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# HOST-DEPENDENT GENETIC STRUCTURE OF PARASITE POPULATIONS: DIFFERENTIAL DISPERSAL OF SEABIRD TICK HOST RACES

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*Abstract.*—Despite the fact that parasite dispersal is likely to be one of the most important processes influencing the dynamics and coevolution of host-parasite interactions, little information is available on the factors that affect it. In most cases, opportunities for parasite dispersal should be closely linked to host biology. Here we use microsatellite genetic markers to compare the population structure and dispersal of two host races of the seabird tick *Ixodes uriae* at the scale of the North Atlantic. Interestingly, tick populations showed high within-population genetic variation and relatively low population differentiation. However, gene flow at different spatial scales seemed to depend on the host species exploited. The black-legged kittiwake (*Rissa tridactyla*) had structured tick populations showing patterns of isolation by distance, whereas tick populations of the Atlantic puffin (*Fratercula arctica*) were only weakly structured at the largest scale considered. Host-dependent rates of tick dispersal between colonies will alter infestation probabilities and local dynamics and may thus modify the adaptation potential of ticks to local hosts. Moreover, as *I. uriae* is a vector of the Lyme disease agent *Borrelia burgdorferi* sensu lato in both hemispheres, the large-scale movements of birds and the subsequent dispersal of ticks will have important consequences for the dynamics and coevolutionary interactions of this microparasite with its different vertebrate and invertebrate hosts.

*Key words.*—*Borrelia burgdorferi* sensu lato, coevolution, *Fratercula arctica*, gene flow, host-parasite interactions, *Ixodes uriae*, *Rissa tridactyla*.

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Parasite dispersal between host populations is likely to be one of the most important factors affecting the dynamics and coevolution of host-parasite interactions (Price 1980; Thompson 1994). Epidemiological models have long recognized the role of spatial processes in such interactions (e.g., Bolker et al. 1995) and recent theoretical studies have emphasized that parasite dispersal between discrete host patches is a key factor in the evolution of local adaptation (Gandon et al. 1996; Lively 1999). Moreover, once established in a host population, the presence of a parasite may directly affect host reproductive success and can subsequently influence proximate host decisions, such as whether to remain at a breeding site or to disperse (Boulinier et al. 2001). However, despite its importance, few empirical studies have examined parasite dispersal (Lively 1999; Boulinier et al. 2001). In many cases, this lack has been related to the difficulty with which such studies could be performed. The development and implementation of genetic markers has now opened up the possibility to examine parasite gene flow at different spatial scales (Nadler 1995), thus allowing inferences to be made about effective parasite dispersal (e.g., Mulvey et al. 1991; Blouin et al. 1995).

The ability of parasites to disperse will depend on a variety of factors including the complexity of the life cycle, the number of propagules produced, the parasitic environment (e.g., endoparasite or ectoparasite), and the presence and duration of free-living stages. Because parasites are closely tied to their hosts, opportunities for dispersal should also depend on the vagility and characteristics of the hosts involved. For example, Blouin et al. (1995) examined the genetic structure of five different nematode parasites from three host species using mitochondrial sequence data. They found that the degree of parasite population structure was related to the host species exploited; nematode species using livestock that were transported between distant locations had less structured populations than a nematode parasite of white-tailed deer. Differential dispersal rates of parasites can have profound implications for the evolution of such interactions, as well as for the epidemiology of medically important diseases. However, the role of host-mediated dispersal in the population dynamics and evolution of host-parasite interactions has, in general, received little attention.

The tick *Ixodes uriae* and its seabird hosts provide an ideal system to examine parasite dispersal and its consequences. This ectoparasite has a vast distribution, being found in circumpolar areas of both hemispheres, and can parasitize a wide variety of colony-nesting seabird species (Guiguen 1988). It typically takes only a single, long blood meal per year during its four-year life cycle and thus spends most of its life in the area surrounding the host breeding site (Eveleigh and Threlfall 1974). Although seabird colonies are often multispecific, different seabird species do not necessarily share the same tick population; the existence of sympatric tick races has been demonstrated recently for two host species (McCoy et al. 2001). In particular, genetic differentiation between tick populations of sympatric black-legged kittiwakes (*Rissa tridactyla*) and Atlantic puffins (*Fratercula arctica*) was much

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greater than that between allopatric populations of either host. This suggested that gene flow between host races, even when found in sympatry, was much lower compared to that between distant populations of the same host. Given the frequent availability of multiple hosts in seabird colonies, the evolution of host specialization in this system can therefore lead to different types of ecological and coevolutionary interactions, both within and between host species. In addition, seabird colonies are discrete in space and dynamic in time such that tick dispersal between different colonies and the local persistence of a tick population over several generations is host dependent. Finally, this ectoparasite is a vector of the Lyme disease agent *Borrelia burgdorferi* sensu lato and seabirds have been suggested to be involved in the maintenance and spread of this bacterium at large spatial scales (Olsen et al. 1993, 1995; Gylfe et al. 1999). Thus, information on the scale and frequency of tick dispersal could help us understand the role of this process in the ecological dynamics and evolution of such host-parasite-microparasite systems.

