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Comparative host–parasite population structures: disentangling prospecting and dispersal in the black-legged kittiwake *Rissa tridactyla*

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Abstract

Although much insight is to be gained through the comparison of the population genetic structures of parasites and hosts, there are, at present, few studies that take advantage of the information on vertebrate life histories available through the consideration of their parasites. Here, we examined the genetic structure of a colonial seabird, the black-legged kittiwake (*Rissa tridactyla*) using seven polymorphic microsatellite markers to make inferences about population functioning and intercolony dispersal. We sampled kittiwakes from 22 colonies across the species' range and, at the same time, collected individuals of one of its common ectoparasites, the tick *Ixodes uriae*. Parasites were genotyped at eight microsatellite markers and the population genetic structure of host and parasite were compared. Kittiwake populations are only genetically structured at large spatial scales and show weak patterns of isolation by distance. This may be due to long-distance dispersal events that erase local patterns of population subdivision. However, important additional information is gained by comparing results with those of the parasite. In particular, tick populations are strongly structured at regional scales and show a stepping-stone pattern of gene flow. Due to the parasite's life history, its population structure is directly linked to the frequency and spatial extent of within-breeding season movements of kittiwakes. The comparison of host and parasite gene flow therefore helps us to disentangle the intercolony movements of birds from that of true dispersal events (movement followed by reproduction). In addition, such data can provide essential elements for predicting the outcome of local co-evolutionary interactions.

Keywords: colonial seabirds, dispersal, ectoparasite, host–parasite interactions, *Ixodes uriae*, microsatellites

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Introduction

Much can be learned through the comparison of the population genetic structures of species that inhabit sympatric ranges. Ecological and evolutionary factors that affect one species will often affect another and the joint consideration of such species can provide important insight into the relative importance of factors in shaping current distributions and population characteristics (Pellmyr *et al*. 1998; Avise 2000; Zink 2002). Indeed, there are numerous examples of comparative studies of species with shared ranges (e.g. Zink 2002; Bernadi *et al*. 2003; Hoffmann & Baker 2003). However, few studies have taken such an approach with interacting species, and particularly with a host and its parasite (Pellmyr *et al*. 1998; Nieberding *et al*. 2004). Depending on the nature of the interaction, such an approach can offer important insight into the ecology of both host and parasite and provide information about effective population sizes, dispersal distances, gene flow rates and the factors that control these parameters. Relative host–parasite dispersal rates are particularly important as they will help define the scale at which co-evolution occurs and may alter the potential of each species to adapt locally (Gandon *et al*. 1996; Gandon & Michalakis 2002).

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Comparative studies of host–parasite population structure to date have found variable results with regard to congruence in population structure and inferences about relative dispersal rates. Parasites have often been found to have more structured populations suggesting lower rates of gene flow (Althoff & Thompson 1999; Delmotte *et al*. 1999; Martinez *et al*. 1999; Burban & Petit 2003), but the reverse has been found (Michalakis *et al*. 1993; Dybdahl & Lively 1996; Davies *et al*. 1999; Mutikainen & Koskela 2002), and in a few cases host and parasite showed similar degrees of population structure (Nadler *et al*. 1990; Mulvey *et al*. 1991; Parker & Spoerke 1998). Only in those systems where host and parasite dispersal are linked has population structure been found to be correlated (Nadler *et al*. 1990; Dybdahl & Lively 1996; Parker & Spoerke 1998). Although many of these studies have examined interactions between few populations or at limited spatial scales, all have revealed important information about the factors acting on both host and parasite.

Despite high rates of site fidelity and socially monogamous mating systems, many seabird species of the Northern Hemisphere are characterized by weakly structured populations. This is largely thought to be due to the recent establishment of colonies since the last glacial period and/or to long-distance dispersal events (Birt-Friesen *et al*. 1992; Moum & Arnason 2001; Patirana 2000; Burg *et al*. 2003). Most studies have focused on mitochondrial genetic markers and a call has been made to explore more contemporary patterns in these species using hypervariable nuclear markers, such as microsatellites (Moum & Arnason 2001). However, these markers have met with variable success in revealing population structure in seabirds (Burg & Croxall 2001, 2004; Roeder *et al*. 2001; Abbott & Double 2003; Riffaut *et al*. 2005) and suggest that large effective population sizes and occasional long-distance dispersal may eliminate the genetic signature of population subdivision in such species. In this way, the incorporation of information from parasites that depend on these hosts for intercolony dispersal may prove particularly useful in providing ecological information on the local functioning of seabird populations.

