

DISPERSAL AND DISTRIBUTION OF THE TICK *IXODES URIAE* WITHIN AND AMONG SEABIRD HOST POPULATIONS: THE NEED FOR A POPULATION GENETIC APPROACH

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ABSTRACT: The aim of this study was to characterize the spatial distribution of the tick *Ixodes uriae* within and among populations of its seabird hosts and to consider the potential insight that could be gained by a population genetic approach to the issue of dispersal of this tick. Analyses of data collected around the Avalon Peninsula, Newfoundland, indicated that both the prevalence and mean abundance of ticks varied significantly among sample locations. Whereas ticks were found on all 4 host species examined (*Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*), infestation prevalence and mean abundance differed among the species. On *R. tridactyla*, ticks were significantly aggregated at the among-nest scale and nestling infestation was spatially autocorrelated. Conversely, ticks were not aggregated among chicks within nests. These results enabled us to make a priori predictions regarding tick dispersal and host specificity and suggest there may be spatial structure of *Ixodes uriae* populations at both macro- and microgeographic scales. Investigating the population genetic structure of ticks within and among populations of hosts with different breeding biologies should provide direct insight into the metapopulation dynamics of such a spatially structured system.

The fact that parasites are typically found aggregated among hosts can be explained, in part, by the heterogeneous spatial distribution of parasites in the environment, i.e., parasites have not colonized all host patches (Medley, 1992). Most parasite populations are thought to function as metapopulations, i.e., they are linked by dispersal and undergo local extinction and colonization of different host patches in the environment (Harrison and Hastings, 1996; Hanski and Gilpin, 1997). The subdivision of parasite populations at different scales has profound implications for the ecology and evolution of host–parasite interactions, for the evolution of virulence (Ebert and Hamilton, 1996), and for the epidemiology of parasitic diseases (Grenfell and Dobson, 1995). Nevertheless, relatively little is known about the population structure of parasites (Nadler, 1995) or the frequency of dispersal among parasite populations (Grosholz, 1993).

The genetic structure of parasite populations is intimately associated with both the evolution of host specificity and the existence of local host adaptation. This structure is, in part, a reflection of the effective movement of individuals or their genes from 1 population to another, i.e., gene flow. Theoretical metapopulation models have shown that migration rates of hosts and parasites may be a major force influencing the degree of local adaptation of parasites and can directly alter coevolutionary outcomes (Gandon et al., 1996). Further, the evolution of habitat selection mechanisms by parasites may result in stricter host specificity (De Meeûs et al., 1993; Adamson and Caira, 1994) and will be affected by both the population structure of parasites and potential host species and by their spatio-temporal distributions in the environment.

The tick, *Ixodes uriae* White, and its hosts are an ideal system to study the importance of spatial aspects of host–parasite interactions. This tick parasitizes seabirds breeding on discrete habitat patches, i.e., colony sites where individual hosts aggregate year after year in dense groups for the breeding season (Furness and Monaghan, 1987). These colonies provide a large

and reliable source of potential hosts for this tick (Barton et al., 1996). *Ixodes uriae* is distributed throughout the circumpolar regions and has been found on at least 52 different seabird host species (Guiguen, 1988). In the north Atlantic, it has been suggested to parasitize common murre (*Uria aalge*) preferentially (Eveleigh and Threlfall, 1974), but it is commonly found on other species such as razorbills (*Alca torda*), atlantic puffins (*Fratercula arctica*), black-legged kittiwakes (*Rissa tridactyla*), and herring gulls (*Larus argentatus*) (e.g., Mehl and Traavik, 1983). In general, this tick is suspected to impact nestling condition negatively (Morbey, 1996) and affect host dispersal and recruitment through its effect on local reproductive success (Monnat and Chastel, 1987; Boulonier and Danchin, 1996; Danchin et al., 1998). Further, *I. uriae* is a vector of several avian arboviruses (Chastel, 1988) and other disease agents such as the spirochaete causing Lyme disease (Olsen et al., 1993).

Ixodes uriae spends most of its life in association with the substrate of the host colony site. It has 3 developmental stages: larvae, nymph, and adult. In each stage, *I. uriae* attaches to the host for single blood meal that lasts for up to 8 days and an entire life cycle typically takes 3–4 yr to complete (Eveleigh and Threlfall, 1974; Barton et al., 1996; for details on the life cycle of *I. uriae* also see Murray and Vestjens, 1967; Steele et al., 1990). This tick is considered to have limited mobility (Barton et al., 1996), and dispersal events within and among host colonies are likely limited to host movements at the end of the breeding season (Danchin, 1992). Thus, the life history of *I. uriae* may favor spatial structuring of its populations at small scales and may promote local adaptation in this host/parasite system.