Here, we investigated the dispersal of *Ixodes uriae* by examining population genetic structure, diversity, and gene flow of ticks among host colonies at different spatial scales. Because the dispersal of this parasite is host-associated and pelagic seabirds tend to be closely tied to the nest site during their short period on land each year, we expected successful tick dispersal to be relatively infrequent and limited in its spatial extent. Given this, the colonization of new host colonies is likely to occur through the introduction of few individuals, resulting in reduced within-population genetic diversity and highly structured populations (McCoy et al. 1999). We also predicted that opportunities for tick dispersal would depend on which host species was exploited. To test this, we compared the genetic structure of tick races of two host species, the black-legged kittiwake (*Rissa tridactyla*) and the Atlantic puffin (*Fratercula arctica*). Based on behavioral observations and breeding characteristics of these hosts, we predicted that puffin ticks should have more opportunities for effective dispersal than kittiwake ticks. Previous work examining the biology of puffins has suggested that movements are frequent between local colonies (about 100 km) and rare at larger scales. Visits to local colonies are almost exclusively by subadults who have not yet established a breeding site (prospectors; Harris 1983). Kittiwake subadults have also been observed to visit different colonies, although most visits have been seen at less than 50 km from the natal colony (Coulson and Nève de Mévergnies 1992; Danchin 1992) and these birds tend to become more closely associated with the natal site as they reach breeding age. Observations of subadult movement to distant colonies ($>$ 2000 km) are rare for both species. These two host species also differ in their behaviors within colonies. Kittiwakes breed on vertical cliff faces in individual nests such that visiting birds have limited access to the nest site area. Puffins, on the other hand, breed in burrows on more moderate slopes and prospecting individuals are able to move freely within the colony. These different behaviors can lead to a higher probability of dispersal for ticks exploiting puffins compared to those exploiting kittiwakes.

To test our predictions, we investigated the scale of tick population structure by examining the distribution of genetic variation at different spatial scales (between local breeding cliffs to between regions) for ticks of both hosts. We discuss our results with respect to their implications for the ecological dynamics and the evolution of local adaptation in this host-parasite system, along with the possible consequences of tick dispersal for the coevolutionary dynamics of tick-borne microparasites.

## Materials and Methods

### *Sampling and Genotyping*

Ticks were sampled from kittiwakes and puffins at 13 different colonies across the North Atlantic (Fig. 1). For two colonies (MN on Hornøya [HN] and Baccalieu Island [BI]), ticks were sampled from the two host species in sympatry. In one large colony (HN), kittiwakes were sampled for ticks in three distinct breeding cliffs (MN, CG, CF). At most sites ticks were collected directly from the birds. However, puffin ticks on Hornøya were also collected from inside the burrow at the nest site using access holes, and on Bleiksøya (BK) by flagging inside burrows (i.e., dragging a cloth through the burrow) in monospecific areas of the colony. An effort was made to collect ticks from at least 30 individual birds/burrows at each site. Collected ticks were stored in 70–90% ethanol until DNA extraction.

For each population, DNA extractions were carried out on a minimum of 24 ticks and ticks were genotyped for eight different microsatellite loci (McCoy and Tirard 2000). Extraction and polymerase chain reaction (PCR) procedures followed those outlined in McCoy and Tirard (2000) and resulting PCR products were run on 6% acrylamide gels using size controls.

### *Data Analysis*

Given that ticks from the two host species considered here seem to have formed isolated groups (McCoy et al. 2001), we analyzed the populations of each host species separately and then compared the two groups (Rousset 1999). All populations and loci for each host species were tested for departure from Hardy-Weinberg expectations using exact probability tests employing a Markov chain method to estimate exact *P*-values (GENEPOP ver. 3.3; Raymond and Rousset 1995). To ensure independence among loci, data were similarly tested for linkage disequilibrium. Where required, significance levels were corrected for multiple tests (Rice 1989). The number of alleles and gene diversities (Nei 1987) were calculated for each tick population. The number of sampled alleles is highly dependent on the number of individuals examined in a population. As such, differences in allelic richness among populations and between host groups were examined by calculating a global estimate across all populations for each locus (based on the common parameter, $\theta$; Chakraborty 1990) and determining the exact probability of sampling more or less alleles in a population given the number of individuals sampled (program provided by L. Excoffier, Dept. of Biology, Zoological Institute, University of Bern, Switzerland). Differences in gene diversity estimates were compared within and between host species using nonpara-