The black-legged kittiwake (*Rissa tridactyla*) is a small, pelagic gull that breeds in large colonies in the temperate and Arctic zones of the Northern Hemisphere. Two subspecies have been described, *Rissa tridactyla tridactyla* in the North Atlantic and *Rissa tridactyla pollicaris* in the North Pacific (Burger & Gochfeld 1996). Variation in plumage characteristics (Chardine 2002) and patterns of local philopatry (Coulson & Nève de Mévergnies 1992; Danchin & Monnat 1992; Boulinier *et al*. 2001; Suryan & Irons 2001) have suggested regional population structure in this species. For example, ring recoveries and observational work has suggested that most kittiwakes disperse within 100 km of their natal colony, although recoveries also occur at distances of 400–900 km (Coulson & Nève de Mévergnies 1992). The mechanism behind dispersal decisions in these birds is poorly understood at large spatial scales, but some insight has been gained through detailed behavioural and demographic studies at small scales (Danchin *et al*. 1998). In particular, young birds (nonbreeders) or failed breeders will often visit colonies during the breeding season (Coulson & Nève de Mévergnies 1992) and are thought to be evaluating the quality of different breeding patches as potential future breeding sites (i.e. prospecting; Cadiou *et al*. 1994; Boulinier *et al*. 1996). As prospecting is correlated with later recruitment to the colony, this behaviour is a direct reflection of local population dynamics (Danchin *et al*. 1998).

The tick *Ixodes uriae* (family Ixodidae) is a common ectoparasite in seabird colonies of the circumpolar regions of both hemispheres (Guiguen 1988). Although this tick has previously been considered a seabird generalist, recent work has shown that it has formed host-associated races throughout its range, including a race specific to the black-legged kittiwake (McCoy *et al*. 2001). Indeed, a detailed genetic study that examined monospecific and heterospecific tick populations of six different seabird species, three of the Northern Hemisphere (*R. tridactyla*, *Fratercula arctica*, *Uria aalge*) and three of the Southern Hemisphere (*Aptenodytes patagonicus*, *Eudyptes chrysocome*, *Eudyptes chrysolophus*), supports the hypothesis that host-race formation is a recurrent phenomenon in this system and suggests that little to no gene flow occurs among sympatric races (McCoy *et al*., unpublished). Dispersal of this tick between isolated seabird colonies can only occur via its host. Because it is highly unlikely that ticks survive on the bird during the 7–8 months they spend at sea each year, intercolony dispersal of the parasite will be confined to the reproductive period of the host. In this sense, gene flow in the tick is a direct reflection of the within-breeding season movements of birds.

In a previous study, we examined the population genetic structure of the kittiwake tick and found that this parasite is structured at regional scales, with significant differentiation between colonies at distances of 200–500 km and strong patterns of isolation by distance (McCoy *et al*. 2003). A study examining mitochondrial control region variation has suggested that kittiwake populations are also structured within the North Atlantic, but at larger spatial scales than for the parasite (Patirana 2000). However, no corresponding structure in the kittiwake was found using a nuclear marker (intron RBP) (Patirana 2000) suggesting that the mitochondrial results could represent historical isolation or sex-biased dispersal.