The aim of the present paper was to characterize the spatial distribution of ticks among and within seabird host species and to determine the potential insight that could be gained by a population genetic approach to the issue of dispersal of *I. uriae* among and within populations of its seabird hosts. Analyses of data on the distribution of the tick at different spatial scales and on hosts with different biologies permitted us to propose a priori predictions that could be tested through a population genetic approach.

MATERIALS AND METHODS

Seabird nestlings were examined for *Ixodes uriae* on a series of colonies situated around the Avalon Peninsula, Newfoundland, Canada, in

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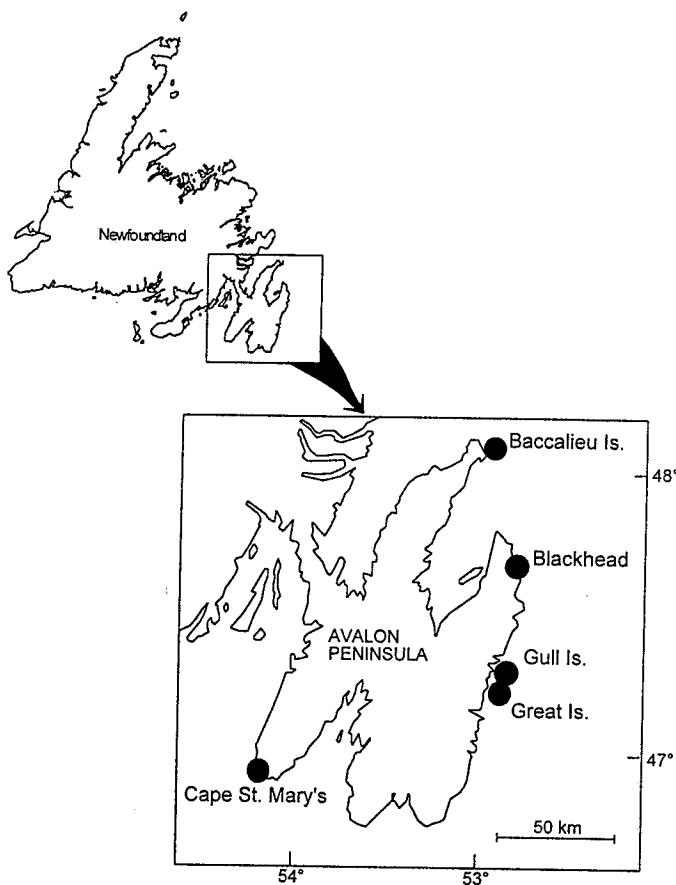


FIGURE 1. Map of colony locations on the Avalon Peninsula, Newfoundland, Canada.

July 1996 and 1997 (see Fig. 1). The sampling period was limited to a 2-wk period each year, thereby reducing the influence of temporal variation in tick activity (Barton et al., 1996). Sampling was performed at numerous locations (or cliffs) within each colony, and 4 different host species were examined where possible, i.e., black-legged kittiwakes, common murres, razorbills, and atlantic puffins. These species all differ in their breeding biology. For example, the location of nestlings differs spatially, with puffins typically nesting on grassy slopes at the top of cliffs, kittiwakes and common murres nesting on the sheer parts of cliffs, and razorbills in small monospecific groups in rock crevices. Thus, the seabird nestlings are found on different substrate types, i.e., nests for kittiwakes, rocky ledges for common murres, rock crevices for razorbills, and dirt burrows for puffins. Similarly, there are temporal differences in the onset and length of the breeding season among these species (Coulson and Thomas, 1985; Harris and Birkhead, 1985). Brood size in kittiwakes ranges between 1 and 3 (Coulson and Thomas, 1985), but the alcids examined (puffin, common murre, and razorbill) lay only 1 egg (Harris and Birkhead, 1985). In all 4 species, nestlings stay on the nest site until fledging. However, kittiwake fledglings typically remain at the colony and return to the natal nest after their first few flights, whereas alcid nestlings go directly to sea at the time of fledging and do not return (Harris and Birkhead, 1985).