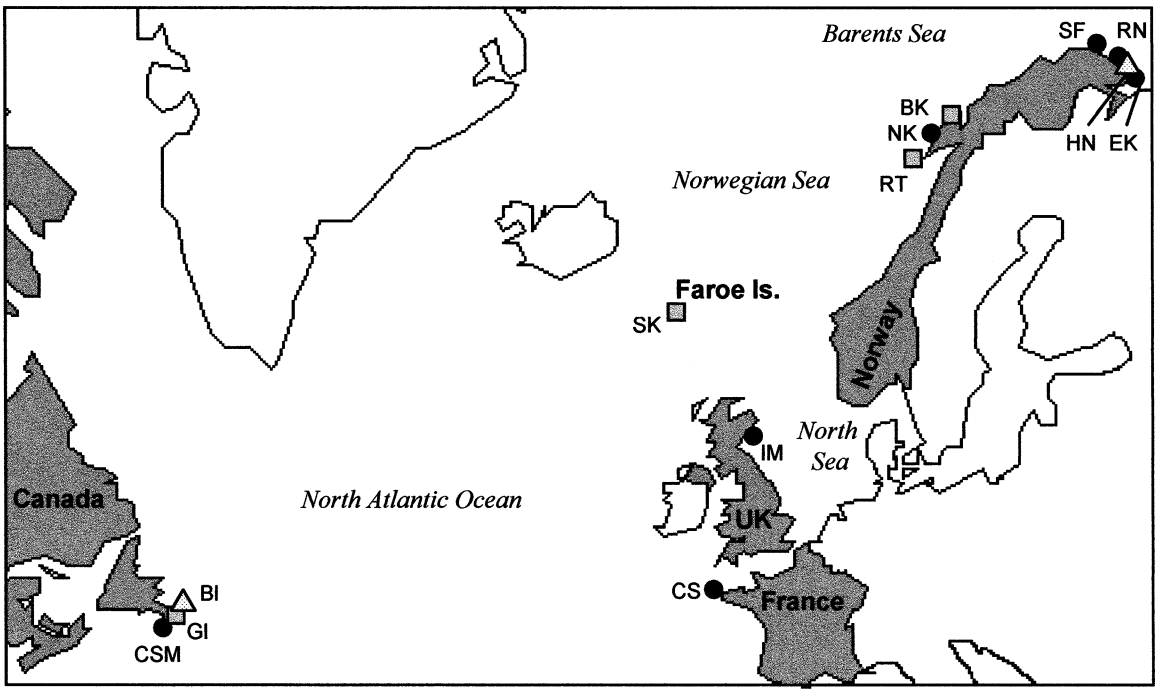


FIG. 1. Sampling locations of *Ixodes uriae* populations. Gray squares indicate the sampling sites of puffin ticks and black circles those of kittiwake ticks. Triangles are sites where ticks from both hosts were sampled. Population codes indicate the following colonies: CSM, Cape St. Mary's, Newfoundland, Canada; GI, Gull Island, Newfoundland, Canada; BI, Baccalieu Island, Newfoundland, Canada; CS, Cap Sizun, France; IM, Isle of May, Scotland; SK, Skuvoy, Faroe Islands; RT, Røst, Norway; NK, Nykvåg, Norway; BK, Bleiksøya, Norway; SF, Syltefjord, Norway; RN, Reinøya, Norway; HN, Hornøya, Norway (containing sites CF, CG, MN); EK, Ekkerøy, Norway.

metric tests (Zar 1996). Allele frequencies are available upon request to K. McCoy.

Hierarchical population structure was quantified using Weir and Cockerham's (1984) estimates of Wright's *F*-statistics. The significance of these values was determined using permutation tests based on resampling alleles or genotypes, either among individuals or populations, using 5000 randomizations (FSTAT ver. 2.9; Goudet 1995). Standard errors were calculated by jackknifing over loci (Goudet 1995).

To describe the clustering of populations, we carried out a principal component analysis (PCA) using the program PCA-GEN ver. 1.2 (1999, J. Goudet, Institute of Ecology, Laboratory for Zoology, University of Lausanne, Switzerland). This analysis uses allele frequencies to define new variables (components) that summarize the variance among populations and then performs permutation tests to evaluate the significance of each component (5000 randomizations). In the first analysis, we examined the clustering of tick populations including all populations of both host groups. We then performed a second analysis for each host group separately to detect potential regional population groups. We investigated the validity of defined regional groups by comparing pairwise estimates of $F_{ST}$ within and among groups. If regional population groups encompassed areas of high gene flow, we expected that average estimates of $F_{ST}$ would be low within groups and high among groups.

To examine the gene flow of ticks at different spatial scales for each host species, we tested for isolation by distance using the correlation between genetic distance, measured as $F_{ST}/(1 - F_{ST})$, and geographic distance of population pairs; correlations were tested for significance using Mantel permutation procedures (Mantel 1967) associated with Spearman-Rank correlation coefficients as test statistics (GENEPOP ver. 3.3). We first show the overall pattern of pairwise differentiation over all distances. However, we only intend this figure to provide a general image of the differentiation between populations. At very large scales, processes other than dispersal are likely to affect estimated differentiation (e.g., mutation; Rousset 1997). Therefore, tests of isolation by distance within each host group were limited to only those populations on each side of the Atlantic, a potentially reasonable scale to consider for the movements of seabirds among colonies. Distances between populations of less than 2 km (corresponding to neighboring cliffs) were not used to calculate correlation coefficients because samples at small spatial scales are not expected to follow the general theory of isolation by distance (Rousset 1997).

