairs), and northern ravens (*Corvus corax*) (several pairs) also occur on the island.

Bird species and quantification of on-host ticks

We sampled a total of 133 adult Atlantic puffins, 152 Atlantic puffin chicks, and 145 herring gull chicks during the breeding seasons of 2004

and 2005. Adult puffins were captured mostly using a large dip-net held in the flight path of birds. Chicks of both species were collected by hand from their breeding sites. Each bird was held briefly in a cotton bag, weighed, and measured, and then searched for ticks using palpation (Danchin, 1992), whereby the entire body surface was gently felt to sense the presence of biting ticks. This method was originally found to be very useful in assessing tick loads on black-legged kittiwake chicks (Danchin, 1992), and was deemed suitable for the assessment of Atlantic puffin chicks. We recognize that the method may underestimate the number of ticks in adult birds, and that this measure would only provide an index of abundance rather than a total count of ticks (Choe and Kim, 1987). Initially, palpation of adult Atlantic puffins showed that ticks could still be collected using a pair of forceps and gently pulling at the base of the hypostome of the feeding tick. Dislodged ticks that inadvertently detached and remained in the bird bag were also retained. Ticks were visually categorized as either nymph or adult female, based on size. Larvae, which are significantly smaller than nymphs, were not included in the analysis because of the difficulty of detecting most individuals on the bodies of live birds.

Quantification of questing tick abundance and behavior

Questing ticks were collected using a 1-m² white flannel flag (adapted from Falco and Fish, 1992) that was dragged along the puffin slopes between 1000 and 1300 hr between 1–8 times every 2 wk during the months of May, June, July, and August in 2004 and 2005. We attempted to collect at least 3 flags worth of samples per week to ensure that the peaks in questing activity were reflected in our samples (Daniels et al., 2000). We were unable to flag for ticks at this rate for the entire sampling period because of periodic bad weather; we attempted to sample at least once a week during these periods. We believe that this did not significantly change our estimates of questing activity because most of the bad weather occurred early or late in the season when tick activity was at a minimum. The number of nymphs and adult females were counted and removed from the flag using forceps and placed in vials