Sampled nestlings were reached by different techniques depending on host species and location. The use of static climbing techniques and a pole with a hook allowed us to reach kittiwake nests containing chicks on large portions of cliffs (see Boulinier and Danchin, 1996), whereas most puffin, common murre, and razorbill chicks were captured by hand. Ticks were found through visual search and skin palpation (Danchin, 1992). Such a method enables the detection of nymphs and adults principally (Danchin, 1992; Boulinier and Danchin, 1996); larvae are too small to be completely sampled in this way. However, this technique provides a repeatable measure of individual infestation, as shown on a

sample of kittiwake nestlings examined multiple times within a breeding season (Boulinier et al., 1997). For each nestling, the total number of ticks detected was recorded. After being examined, nestlings were quickly returned to their nest, and colony disturbance was kept to a minimum. Searching for ticks on nestlings allowed us to attribute ticks to precise sites both among and within a sampling location.

A nested analysis-of-variance (PROC GLM, SAS, 1990) was conducted to compare the mean abundance of ticks (mean number of ticks per chick) detected on nestlings among colonies and among sample locations within colonies. Only kittiwake nestlings were used for this analysis as they were the most extensively sampled host species. To examine the effect of host species on tick abundance, we used a mixed-model ANOVA (PROC GLM, SAS, 1990) with sample location as a random factor. Only those sample locations where more than 1 host species was present were included. Tick abundance was log transformed ($\log[x + 0.5]$) to better fit the assumptions of linear models. Logistic analysis (PROC CATMOD, SAS, 1990) was used to examine the influence of host and sample location on the prevalence of infestation (the proportion of individuals that were infested). To help meet desirable sample sizes for this analysis, only those locations where more than 20 chicks were examined were included. The 3 alcid species were pooled at a given sample location to increase the number of populations that could be used in the analysis. Although pooling these species may cover some important biological differences, phylogenetic relatedness has been shown to influence parasite community structure (Choe and Kim, 1987) and, thus, we felt this grouping was appropriate. Only data for 1997 were used in the ANOVA and logistic analyses as only kittiwakes were sampled in 1996; sampling among all species was more extensive in the second year.

To examine the spatial distribution of ticks, aggregation at 2 embedded scales was first calculated using a modified measure of aggregation derived from Lloyd's (1967) index of patchiness (Ives, 1991; Boulinier et al., 1996). This enabled us to test for an aggregation of ticks both among and within nests within a sample location. Such a method avoids confounding different levels of aggregation by pooling samples together. Only data from locations where there was a large number of chicks and nests examined were used (arbitrarily decided to be samples with a minimum of 30 chicks and 20 nests). To determine if the aggregation measures departed significantly from that expected for a random distribution of ticks within and among nests, confidence intervals under the null hypothesis of a random distribution of ticks were obtained. For each sample used in the analysis, 100 simulation data sets were generated and the different aggregation measures with their confidence intervals were calculated. If a given aggregation measure was above the corresponding upper confidence limit calculated for the randomly distributed ticks, ticks were considered to be aggregated significantly at that scale (for details see Boulinier et al., 1996).

To investigate the patchiness in tick distribution among nests within a cliff, i.e., whether infested nests were aggregated in space, we analyzed the spatial autocorrelation of tick infestation (Sokal and Oden, 1978). This was done by calculating Moran's *I* for nestlings situated at different distance classes (Cliff and Ord, 1981). Moran's *I* varies between +1 and -1 and corresponds to the correlation of the studied variable among nestlings situated at different distance classes. A correlogram showing variation of Moran's *I* with distance class can then be drawn to infer the potential patchiness in the level of the studied variable (Sokal and Oden, 1978). Such methods have been used to investigate the spatial distribution of diseases (e.g., Cliff and Ord, 1981; Real and McElhany, 1996) and the spatial genetic structure of populations (e.g., Slatkin and Arter, 1991; Epperson and Li, 1996). Maps of kittiwake breeding cliffs were drawn for sample locations where large numbers of nestlings were examined. Coordinates of nest sites were used to compute distance matrices and spatial autocorrelation statistics using software "R" (Legendre, 1993). The threshold for significant *P* values for Moran's *I* was set at the 0.05 level (unilateral tests). Correlograms with positive Moran's *I* for short distance classes and negative ones for increasing distances would suggest a patchy distribution of ticks among nests within a cliff.