## RESULTS

After correction for multiple tests, all population-locus combinations were in Hardy-Weinberg equilibrium (Table 1). Without the correction, there were slight deviations for certain combinations that may suggest inbreeding or substructuring in some populations. For this reason, alleles were not considered to be independent for testing the significance of population differentiation such that permutation tests of $F_{ST}$ estimates used the genotype as the randomization unit instead of the allele (Goudet 1995). No linkage disequilibrium was found between any of the eight loci used.

TABLE 1. Average estimates of variability parameters (±standard error) of tick populations for eight microsatellite loci. Colony locations, indicated by abbreviations in parentheses, are shown on Fig. 1. $H_{HW}$ refers to estimates of $F_{IS}$ for each population and the corresponding *P*-values to overall tests for Hardy-Weinberg equilibrium. Note that all individual population-locus combinations were in Hardy-Weinberg equilibrium after correction for multiple tests (Rice 1989). *n*, number of individuals genotyped; $n_a$, number of alleles; *h*, gene diversity (Nei 1987); $H_o$, observed heterozygosity.

| Kittiwake | *n*(SE) | $n_a$(SE) | *h*(SE) | $H_o$(SE) | $H_{HW}$ | *P* |
|---|---|---|---|---|---|---|
| NW, Baccalieu Is. (BI), Canada | 19.88 (1.14) | 4.38 (1.02) | 0.45 (0.12) | 0.44 (0.12) | 0.139 | 0.024 |
| Cape St. Mary's (CSM), Canada | 34.25 (0.67) | 5.25 (1.22) | 0.48 (0.10) | 0.42 (0.10) | 0.114 | 0.002 |
| MN, Hornøya (HN), Norway | 25.88 (1.32) | 5.88 (1.03) | 0.59 (0.09) | 0.53 (0.09) | 0.091 | 0.561 |
| CG, Hornøya (HN), Norway | 29.25 (0.80) | 7.50 (1.57) | 0.62 (0.09) | 0.55 (0.08) | 0.108 | 0.003 |
| CF, Hornøya (HN), Norway | 20.50 (0.50) | 6.00 (1.07) | 0.65 (0.06) | 0.58 (0.06) | 0.112 | 0.441 |
| Ekkerøy (EK), Norway | 22.88 (0.13) | 6.25 (1.11) | 0.57 (0.09) | 0.58 (0.09) | −0.008 | 0.754 |
| Reinøya (RN), Norway | 20.88 (0.30) | 6.38 (1.08) | 0.59 (0.08) | 0.60 (0.10) | −0.013 | 0.743 |
| Syltefjord (SF), Norway | 23.63 (0.18) | 6.75 (1.13) | 0.66 (0.06) | 0.64 (0.08) | 0.028 | 0.107 |
| Nykvåg (NK), Norway | 22.63 (0.18) | 5.50 (0.85) | 0.56 (0.09) | 0.48 (0.07) | 0.156 | 0.082 |
| Cap Sizun (CS), France | 23.63 (0.32) | 5.50 (0.98) | 0.58 (0.10) | 0.54 (0.10) | 0.057 | 0.524 |
| Isle of May (IM), Scotland | 29.00 (1.22) | 5.75 (1.28) | 0.47 (0.11) | 0.40 (0.10) | 0.177 | 0.194 |
| Average | 24.76 (1.34) | 5.92 (0.25) | 0.57 (0.02) | 0.52 (0.02) | 0.086 | <0.001 |
| Puffin | | | | | | |
| NW, Baccalieu Is. (BI), Canada | 32.63 (0.18) | 7.25 (1.98) | 0.60 (0.11) | 0.67 (0.08) | 0.009 | 0.268 |
| Gull Is. (GI), Canada | 25.75 (0.16) | 6.63 (2.05) | 0.55 (0.11) | 0.55 (0.10) | 0.127 | 0.184 |
| MN, Hornøya (HN), Norway | 30.38 (0.50) | 7.75 (2.23) | 0.59 (0.12) | 0.51 (0.12) | 0.132 | 0.052 |
| Bleiksøya (BK), Norway | 24.00 (0.0) | 6.88 (1.53) | 0.54 (0.12) | 0.50 (0.11) | 0.066 | 0.059 |
| Røst (RT), Norway | 25.50 (1.45) | 6.25 (1.37) | 0.54 (0.13) | 0.42 (0.10) | 0.217 | 0.024 |
| Skuvoy (SK), Faroe Is. | 24.00 (0.0) | 6.50 (1.60) | 0.53 (0.13) | 0.57 (0.12) | 0.052 | 0.863 |
| Average | 27.04 (1.47) | 6.88 (0.22) | 0.55 (0.01) | 0.54 (0.03) | 0.097 | 0.002 |