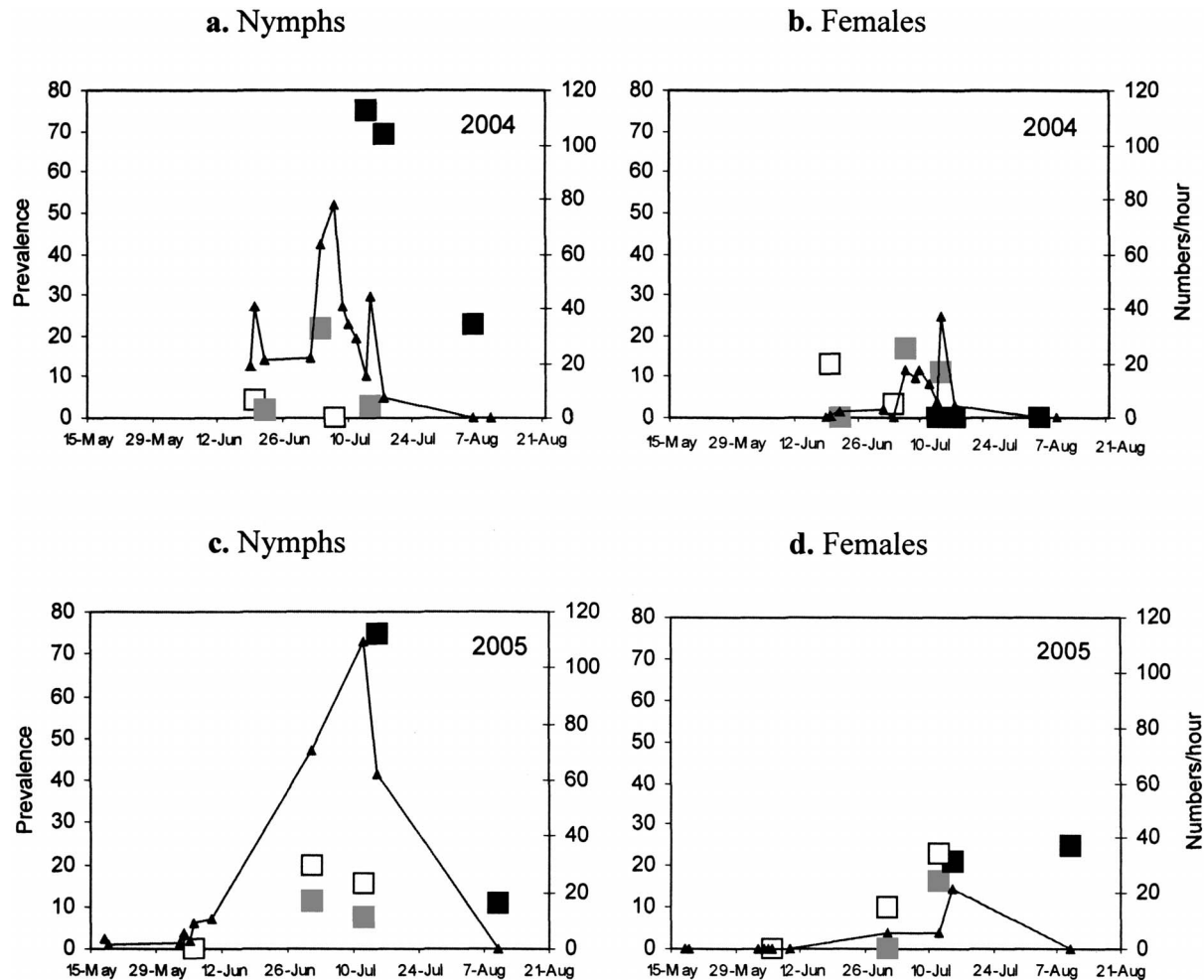


FIGURE 2. Variation in the abundance of (a) questing nymphs (2004), (b) questing females (2004), (c) questing nymphs (2005), and (d) questing females (2005) of *Ixodes uriae* in relation to their proportion on different hosts. (Herring gull chicks = grey squares; Atlantic puffin adults = white squares; Atlantic puffin chicks = black squares).

for identification. The flag was dragged between 30–120 min, with an interval of 30 sec between tick checks. The frequency of tick occurrence was indexed quantitatively as the number of nymphs and adult females captured per hour of dragging (Falco and Fish, 1992; Rand et al., 2003). The relative seasonal abundance of questing ticks was then presented as the mean number of ticks captured per hour.

Statistical analyses

We used Quantitative Parasitology 2.0 software, specifically developed to account for aggregated parasite distributions and allow distribution-free statistical tests to compare parasite loads (Reiczigel and Rózsa, 2001). We quantified mean intensity (mean number of ticks per infected host), prevalence (proportion of hosts that were infected) and median intensity (most commonly occurring abundance of ticks per host) because no single measure of parasite 'load' is appropriate and a combination is recommended (Rózsa et al., 2000). Confidence intervals (at 95% confidence level) for mean intensities were computed using bootstrap techniques with 2,000 replications (Rózsa et al., 2000). Exact confidence intervals (at 95% confidence level) were calculated for prevalence using the Clopper–Pearson method. Confidence intervals for median intensities were also calculated, with the exact confidence level being reported, rather than the desired level, because of the discrete nature of the data (Rózsa et al., 2000). Mean intensities of different hosts were compared using bootstrap *t*-tests, with *P* values generated from 2,000 replications (Rózsa et al., 2000). Prevalence of ticks on different hosts was compared using Fisher's exact test, with the exact

P value reported whenever possible. Median intensities were compared using Mood's median test. A α level of 0.05 was used to determine significance in each case. Spearman's rank correlation (2-tailed) was used to examine associations between on-host and questing ticks.