Here, we used a comparative approach of host and parasite population structures to make inferences about the population functioning and dispersal of kittiwakes. Kittiwakes and their ticks were sampled in the same colonies from across their range and genotyped at several polymorphic microsatellite loci. Using this data, we first examined

host population structure to make inferences about population subdivision and effective dispersal in this seabird. Next, we carried out a similar independent analysis for the parasite and then compared the genetic structures of the interacting species. Our aims were to determine (i) whether prospecting in the kittiwake was correlated with effective dispersal and (ii) the potential for host/parasite local adaptation at the considered spatial scales. If parasite dispersal reflects that of its host (i.e. kittiwakes actively disperse to the areas that they visit during the breeding season), host–parasite population structures should be correlated. If structures are uncorrelated, kittiwake movements within the breeding season either do not match their habitat choice or gene flow has eliminated the genetic signature of local population function.

Materials and methods

Study species

The biogeographical population size of the black-legged kittiwake (family Laridae) numbers more than 4 million breeding pairs (Heubeck 2004). Colonies range in size from tens to several thousand breeding pairs and are typically found in isolated areas where birds build their nests on steep sea cliffs. After reaching adulthood at 3–5 years of age, individuals can reproduce for more than 10 years (e.g. Danchin & Monnat 1992). Natal philopatry is relatively high in this species (36–56%, Coulson & Nève de Mévergnies 1992; Danchin & Monnat 1992), as is breeding site fidelity (80–99%, Danchin & Monnat 1992; Boulinier *et al*. 2001). In Britain, 80% of kittiwakes have been reported to recruit to their natal colony or to within 50 km of this colony (Coulson & Nève de Mévergnies 1992). However, these parameters may vary depending on the quality of the breeding patch (Danchin & Monnat 1992; Danchin *et al*. 1998; Boulinier *et al*. 2001) and the reproductive success of individuals is directly linked to the quality of the local environment (food resources, parasitism and predation). Kittiwakes are only associated with land during the 4–5 months of the breeding season and overwinter at sea. During the winter, these birds move widely across the North Atlantic, with individuals from northern European colonies frequently being recovered off the coasts of Newfoundland and Greenland (Barrett & Bakken 1997) and the northwestern populations moving further south down the coast (Coulson 2002).

Ixodes uriae is a hard tick commonly found in seabird colonies throughout the circumpolar regions of both hemispheres. Although recorded from many different species of colonial seabirds (Guiguen 1988), host-associated races of this parasite have recently been demonstrated, and notably for the black-legged kittiwake (McCoy *et al*. 2001). This race seems to be specific to kittiwakes as other common local seabird species are either only rarely infested (*Larus marinus*, *Larus argentatus*; K. McCoy, unpublished) or have distinct races of their own (*Fratercula arctica*, *Uria aalge*, McCoy *et al*. unpublished). *Ixodes uriae* typically takes only a single, long blood meal per year (3–12 days, McCoy *et al*. 2002) during its 4-year life cycle and thus spends most of its life in the area surrounding the host's breeding site. 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. Infestation by this parasite is known to reduce the reproductive success of host individuals (e.g. Morbey 1996; Bergstrom *et al*. 1999) that may, in turn, modify the population dynamics of the host (Boulinier & Danchin 1996; Boulinier *et al*. 2001). In addition to these direct effects, this ectoparasite is also a vector of numerous arboviruses and bacteria (Chastel 1988), including the agent responsible for human Lyme disease *Borrelia burgdorferi sensu lato* (Olsen *et al*. 1993). The effect of these microparasites on seabird dynamics is largely unknown, but clearly the scale and frequency of seabird and tick dispersal will have important implications for the dynamics of the host–parasite interaction and for disease epidemiology.

Sampling

Kittiwakes. Individuals were sampled in 22 populations across the range of the species over a 10-year period (Fig. 1, Table 1). Young birds, still constrained to the nest, were sampled in preference, but in certain locations, only breeding adults could be obtained. As kittiwakes breed in vertical cliff areas, static climbing techniques were employed to reach nests in several of the colonies. In most populations, sampling consisted of taking a small blood sample (0.1–0.3 mL) from the brachial vein using a sterile syringe rinsed with heparin. Blood samples were stored in a Tris-EDTA buffer. In some populations, DNA was extracted from muscle tissue or growing feathers stored in 70–90% ethanol. All manipulated birds were either ringed or temporarily marked to avoid sampling the same individual twice.