The average number of alleles per locus varied from 4.38 (±1.02) to 7.50 (±1.57) for kittiwake tick populations and from 6.25 (±1.37) to 7.75 (±2.23) for puffin tick populations (Table 1). After accounting for the number of individuals sampled and the number of tests performed, no population for either host group deviated from the global expectations of each locus. That is, no population showed reduced allelic richness compared to the global estimate. Similarly, when allelic richness was compared between host groups, neither group showed deviations from the expected richness at any locus (all $P > 0.25$). Gene diversities did not vary significantly among populations in either host group (Kruskal-Wallis test, kittiwake ticks $\chi^2_{10} = 4.48$, $P = 0.92$ and puffin ticks $\chi^2_5 = 0.41$, $P = 0.99$; Table 1) and were not significantly different for tick populations of the two host species (Wilcoxon two-sample test, $z = -0.65$, $P = 0.51$). Overall, these results suggest that there has been ample time since colonization for similar levels of diversity to be established in populations of both host groups.

TABLE 2. Average pairwise estimates of $F_{ST}$ (±standard error) within and among regional groups of tick populations for kittiwake and puffin hosts. *n* refers to the number of comparisons within each group. Overall $F_{ST}$ (±standard error) refers to estimated differentiation including all populations of each tick race.

| Host | Regional group | *n* | Average pairwise $F_{ST}$ |
|---|---|---|---|
| Kittiwake | Barents | 15 | 0.0034 ± 0.0013 |
| | West Atlantic | 1 | 0.0299 ± 0.0000 |
| | North-Norwegian | 3 | 0.0497 ± 0.0071 |
| | Among groups | 36 | 0.1144 ± 0.0212 |
| | Overall $F_{ST}$ | | 0.060 ± 0.011 |
| Puffin | East Atlantic | 6 | 0.0107 ± 0.0030 |
| | West Atlantic | 1 | 0.0051 ± 0.0000 |
| | Among groups | 8 | 0.0529 ± 0.0018 |
| | Overall $F_{ST}$ | | 0.034 ± 0.009 |

Kittiwake ticks tended to show greater overall structure than puffin ticks; $F_{ST}$ estimates were almost double for kittiwake tick populations despite the fact that there were many more nearby populations included in the calculation for this host species (Table 2; but also see Fig. 3a). The PCA including all tick populations of both host groups showed two significant axes explaining 58.61% of the total inertia (41.33% and 17.28% inertia for axes 1 and 2 respectively) and isolated tick populations from the two host species (Fig. 2). Tick populations were then reanalyzed separately for each host species. The PCA of kittiwake ticks showed two significant axes explaining 64.89% total inertia (43.03% and 21.86% inertia for axes 1 and 2 respectively). This analysis clustered populations into three broad regional groups: one found in the Barents Sea (Barents group), one composed of the two colonies in Newfoundland (West Atlantic group) and one made up of the three colonies in the North and Norwegian Seas (North-Norwegian group; Fig. 2: results mapped onto first analysis). The first two components of the PCA explained 73.50% inertia for puffin tick populations; however, this was mostly due to the first component, which showed 58.19% inertia and was the only significant axis. Based on this first axis, puffin tick populations clustered into two groups: East and West Atlantic (Fig. 2: results mapped onto first analysis).

For both tick races, regional population groupings of ticks were supported by lower average values of $F_{ST}$ within groups compared to among groups (Table 2). However, there were still several significant pairwise $F_{ST}$ estimates within regional groups. For puffin ticks, there was significant differentiation between the populations of Røst and Bleiksøya ($F_{ST} = 0.020$, $P < 0.001$). For kittiwake ticks, only the Barents group