RESULTS

Questing activity

The questing of ticks in search of suitable hosts varied between the 2 yr of our study (Fig 2). First activity of tick nymphs was noted on 19 June 2004 compared to 18 May 2005 (Fig. 2a, c). Nymph activity reached a peak (79 and 110 individuals/hr in 2004 and 2005, respectively) at around mid-July in both years, although peaks of smaller magnitude occurred before and after the highest peak in 2004. Female ticks quested later in the season, compared to nymphs, starting at around late June and early July (Fig. 2b, d). Questing females did not reach the massive peaks observed in nymphs, with 12 and 21 individuals/hr captured in 2004 and 2005, respectively. Questing of both nymphs and females ended by early August in both years.

TABLE I. Variation in the prevalence, mean intensity, and median intensity of *Ixodes uriae* nymphs and adult females on seabird hosts. C.I. indicates confidence interval. N.D. indicates confidence intervals that could not be computed because of low numbers of ticks. Values in parentheses indicate the exact confidence, in percentage, of the confidence interval of median intensity.

Nymphs	2004			2005		
	Puffin (adult)	Puffin (chick)	Gull (chick)	Puffin (adult)	Puffin (chick)	Gull (chick)
n	55	42	87	43	56	58
Prevalence (%)	1.8*	57.1†	12.6‡	23.3	30.4	8.6‡
C.I.	0.09–9.72	40.96–72.28	6.48–21.50	11.75–38.64	18.77–44.10	2.85–18.99
Intensity (no./infected host)	1	3	3.91	2.1	2.41	1.8
C.I.	N.D.	2.21–4.29	1.91–7.64	1.30–3.10	1.47–3.94	1.00–3.00
Median (no./infected host)	1	2	2	1.5	2	1
C.I.	N.D.	1–4 (99.7%)	1–6 (96.7%)	1–4 (98.8%)	1–2 (99.3%)	1–4 (93.8%)
Females						
n	55	42	87	43	56	58
Prevalence (%)	7.3*	0	13.4	34.9	8.9	15.5
C.I.	2.01–17.59	0	7.33–22.86	21.00–50.93	2.96–19.62	7.34–27.43
Intensity (no./infected host)	2.25	0	1.42	1.8	1.4	1.78
C.I.	1.00–2.75	0	1.08–1.83	1.27–2.80	1.00–1.60	1.22–2.89
Median (no./infected host)	2.5	0	1	1	1	1
C.I.	N.D.	0	1–2 (99.7%)	1–2(98.2%)	1–2 (93.8%)	1–2 (97.9%)

* Significantly different from adult puffins in 2005.

† Significantly different from adult puffins in same year.

‡ Significantly different from puffin chicks in same year.

On-host ticks and questing

Nymphs and females feeding on hosts varied with time of year and between species (Fig. 2). Mean intensity, median intensity, and prevalence of nymphs and female ticks, pooled over the entire field season, showed distinct patterns across host species and host age (Table I). Mean intensity and median intensity of nymphs and ticks did not vary statistically in any of the 3 host types ($P \ll 0.05$ in all cases of bootstrap t -tests and Mood's median tests; Table I). Nymphs were seen to feed opportunistically on adult puffins and herring gull chicks during the early part of July (in both years) although this did not necessarily relate to tick questing (e.g., Fig. 2c). The prevalence of nymphs did not vary significantly on herring gull chicks between the 2 yr (Fisher's exact test, $P = 0.591$; Fig. 1a, c; Table I). Nymph prevalence on herring gull chicks was significantly correlated with questing activity (Spearman's rank correlation, $P < 0.01$ in both years). The prevalence of female ticks on herring gull chicks was also low, but was not significantly correlated with questing activity ($P \gg 0.05$ in both years).

The prevalence of nymphs on adult puffins was significantly lower in 2004 (Fisher's exact test, $P = 0.001$; Fig. 2a, c), whereas intensity and median abundance did not vary (Table I). Adult puffins had a higher prevalence of female ticks in both years, but prevalence was significantly correlated with questing activity only in 2005 (Fig. 2c, d; Spearman's rank correlation, $P < 0.01$). Similarly, increased abundance of questing nymphs was related to a significantly higher prevalence of nymphs on adult puffins only in 2005 (Spearman's rank correlation, $P < 0.01$), but not in 2004 (Table I; Fig. 2c; Spearman's rank correlation, $P \gg 0.05$).