RESULTS

Over both years, a total of 383 nestlings from 4 host species was examined for ticks, and a total of 1,549 *I. uriae* individuals

TABLE I. Prevalence (P) and mean abundance (A) of infestation of seabird nestlings by *Ixodes uriae* from different sample locations on the Avalon Peninsula, Newfoundland, Canada.

Colony*	Sample	Host†	Date	nn‡	ns§	P	A	SD
Cape St. Mary's	False Cape	BLKI	08.07.96	16	11	0.69	2.69	3.26
		BLKI	11-12.07.97	45	34	0.56	2.78	3.54
Gull Is.	Lighthouse	BLKI	10.07.96	8	6	1.00	30.88	31.40
		BLKI	09-12.07.97	53	34	0.91	8.40	12.47
	Northeast	BLKI	18.07.96	13	12	0.54	1.15	1.68
		BLKI	17.07.97	13	11	0.62	1.23	1.48
		COMU	17.07.97	4	4	0.25	0.50	1.00
		ATPU	17.07.97	11	11	1.00	4.18	5.00
	South 3	BLKI	18-20.07.96	20	16	0.80	5.70	6.97
		BLKI	16.07.97	28	25	0.86	3.43	3.58
	South tip	ATPU	16.07.97	16	16	0.06	0.38	1.50
		RAZO	16.07.97	9	9	0.67	2.00	2.12
Black Head Great Is.	East	RAZO	17.07.97	9	9	0.67	2.11	2.52
		COMU	17.07.97	12	12	0.33	0.33	0.49
	Southeast	BLKI	18.07.97	21	21	0.77	1.62	1.57
	Center	BLKI	08.07.97	11	9	0.27	0.27	0.47
	Southeast	BLKI	19.07.97	22	22	0.36	0.50	0.91
		ATPU	19.07.97	22	22	0.68	1.82	2.36
Baccalieu Is.	Bull Gulch	BLKI	20.07.97	17	13	0.41	2.35	4.27
	Ned Walsh	BLKI	21.07.97	20	16	0.85	6.90	13.46
		ATPU	21.07.97	13	13	0.77	6.69	7.47

* Colony names correspond to those of Brown et al. (1975).

† BLKI = black-legged kittiwake, ATPU = atlantic puffin, RAZO = razorbill, COMU = common murre.

‡ nn = Number of nestlings.

§ ns = Number of nest sites

SD = standard deviation of tick density on nestlings.

was detected. *Ixodes uriae* was found on all host species and at all sample locations (Table I). All 3 stages of the tick were present, but larvae were rarely detected. For a sample of 79 kittiwake and 54 alcid chicks, ticks were classified by stage. Significantly more nymphs were found on alcid nestlings (204 compared to 64 on kittiwakes), whereas most ticks on kittiwakes were adults (158 compared to 5 on alcids; $\chi^2 = 213.64$, $P < 0.001$). In 1997, we recorded the number of dead ticks on hosts and found them most frequently on kittiwake nestlings; 4% of parasitized nestlings had at least 1 dead tick (9 chicks of 230).

The mean abundance of *I. uriae* among sample locations varied from 0.33 to 30.88 ticks per host individual (Table I). The mean abundance of tick infestation of kittiwake nestlings was significantly influenced by sample location within colony ($F_{4,221} = 9.17$, $P = 0.001$), but did not vary among colonies once

variation due to sample location was accounted for ($F_{4,4} = 1.12$, $P = 0.456$). In a second analysis, using only locations with more than 1 sampled species, host species was also found to influence tick abundance significantly ($F_{3,57} = 5.28$, $P = 0.003$); kittiwakes had the highest abundance of ticks, whereas common murrens had the lowest (Table II).

The prevalence of tick infestation was also variable among sample locations, from 0.06 to 1.00 (Table I), and was significantly influenced by both host species (kittiwake or alcid) ($\chi^2_1 = 12.09$, $P < 0.001$) and sample location ($\chi^2_7 = 35.22$, $P < 0.001$). The average prevalence of infestation across all sample locations was similar for kittiwakes and razorbills; common murrens tended to have the lowest prevalence (Table II). These results suggest that there was a relatively strong component due to host species in the distribution of ticks as, even when the alcids were pooled, a difference was found between this group and kittiwakes.