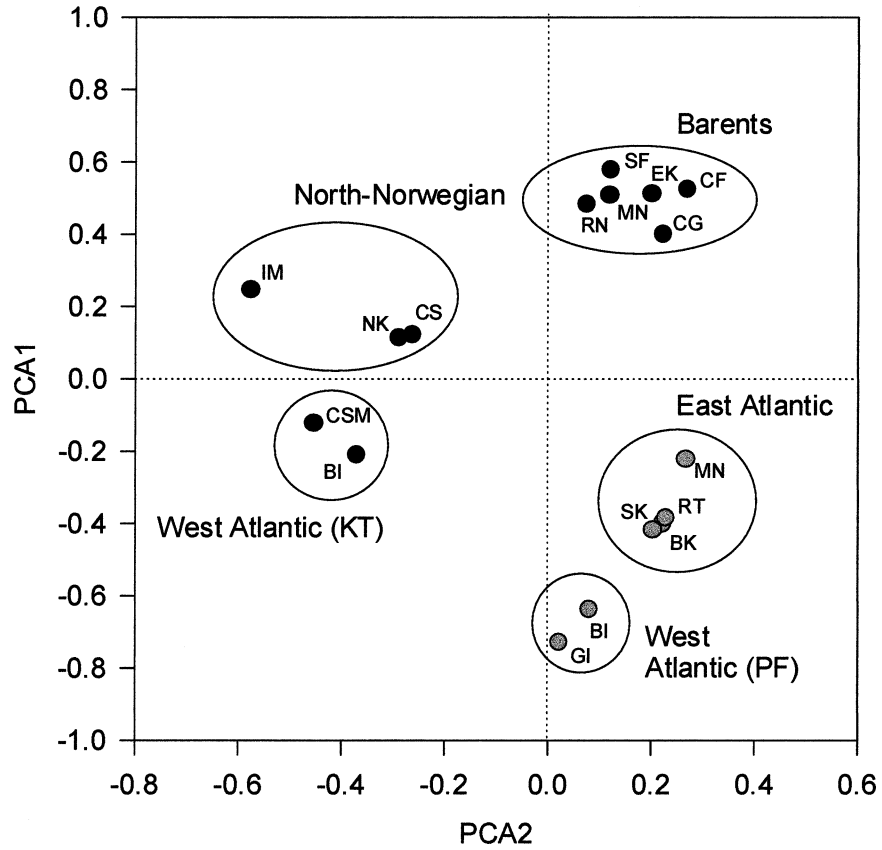


FIG. 2. Factor map of the two main axes of the principal component analysis (PCA) of population allele frequencies of kittiwake and puffin ticks. Both PCA1 (inertia = 41.33%) and PCA2 (inertia = 17.28%) axes were significant ($P < 0.05$), and clustered tick populations according to host species (kittiwake, black circles; puffin, gray circles). A second analysis, conducted separately for each host group, was used to identify regional population groups (encircled populations). See Results for the details of the individual analyses. Population codes as in Figure. 1.

showed no genetic structure among populations. Within the other two groups, all populations were significantly differentiated (West Atlantic: Baccalieu Island and Cape St Mary's, $F_{ST} = 0.030$, $P < 0.001$; North-Norwegian: Isle of May and Nykvåg, $F_{ST} = 0.0510$, $P < 0.0001$; Cap Sizun and Nykvåg, $F_{ST} = 0.049$, $P < 0.0001$; Cap Sizun and Isle of May, $F_{ST} = 0.049$, $P < 0.0001$).

Population differentiation was almost always greater between kittiwake tick populations than between puffin tick populations, regardless of spatial scale (Fig. 3a). At the scale of each side of the Atlantic (i.e., not including transatlantic distances), significant isolation by distance was found for kittiwake tick populations, but not for puffin tick populations ($P = 0.004$ and $P = 0.917$, respectively; Fig. 3b). These results match those presented above and suggest that the frequency and/or extent of tick dispersal is greater for ticks that exploit puffins than for those that exploit kittiwakes.

## DISCUSSION

Although few studies to date have addressed parasite population structure (Lively 1999; Boulinier et al. 2001), those that have typically find that genetic variability and gene flow between discrete parasite populations is higher than was historically predicted (Price 1977) and suggest that the host plays an essential role in determining these population characteristics (e.g., Mulvey et al. 1991; Blouin et al. 1995, 1999). In line with this, previous studies examining population structure in Ixodid ticks have found relatively high within-population variation and little structuring at large spatial scales; the latter being presumably related to high host vagility (e.g., Hilburn and Sattler 1986; Delaye et al. 1997; Lampo et al. 1998; Kain et al. 1999). Similarly, in another host-ectoparasite system involving the chewing louse *Geomydoecus actuosi* and its pocket gopher host *Thomomys bottae*, low genetic variation within parasite populations and high population structuring (and substructuring) has been directly linked to host movement and social behavior (Nadler et al. 1990).

Unlike other Ixodid tick species, we expected that *Ixodes uriae* would show reduced within-population variation and high population structuring due to the short period of time this parasite spends on its host each year, its low inherent vagility, and the limited movement of breeding seabirds on land (McCoy et al. 1999). Instead, we found that tick populations of both host races were characterized by relatively high genetic variation and low population subdivision over a large spatial range. We also predicted that the population structure of *I. uriae* should depend on which host species it exploits. This prediction was supported; estimates of population differentiation were almost two times greater between