Ticks. During the sampling of kittiwakes, we also attempted to collect a sample of their ectoparasites. We obtained tick samples for 14 of the 22 kittiwake populations from a variable number of host individuals (Fig. 1, Table 1). Some colonies were not infested or were unable to be sampled. Others were only lightly infested and, in these areas, parasite sample sizes were too low to be considered representative. Only the Newfoundland (NF) tick and kittiwake samples came from separate locations, although both were sampled from the Avalon Peninsula. Ticks are most readily found on chicks by visual search and skin palpation, but can also be found in the head region of adult

Fig. 1 Populations sampled across the range of the black-legged kittiwake *Rissa tridactyla*. Colonies where *Ixodes uriae* was also sampled are indicated by white circles. Abbreviations of sample locations are indicated in Table 1.

birds. Collected ticks were stored in 70–90% ethanol prior to DNA extraction. Genotyped ticks included individuals from as many different birds as possible to ensure a representative population sample (Table 1).

Molecular methods

Genomic DNA of kittiwakes was obtained using a commercial kit (Perfect gDNA Blood Mini Isolation Kit, Eppendorf). The same kit was used for solid tissue and feather samples. Kittiwakes were genotyped for seven dinucleotide microsatellite loci. Six of these markers were isolated specifically from this species (K6, K16, K31, K32, K67, K71; Tirard *et al.* 2002) and one was developed for the common guillemot, *Uria aalge* (HC6; GenBank Accession no.: AY359959). For all loci, polymerase chain reactions (PCR) and amplification conditions were carried out as described in Tirard *et al*. (2002). PCR products were visualized and sized on an automated DNA sequencer (ABI Prism 310) using GENESCAN version 3.1.2 (ABI) and ROX 400HD size standard (ABI).

For ticks, a high-salt DNA extraction method was employed as described in McCoy & Tirard (2000). Ticks were then genotyped at eight dinucleotide microsatellite loci (T3, T5, T22, T35, T38, T39, T44, T47; McCoy & Tirard 2000). PCR procedures followed those outlined in McCoy & Tirard (2000) and resulting PCR products were run on 6% acrylamide gels using size controls.

Data analyses

To compare population structures of host and parasite, analyses were first carried out individually for each species. We then contrasted the results of the two and tested whether their genetic structures were correlated and related to geographical distance.

All populations and loci were tested for departure from Hardy–Weinberg equilibrium using exact probability tests as implemented in GENEPOP version 3.3 (Raymond & Rousset 1995). To ensure independence among loci, data were similarly tested for linkage equilibrium (10^7 iterations). Significance levels were corrected for multiple tests (Rice 1989). Allelic richness, gene diversity (Nei 1987), and expected heterozygosity were calculated for each population using the program FSTAT version 2.9.3 (Goudet 1995). As the number of detected alleles is highly dependent on the number of individuals sampled, allelic richness was calculated by estimating the expected number of alleles for a given locus in a subsample of $2n$ genes, where n is fixed at the smallest number of individuals typed for a sample. Differences in diversity estimates were compared among

Table 1 Sampling locations of kittiwakes and their parasitic tick. Abbreviations are indicated in brackets for each sampled population, along with its location, the sample year(s) and number of kittiwakes (N_{KT}) and ticks (N_T) genotyped. The number of hosts that ticks were collected from is indicated in brackets