There were 2 sample locations for which we had a large enough number of kittiwake nestlings and nests to calculate measures of aggregation (Cape St. Mary's, False Cape, and Lighthouse locations in 1997, see Table I). Parasites were globally aggregated among nestlings, with a few nestlings hosting most of the parasites (J; Table III). When aggregation was partitioned to among and within nests, we found that almost all of the aggregation could be attributed to the among-nest scale (J_k/J ; Table III); there was no significant aggregation at the within-nest scale at either sample location (EJ_j ; Table III).

For the same 2 cliffs used to calculate the aggregation measures, we were also able to determine if there was a spatial autocorrelation of tick infestation. We found evidence of a

TABLE II. Average prevalence (\pm standard deviation) and abundance (\pm standard deviation) of ticks on chicks of different seabird species across all sample locations on the Avalon Peninsula, Newfoundland in 1997.*

Species	No. chicks	Total ticks	Avg. prevalence (\pm SD)	Avg. abundance (\pm SD)
BLKI	230	908	0.68 (± 0.47)	3.95 (± 8.03)
COMU	16	6	0.31 (± 0.48)	0.38 (± 0.62)
RAZO	18	37	0.67 (± 0.49)	2.06 (± 2.26)
ATPU	62	179	0.60 (± 0.50)	2.89 (± 4.80)

* Species abbreviations as in Table I.

TABLE III. Aggregation of *Ixodes uriae* among kittiwake (*Rissa tridactyla*) nestlings at the within and among-nest scales in 2 colonies on the Avalon Peninsula, Newfoundland, Canada.*

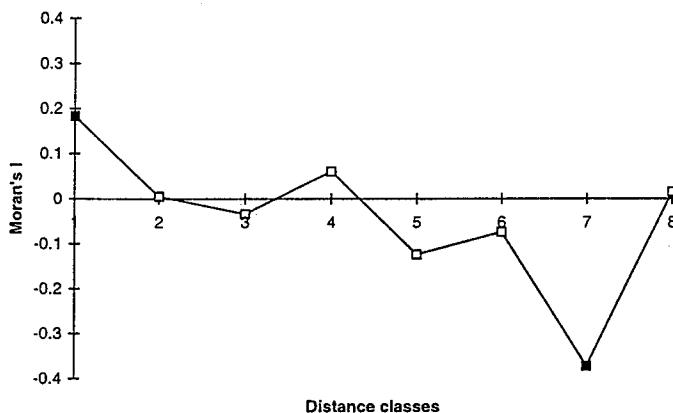
Location	nn	ns	J (CI)	J_k (CI)	EJ_j (CI)	J_k/J
Cape St. Mary's, False Cape	45	34	1.24 (-0.36; 1.02)	1.10 (-0.37; 0.80)	0.14 (-0.20; 0.41)	0.88
Cape St. Mary's, Lighthouse	53	34	2.05 (-0.27; 0.47)	1.93 (-0.28; 0.33)	0.12 (-0.11; 0.17)	0.9

* J and J_k measure the total and among-nest aggregation of ticks, respectively, EJ_j indicates the weighted average of the within-nest aggregation of ticks among chicks (where $EJ_j = J - J_k$). An aggregation measure is considered significant (marked in bold) if it is above the upper confidence limit; nn = number of chicks per sample; ns = number of nest sites per sample; (CI) = confidence intervals at 98% under the null hypothesis of a random tick distribution.

patchy infestation in both locations as indicated by the shape of the spatial correlograms (Fig. 2). There were significant positive correlations of tick infestation of nestlings among nests situated close together in space, but significant negative correlations between nests situated far apart (Fig. 2). We did not

have enough data to examine temporal autocorrelation of tick infestation, but the lighthouse location at the Cape St Mary's Ecological Reserve was the most heavily infested by *I. uriae* in both years and other locations, where kittiwakes were examined in both years, showed similar consistent patterns between the years (Table I).