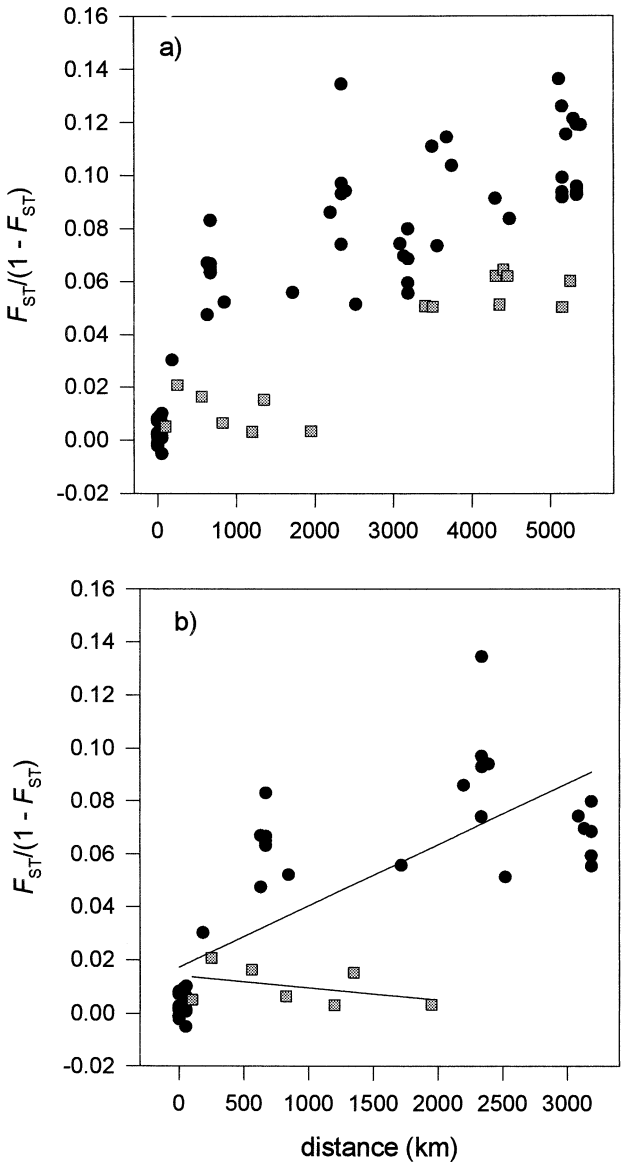


FIG. 3. Pairwise genetic distance ($F_{ST}/(1 - F_{ST})$ and geographic distance (km) between populations of kittiwake ticks (black circles) and puffin ticks (gray squares) over all distances (a), and between populations along each coast (b). At the scale of the Atlantic coast, only kittiwake tick populations showed significant isolation by distance (kittiwake ticks: $F_{ST}/(1 - F_{ST}) = 0.023 + 0.000021$ [distance km], $P = 0.004$; puffin ticks: $F_{ST}/(1 - F_{ST}) = 0.020 - 0.000087$ [distance km], $P = 0.917$).

kittiwake tick populations compared to puffin tick populations. Further, kittiwake tick populations showed some evidence of isolation by distance, but this was not the case for puffin ticks. These results strongly suggest that the frequency and/or extent of dispersal opportunities for puffin ticks is much greater than that for kittiwake ticks.

Low genetic differentiation among tick populations could also be accounted for by a recent population expansion rather than by frequent dispersal between established populations. Rapid population expansion can be characterized by a reduced within-population diversity compared to global diversity linked to founder events (Hedrick 2000). Here, we found that estimates of genetic diversity were similar among populations. This argues that gene flow between subdivided groups, rather than colonization events, may be responsible for patterns of population structure. Furthermore, diversity estimates of tick populations were similar for both host groups suggesting that race formation is old enough to have lost its signature in microsatellite diversity. Thus, it is likely that the differences we find in the population structure of the two host races reflect differential rates of gene flow and not historical factors.

The only way for ticks to disperse between discrete host colonies is through host movements during the breeding season. Very little is known about such movements in seabirds because most data come from band returns and depend on the intensity of marking and observation in different colonies (Harris 1983). Information on the dispersal of parasites can directly inform us about intercolony movements in such species. This is particularly interesting given that such movements do not necessarily result in the effective dispersal of host individuals and thus leave no genetic signature behind. Assuming that the probability of successfully dispersing ticks is low, our results suggest that movements at large scales ($>$ 100 km) may be more frequent than observed for both of the seabird species considered here (see introduction). For puffin ticks, we found no significant genetic structure between populations more than 1000 km apart (e.g., SK, Faroe Islands, and MN, Hornøya). However, the greater population differentiation of kittiwake ticks suggests that movements of this host species occur within somewhat smaller areas. These regions do not seem to be a simple function of geographic distance (e.g., Nykvåg in the North-Norwegian group rather than the Barents group), but instead may be related to historical feeding or wintering sites at sea. Except for the Barents region, we found that kittiwake tick populations within the other regional groups were significantly differentiated (see Results). The inclusion of more populations from these regions will most likely reveal other local homogeneous groups within these geographical areas. Similarly, within regions, the gene flow of ticks does not seem to be equal between all host colonies; in several instances, we found significant differentiation between nearby populations and no differentiation between more distant populations. For example, the puffin tick populations of Bleiksøya and Røst (250 km apart) showed some weak differentiation, whereas there was no significant structure between the populations of Bleiksøya and Skuvoy (1350 km apart). These patterns of host movement may be a result of ecological factors such as colony size or local breeding success with, for example, larger or more successful colonies attracting more visiting birds (Boulinier et al. 1996).