Location	Population	Location	Sample year	N_{KT}	N_T
Alaska, USA	Middleton Island (MI)	59°26′N, 146°20′W	2002	40	30 (30)
Canada	Newfoundland (NF)	47°15′N, 52°46′W	1992	23	36* (20)
	Prince Leopold (PL)	74°00′N, 90°00′W	1993	10	—
Greenland	Hakluyt (HI)	77°26′N, 72°42′W	2001	10	—
Iceland	Flaty (FT)	65°22′N, 22°56°W	2001	24	—
Scotland	Colonsay (CO)	56°06′N, 06°10′W	2001	30	—
	Whinnyfold (WF)	57°23′N, 01°51′W	2001	28	35 (19)
	Orkneys (OK)	59°08′N, 03°20′W	2001	18	24 (5)
	Fair Isle (FI)	59°32′N, 01°37′W	2001	29	42 (18)
	Foula (FO)	60°08′N, 02°05′W	2001	30	18 (6)
	Sumburgh Head (SH)	59°51′N, 01°16′W	2001	30	25 (12)
Ireland	Rockabill (RB)	53°36′N, 06°01′W	2001	32	—
France	Cap Sizun (CS)	48°02′N, 04°44′W	1995–2000	66	25† (15)
Norway	Nykvåg (NK)	68°45′N, 14°30′E	2000	20	24 (14)
	Bjarkøya (BJ)	69°01′N, 16°30′E	2000	16	0
	Gjesvær (GJ)	71°10′N, 25°20′E	2000	29	9 (9)
	Syltefjord (SF)	70°40′N, 30°20′E	2000	22	24 (24)
	Reinøya (RN)	70°22′N, 31°08′E	2000	30	22 (22)
	Hornøya (HN)	70°22′N, 31°10′E	2000	39	30 (30)
	Ekkerøy (EK)	70°05′N, 30°06′E	2000	30	23 (23)
Spitzberg	Krykkjefjellet (KF)	78°55′N, 11°57′E	1999	27	0
	Ossiansarsfjellet (OS)	78°57′N, 11°57′E	1999	29	0

*Parasites sampled in 1997 in same region.
†Parasites all sampled in 1997.

populations using a Kruskal–Wallis test and between kittiwakes and ticks using a Wilcoxon 2-sample test (Zar 1996).

Hierarchical population structure was quantified using Weir & 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 2.9.3; Goudet 1995). Standard errors were calculated by jackknifing over loci (Goudet 1995).

To describe the geographical clustering of populations, we carried out a principal component analysis (PCA) using the program PCA-GEN version 1.2 (1999, J. Goudet, Institute of Ecology, 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 a first analysis, we included all populations of the host or parasite. In a second, we removed the Pacific population of Middleton Island (MI) to examine structure within the North Atlantic only. Regional population groupings were identified from the PCA and were verified using assignment tests. In particular, a Bayesian approach was used to directly assign each individual to the regional group where the likelihood of its multilocus genotype was the highest (program GENECLASS version 1.0.02; Cornuet *et al*. 1999). We then calculated the percentage of correct assignments to each group.

Isolation by distance was tested using the correlation between genetic distance, measured as $F_{ST}/(1 - F_{ST})$, and geographical distance of population pairs (log transformed). Geographical distance was measured as the shortest distance between populations. However, because kittiwakes do not typically fly inland, we also used a relative measure of the geographical distance between colonies by sea. Correlations were tested for significance using Mantel permutation procedures (Mantel 1967) associated with Spearman rank correlation coefficients as test statistics (GENEPOP 3.3). At very large spatial scales, processes other than dispersal are likely to affect estimated differentiation (i.e. mutation; Rousset 1997). Therefore, tests of isolation by distance were limited to North Atlantic populations only. Genetic distances between colonies of less that 5 km (corresponding to neighbouring 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). To take into account any possible effects of sampling year, we also carried out partial Mantel tests that included the difference in the sampling year of each population pair (FSTAT 2.9.3; Goudet 1995).

The population structures of kittiwakes and their ticks were directly compared by testing for a correlation in the pairwise genetic distances between populations where both species were sampled (14 populations, Table 1). The correlation was tested for significance using the same procedure as outlined for tests of isolation by distance. A positive correlation between estimates of genetic distance would suggest that the colonies that kittiwakes prospect in during the breeding season are the same as those that they disperse to.

Results

Kittiwakes

After correction for multiple tests, all populations and loci were in Hardy–Weinberg equilibrium. Without correction, two populations deviated slightly from expectations (RN, $P = 0.02$ and FI, $P = 0.04$). For this reason, we did not consider alleles independent for testing the significance of population differentiation; 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 seven loci used (all $P > 0.05$).