Puffin chicks showed the highest prevalence of nymphs in both years and this was well synchronized with the peak questing activity of nymphs (Fig. 1a, c; Table I; Spearman's rank correlation, $P < 0.01$ in both years). The prevalence of nymphs

on puffin chicks did not vary between the years (Fisher's exact test, $P < 0.05$; Table I). Female ticks were not found on puffin chicks in 2004 and occurred in low prevalence (compared to nymphs) in 2005, although this was not correlated with questing (Spearman's rank correlation, $P \gg 0.05$). Prevalence of nymphs over the entire season was significantly higher in puffin chicks compared to adults in 2004 and herring gull chicks in both years (Table I).

DISCUSSION

The preferred host of *I. uriae* is considered to be the common murre, although the tick species thrives on colonies of seabirds even when murre are absent (Eveleigh and Threlfall, 1974; Morbey, 1996; Muzaffar and Jones, 2004). Gull Island harbors substantially larger populations of both breeding Atlantic puffins and herring gulls compared to common murre; however, ticks were extremely abundant on grassy slopes occupied by breeding puffins and gulls, and both of these seabird species were utilized extensively as hosts.

Questing or host-seeking activity is an important aspect of tick biology and is crucial to our understanding of the epidemiology of tick-borne diseases (Rand et al., 2003; Ogden et al., 2005). Olfactory, thermal, tactile, and visual cues may all serve as stimuli for ticks to assist in seeking out and feeding on suitable hosts (Sonenshine, 1991). Questing strategies are broadly categorized as either 'active' or 'passive' and many tick species may use a combination of both strategies to find hosts (Balashov, 1972; Sonenshine, 1991). Some nonnidicolous tick species climb onto vegetation and wait to grab onto passing hosts. Other species use the hunter technique whereby they actively crawl and run towards their hosts. Nidicolous species use cues that are similar to those used by nonnidicolous species, although the behavior and the extent to which they respond to such cues (or their combinations) vary among species (Sonenshine, 1991).

The exact questing strategy varies between species and in many cases between the different stages within a species (Sonenshine, 1991). Ticks that actively quest for hosts go through periods of questing followed by inactivity (quiescence), which varies on a daily as well as a seasonal basis (Burkot et al., 2001; Bown et al., 2003; Perret et al., 2003).

Eveleigh and Threlfall (1974) established the life cycle of *I. uriae* and quantified the abundance of larvae, nymphs, and adults in soil samples from Gull Island, Newfoundland. They measured the increase in the abundance of different tick stages from soil samples and equated this to 'activity,' although this did not differentiate between questing and inactive ticks in soil samples. Patterns of abundance were characterized by a marked peak of larvae and nymphs in early July, whereas adult males and females were generally lower in abundance relative to nymphs and larvae, and were most abundant late in the season (August) (Eveleigh and Threlfall, 1974). Barton (1996) reported earlier activity of *I. uriae* on the Isle of May (Scotland). He collected soil samples on a monthly basis over 2 yr and used the proportion of engorged ticks in a sample as an indication of activity. Ticks of all stages were found to be most active in the months of May and June. Our observed seasonal patterns of abundance of questing nymphs and adult females were similar to the patterns of abundance observed by Eveleigh and Threlfall (1974). In both years, nymph questing activity peaked around mid-July, although the magnitude of the peaks was different in each year. Additionally, in 2004, there were peaks earlier and later in the season that were of lower magnitude. Such changes in tick activity patterns were likely weather-driven, with fewer ticks being active in wet or cold conditions (Muzaffar, 2003–2006, pers. obs.). In nonnidicolous species, the influence of environmental factors on feeding and host-seeking activities has been determined in many tick species. Harlan and Foster (1990) showed that questing activity (determined by drag sampling) of *Dermacentor variabilis* was significantly affected by ambient temperature, and to a lesser extent, by relative humidity and vapor pressure. The variation in questing activity patterns in *Ixodes scapularis* and *Amblyomma americanum* were related to temperature and relative humidity, the former species being most active under conditions of low temperature and high relative humidity whereas the reverse was true for the latter species (Schulze et al., 2001). Species such as *Ixodes persulcatus* and *Ixodes ricinus* were more active under conditions of optimal temperature and relative humidity ranges characteristic of each species (Balashov, 1972). In nidicolous species such as *Ixodes trianguliceps*, temperature and other environmental factors influence the development of stages rather than questing (Randolph, 1975).