From our data on parasites, it seems that the frequency and/or extent of visits to different colonies is higher for puffins compared to kittiwakes. This is reasonable based on the characteristics of the two species as described above. However, it may also be that there is a host-associated probability of successful parasite dispersal. For example, a visiting puffin tends to move around within the colony and may even visit occupied burrows (Harris 1983). Any ticks that drop off during such a visit have a high probability of finding an appropriate host. Kittiwakes, on the other hand, nest on the vertical

areas of cliffs and usually defend their nest sites, such that prospecting birds will often land outside the actual breeding site during visits (Cadiou et al. 1994). This behavior should reduce the probability that these birds pick up local ticks and that engorged ticks that detach during visits find a suitable host for the next blood meal.

Frequent dispersal at large scales will directly alter the population dynamics of *I. uriae*. For example, for both host species, there should be a high probability for ticks to colonize breeding sites. Thus, noninfested breeding areas may be more a function of off-host microhabitat suitability or the presence of susceptible hosts than a lack of a colonization event. It will also mean that the buildup of local populations may occur rapidly due to dispersal in combination with local intrinsic growth. This influx of individuals may introduce novel alleles to populations that enable the rapid adaptation of ticks to local hosts (Gandon et al. 1996). Indeed, local adaptation of *I. uriae* to kittiwake hosts has been shown experimentally at a small scale (McCoy et al. 2002). However, the outcome of local interactions may depend on the amount of exchange between ticks of different host types (Lajeunesse and Forbes 2002). For example, gene flow between ticks of different alcid species (e.g., puffins and razorbills *Alca torda*), may block parasite adaptation to either host due to diffuse selection. Gene flow between host types could also help explain differential patterns of host-mediated dispersal. Based on previous results (McCoy et al. 2001), we have assumed in the present study that no gene flow occurs between ticks exploiting different host species. However, we can not yet say how gene flow between other potential tick races (i.e., ticks of other sympatrically occurring seabird species) may affect population structure and patterns of dispersal in these groups. The geographical patterns and extent of host race formation in the seabird tick is currently being investigated.

Parasite dispersal at large scales can also modify the population dynamics of their hosts. Previous observational studies have suggested that *I. uriae* may directly affect the reproductive success and local recruitment of host individuals (Boulinier and Danchin 1996) and, in extreme cases, may lead to the abandonment of breeding areas (e.g., King et al. 1977). Thus, the local spread of ticks and their ability to track host defenses may impact proximate host decisions, such as whether to attempt to breed in an area or to disperse (Boulinier et al. 2001). Clearly, the differential patterns of tick dispersal that we have shown here for the two host races should have important consequences for the nature and outcome of the interactions between these ectoparasites and their different seabird hosts. In mixed colonies, these interactions may also have direct consequences for the results of local interspecific competition for breeding sites (e.g., parasite-mediated or apparent competition).

The extent and frequency of tick dispersal will also have implications for the microparasites that they may harbor. For example, the spirochete responsible for Lyme disease in humans, *Borrelia burgdorferi* sensu lato, has been recorded in several seabird colonies in the North Atlantic, including some of the areas considered in this study (e.g., Olsen et al. 1993, 1995; Gylfe et al. 1999; Gasparini et al. 2001). Seabirds and *I. uriae* ticks have been suggested to maintain an independent and widespread enzootic cycle of *Borrelia* that may interact with local mammalian cycles (Olsen et al. 1993; Gylfe et al. 1999). Even though seabirds may frequently visit neighboring colonies, local movements are not equivalent to effective dispersal or gene flow. Most seabirds show relatively high levels of natal philopatry (e.g., 36% in kittiwakes; Coulson and Nève de Mévergnies 1992 and 60% in puffins; Harris 1983) and very strong breeding philopatry (>80–90% in puffins and kittiwakes; Harris 1983; Boulinier et al. 2001). This suggests that the spread of *Borrelia* to new colonies may be principally through ticks that are dispersed by the birds, rather than by the birds themselves. In this way, the breeding dispersal of birds does not necessarily give us an indication of the potential spread of this disease agent. Instead, we may need to consider the dispersal of the disease vectors. Only a few seabird colonies have been tested for the presence of *Borrelia* to date. Our results suggest that we may find it already established in most colonies in which ticks are present. Furthermore, as the genetic variation of *B. burgdorferi* sensu lato appears to be associated with both its pathogenicity and its tick vector specificity (Baranton et al. 2001), tick dispersal at different spatial scales and between different host types will need to be considered when investigating the dynamics and evolutionary history of this micropathogen in relation to both its vertebrate and invertebrate hosts (Wang et al. 1999; Randolph et al. 2002). For example, differential dispersal rates of tick races could result in different levels of *Borrelia* strain diversity in each host species, which may, in turn, alter the ability of hosts to respond efficiently to infection.

In conclusion, we have shown that the dispersal of seabird ticks among host populations is likely more frequent at large scales than could be predicted based on observed host movements, and that different host species provide different opportunities for this dispersal to occur. These results have direct implications for the ecological dynamics and coevolutionary interactions in this system with subsequent consequences for the epidemiology of tick-borne diseases, such as Lyme disease. More generally, these results point to the wealth of information that can be gained about host life-history characteristics by considering those of their parasites and, conversely, the importance of considering host behavior when investigating the evolutionary biology of parasites.

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