Estimates of allelic richness per population were variable with the highest value in the Pacific population MI (6.10 ± 1.14) and somewhat lower values in the Atlantic populations (average richness $= 4.12 \pm 0.10$). However, this variation among populations was not statistically significant (Kruskal–Wallis test; $P = 0.999$). Similarly, neither gene diversities nor observed heterozygosities varied significantly among kittiwake populations (Kruskal–Wallis test; $P = 0.999$ and $P = 1.0$ for gene diversity and observed heterozygosity, respectively).

The first two axes of the PCA including all kittiwake populations accounted for 53.02% of the total inertia (40.63% and 12.39%, respectively, for PC1 and PC2). However, only PC1 explained a significant proportion of the total inertia and clearly separated the Pacific population (MI) from the Atlantic populations (Fig. 2A). This separation corresponds to the described subspecies and was supported by assignment tests; 99.67% of kittiwakes were correctly assigned to their respective ocean basin. When the Pacific population was removed from the PCA, no regional structure was evident and neither PC1 nor PC2 could explain a significant amount of the total inertia ($P > 0.05$) (Fig. 2C).

Significant differentiation was found among kittiwake populations ($F_{ST} = 0.021 \pm 0.002$, $P < 0.0002$), but most of this was due to differences between the Pacific and Atlantic populations. Indeed, all pairwise F_{ST} estimates between population MI and the Atlantic populations were highly significant (Table 2). Among the Atlantic populations, the overall estimate of differentiation was lower, although still significant ($F_{ST} = 0.006 \pm 0.003$, $P < 0.0002$). There were several pairwise estimates of F_{ST} that were significant at the $P < 0.05$ threshold, but only two remained significant after correction for multiple tests (Table 2).

In agreement with the overall population structure of kittiwakes, a weak correlation was found between genetic distance and log geographical distance ($P = 0.048$) (Fig. 3A). This pattern was similar if geographical distance was measured as the shortest distance between populations ($P = 0.064$) instead of the shortest distance by sea. The relationship with distance did not improve by the inclusion of sampling year as an independent variable (partial Mantel test: distance, $P = 0.162$; difference in sample years, $P = 0.496$). These results suggest that kittiwake populations either function under an island-type model of dispersal or that dispersal is frequent enough to weaken signs of isolation by distance.

Ticks

Most tick populations and loci were found to be in Hardy–Weinberg equilibrium. After correction for multiple tests, only one population (NF, $P = 0.0013$) deviated from equilibrium due to a slight deficit of heterozygotes at a single locus (T39). However, overall patterns suggested no global problems with any one population or locus. Nonetheless, as with the kittiwakes, we did not consider alleles independent for testing the significance of population differentiation and permutation tests of F_{ST} estimates used the genotype as the randomization unit instead of the allele (Goudet 1995). No overall linkage disequilibrium was detected among loci. However, significant disequilibrium was evident between two loci (T22 and T44, $P = 0.00077$) in population MI. This population is the only one included from the Pacific Ocean and suggests that the markers may have experienced different evolutionary histories in the different ocean basins. All analyses that follow include both loci, but the elimination of either locus does not change the general results.

Estimates of allelic richness showed similar levels of variation across populations (Kruskal–Wallis test; $P = 0.948$; average richness $= 4.21 \pm 0.11$). Likewise, neither gene diversities nor observed heterozygosities varied significantly among tick populations (Kruskal–Wallis test; $P = 0.988$ and $P = 0.922$, respectively).

Principal component analyses of tick populations accounted for much more variation in allele frequencies than did those for kittiwake populations. The first axis alone of the PCA including all tick populations accounted for 59.32% of the total inertia and clearly isolated the Pacific (MI) and Atlantic populations (Fig. 2B). This separation corresponds to that found for the kittiwake (Fig. 2A) and suggests strong isolation of both host and parasite between ocean basins. However, unlike for the host, when the Pacific population was excluded from the PCA, clear regional structure was found among tick populations in