Ixodes uriae ticks do not quest by climbing on to vegetation as do many other *Ixodes* species (Balashov, 1972; Eveleigh and Threlfall, 1974); many seabird colonies have limited vegetation, which limits such a strategy (Barton, 1996; Eveleigh and Threlfall, 1974). Visual cues could be a factor because the puffin slopes were typically covered in puffins on some days and herring gulls had a great deal of activity on and around their nest sites. Most hard ticks, including species of eyeless *Ixodes*, have photoreceptors that aid in responding to shades of light (Sonenshine, 1991; Fourie et al., 1993). *Ixodes rubicundus* ticks respond to variations in shadowing more than to carbon dioxide or host odors (Fourie et al., 1993), although the latter 2 cues

are also very important (Balashov, 1972). *Ixodes ricinus* ticks use the onset of darkness as a cue to initiate questing, but olfactory cues (such as carbon dioxide gradients) are more important in host detection (Balashov, 1972; Perret et al., 2003). The relative importance of different cues that aid in host detection remains unclear in *I. uriae* and laboratory experiments are required to illuminate these behavioral attributes.

Ixodes uriae ticks exhibited differential host preference. The prevalence of both nymphs and female ticks on herring gulls in relation to questing activity suggested no preference for this species as a host for the tick. Prevalence patterns of female ticks on adult puffins, in contrast, suggested that the ticks were likely preferentially feeding on adult puffins during the early part of the season, when the birds were still incubating their eggs. Because there was no clear relationship between questing activity of female ticks and prevalence on adult puffins (significant in 2004 but not 2005), it would seem likely that the feeding was taking place without aggressive questing, i.e., ticks were passively waiting in burrows. Nymphs, however, did not feed preferentially on adult puffins because large numbers of questing nymphs in 2004 did not result in high prevalence on adult puffins.

Prevalence of nymphs on puffin chicks suggested a preference for these hosts. Eveleigh and Threlfall (1975) sampled 15 puffin chicks and stated that puffin chicks were not important in the life cycle of *I. uriae* because very few ticks were found on these chicks. Puffins are highly variable in the timing of hatching and we suggest that their chicks are important particularly when both nymphs and puffin chick abundance were synchronized. High prevalence of nymphs on puffin chicks indicated that other cues (such as olfactory) were likely responsible for helping nymphs detect, approach, and attach to these hosts in their natal burrows. The correlation between questing activity and prevalence on puffin chicks also suggested that the nymphs were using a more aggressive mode of questing.

Clearly, a great deal of variation exists in the ecology and behavior of *I. uriae* ticks throughout their range. The role of ticks in various aspects of host ecology and the maintenance of diseases in seabird colonies remain unknown. Our study shows that questing behavior varies between nymph and adult female stages of *I. uriae*, thereby making different host species susceptible to infestations during different times of the breeding season. Additionally, different stages feed preferentially on different hosts. This particular aspect is of great ecological and epidemiological significance because the nymphs of other *Ixodes* species, e.g., *I. scapularis*, are very important as reservoirs of *Borrelia burgdorferi*, and feeding behavior of nymphs are critical in the perpetuation this pathogen. The recent documentation of the presence of *Borrelia garinii* from ticks from puffins in Gull Island (Smith et al., 2006) underscores the importance of our study. One important gap in our investigation is the questing activity of larvae of *I. uriae*, which would add greatly to our understanding of seabird–tick interactions. Therefore, we urgently need more information on the behavior, ecology, and host preference of all the different life stages of *I. uriae* to better evaluate and understand the impact of an emerging disease in the seabird colonies of the northwest Atlantic.

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