A) Lighthouse



B) False Cape

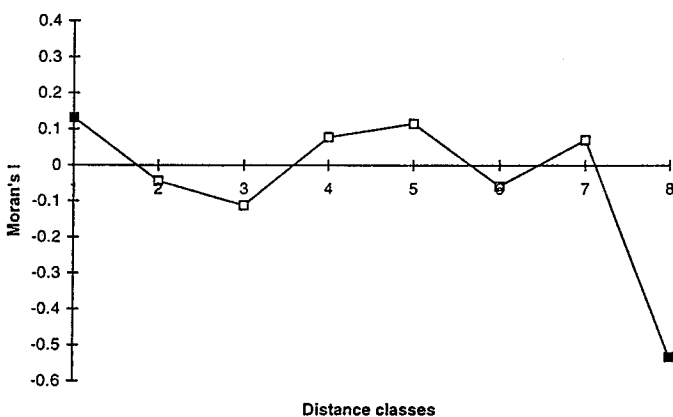


FIGURE 2. Spatial correlograms of kittiwake nestling infestation by the tick *Ixodes uriae* in nests situated at different distances within 2 cliffs of Cape St Mary's Ecological Reserve (A, Lighthouse; B, False Cape). Black squares are significant Moran's I showing a positive or negative correlation of level of infestation by the tick for the distance classes considered. Distance classes correspond to equidistant classes inferred from the sketch maps of the cliffs. Each portion of cliff corresponded roughly to a square of 100 m².

DISCUSSION

Various factors contribute to the distribution of parasites among hosts. In many cases, however, and despite the potential importance of patchiness to the distribution of hosts and pathogens, spatial aspects are rarely investigated (Nadler, 1995; Real and McElhany, 1996). Here, we report a strong effect of sample location on the prevalence and abundance of infestation by *Ixodes uriae*. On a smaller scale, we show evidence of an aggregation of *I. uriae* among nests within a cliff, with nests closer to infested nests having a high probability of also being infested (spatial autocorrelation of infestation). Mean abundance of ticks varied among all 4 species examined and prevalence was significantly influenced by whether the host was a kittiwake or alcid. A larger sample of the alcid species would have allowed us to further tease apart differences in tick prevalence within this group. Overall, the results underline the strong spatial variability in the level of infestation of nestlings at different scales (within a cliff and among cliff samples) and among different host species and suggest the importance of local, and among, patch dynamics of tick infestation on seabird colonies.

Whereas the pattern we found tells us little about the dispersal of *I. uriae* within, and among, host populations, it does point out the need to investigate further dispersal processes operating among hosts and at different spatial scales in order to understand the dynamics of the system. Long-term surveys of infestation dynamics from an initially uninfested, monospecific colony of hosts would provide direct information about some of the processes involved. For example, such a survey in a kittiwake colony provided evidence that both local tick population growth within cliffs, and the influx of ticks from nearby cliffs contributed to the rapid spread and local build-up of resident tick populations (T. Boulinier, J.-Y. Monnat, and E. Danchin, unpubl. obs.). Nevertheless, the quantification of tick dispersal through direct observation appears impossible with such parasites, and these methods will not inform us about the level of dispersal among different host species. Further, direct measures of dispersal are limited by the time scale they encompass and, on evolutionary time scales, inferences based on these

measures are restricted (Slatkin, 1987). Indirect measures of dispersal are, therefore, necessary to answer questions related to gene flow and when dealing with intractable species such as parasites.

Questions linked to the evolution of host specificity and local adaptation (Adamson and Caira, 1994; Gandon et al., 1996) also need consideration as they directly affect the population dynamics of the parasite. Host specificity may be associated with differential susceptibility among hosts that can vary both among host species and among individuals within a given host species (e.g., Boulinier et al., 1997; Sorci et al., 1997). Our finding of several, partially fed, dead ticks attached to hosts suggests that such processes are operating and are impacting individual tick survival. Likewise, the timing of tick activity in the field has been suggested to be controlled to a certain extent by host species (Barton et al., 1996). Eveleigh and Threlfall (1974) considered host preference by examining tick prevalence in the field and by determining the proportion of ticks that successfully fed on different seabird hosts in the laboratory; they suggested that common murres were the preferred hosts of *I. uriae*. However, their observations were based on data collected from 1 colony, Gull Island, and from the examination of feeding success on 1–2 individuals of each host species. Due to variability in host susceptibility to tick infestation and the potential for local host adaptation, their results might not reflect the general pattern. In fact, our results, at least in part, do not support these findings as we found the highest prevalence and mean abundance of ticks in kittiwake nestlings and the lowest in common murres (Table II). A similar pattern of prevalence and mean abundance has been found in colonies in northern Norway (K. McCoy, unpubl. obs.). Further experiments of host choice and tick engorgement success on individuals of different host species might help to indicate the potential structuring of parasite populations among different host species and the existence of local adaptation.

A population genetics approach could provide important elements to help address several of these questions. Population genetic structure is determined by the relative forces of genetic drift, natural selection, and gene flow. In general, gene flow is considered to reduce the genetic differentiation that natural selection and drift promote (Slatkin, 1987). In parasite populations, isolating factors such as low dispersal ability, habitat patchiness, length of association, and host specificity can produce genetic structure at fine spatial scales. For example, using allozymes, chewing lice (*Geomydoecus actuosi*) of pocket gophers were found to be highly structured within and among host localities (Nadler et al., 1990). Conversely, in 2 previous studies on ticks (*Ixodes ricinus* [Delaye et al., 1997] and *Amblyomma americanum* [Hilburn and Sattler, 1986]), no population structure was found, despite the fact that disease agents transmitted by these ticks can have small geographic foci and that surveys were performed over broad geographic areas. The results of these studies have been attributed to both low host specificity and high host mobility (Hilburn and Sattler, 1986) and to the limited ability of protein markers to detect variation in these species (Delaye et al., 1997). With the development of techniques to examine highly polymorphic genetic markers, such as microsatellites, and to amplify small amounts of tissue (using PCR-based techniques), new opportunities to examine popula-

tion structure at finer scales are now available (Nadler, 1995; Parker et al., 1998).

Nadler (1995) suggested that certain life-history traits of parasites could be used to make general predictions about the distribution of genetic variation over geographic space. For example, factors such as high host vagility, low host specificity, and frequent metapopulation extinction and recolonization events, could all act to reduce genetic structure in parasite populations. Conversely, sedentary hosts, host patchiness in space and time, small effective parasite population size, and parasite transmission relying on physical contact between hosts should all promote structuration.

We found that *I. uriae* populations in Newfoundland seabird colonies were spatially subdivided and aggregated at both among and within cliff scales. Individual dispersal abilities in these ectoparasites appear to be limited (e.g., Barton et al., 1996), and dispersal events likely occur when fledglings move around the colony at the end of the breeding season (Danchin, 1992). Although the high vagility of birds should increase dispersal of their parasites, considering that *I. uriae* remain on the host for only short feeding bouts each year and are found in the highest numbers during the incubation and chick-rearing periods when birds stay close to the nest (Danchin, 1992; Barton et al., 1996), we still might expect dispersal events of ticks to be random and relatively rare. Based on these ecological characteristics, we may expect to see strong genetic subdivision of populations among cliff localities and, potentially, even within cliffs. Further, different seabird host species can have very different life histories. For example, young kittiwakes stay on the breeding grounds for several days after fledging and may visit different colony sites. This period could represent the main opportunity for ticks to disperse (Danchin, 1992). Conversely, young common murres leave the colony directly to go to sea and do not return for several years (Harris and Birkhead, 1985). This behavior renders them less likely to promote tick dispersal. We could thus predict tick populations to be less structured among subpopulations of hosts such as kittiwakes than among subpopulations of hosts like common murres.

In relation to local adaptation of parasites and the evolution of host specificity, a population genetic examination of *I. uriae* would permit us to answer several important questions. For example, there is currently debate about the relative importance of host adaptation versus habitat adaptation in the evolution of ticks (Klompen et al., 1996). *Ixodes uriae* is not a priori host specific in that it can parasitize many different seabird species and has been known to feed on other, nonavian hosts, e.g., humans (Mehl and Traavik, 1983). However, the ability of this tick to contact different host species is limited as it spends most of its life in the substrate of the seabird host's nest. Further, breeding seabirds can show relatively high breeding-site fidelity and natal philopatry (Furness and Monaghan, 1987), and some seabirds have been shown to form kin groups (Friesen et al., 1996). Such factors may limit the potential for ticks to contact unrelated hosts both within and among species. These aspects should promote local adaptation in this system and may result in structuring among host species within mixed colony sites.

Thus, a population genetics approach to the issue of *I. uriae* dispersal would provide a powerful tool to investigate several important questions related to the ecology and evolution of host-parasite interactions. A better understanding of these sys-

tems would have direct implications for other important issues such as the evolution of virulence and the epidemiology of tickborne disease. Studying parasite population genetics and linking results with ecological attributes will rely on careful sampling of the parasite in relation to what is known about its spatiotemporal distribution, and on a good knowledge of the life history and behavior of the different host species involved. In the end, such studies should be fruitful both in examining the validity of current ideas about host–parasite associations and in generating further understanding about the interrelationships between the different biological factors that affect natural populations.

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