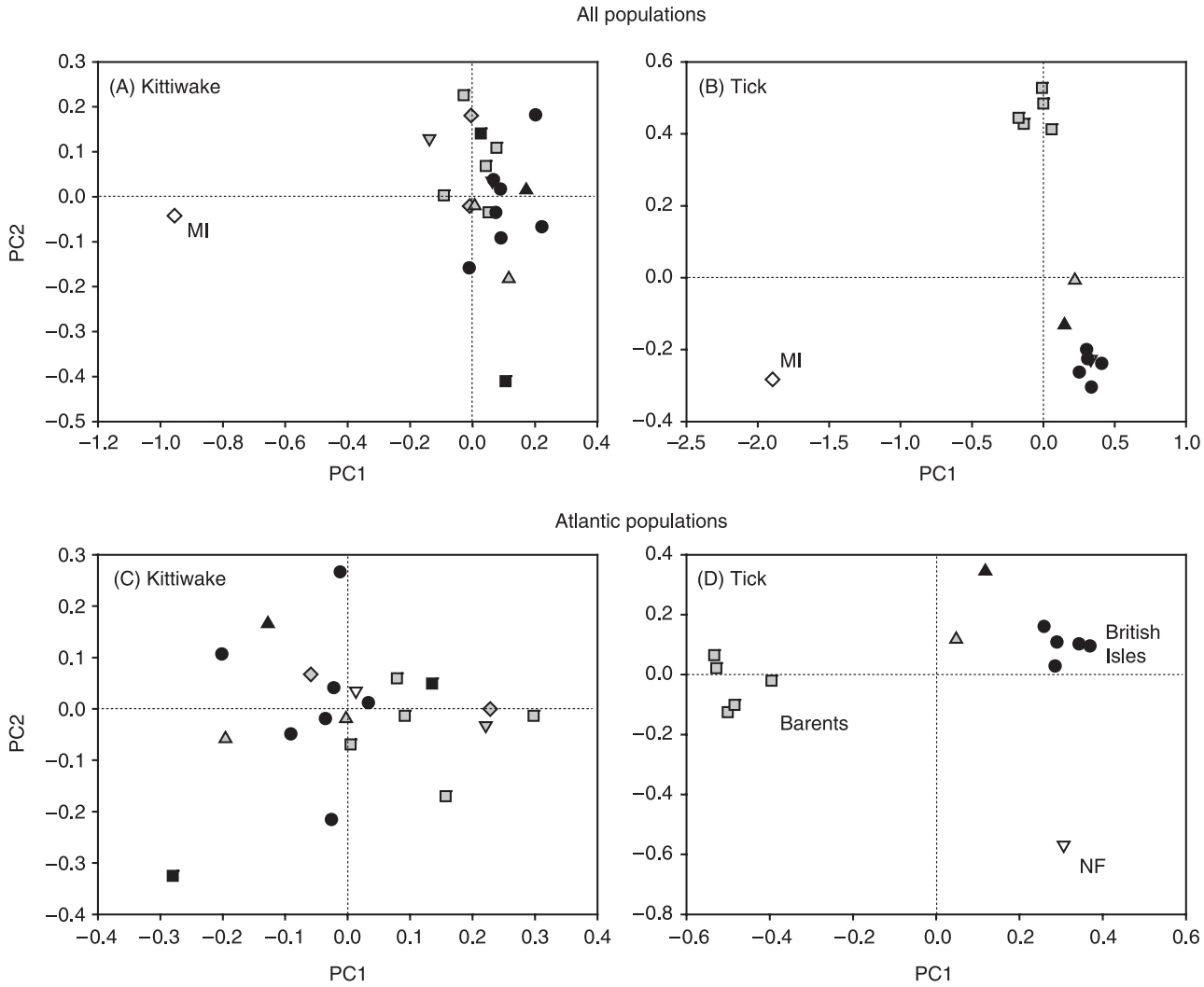

Fig. 2 Factor maps of the principal component analyses (PCA) of host and parasite. (A) All kittiwake populations included (PC1 inertia = 40.63%, $P < 0.0002$; PC2 inertia = 12.39%, $P = 0.9884$). (B) All tick populations included (PC1 inertia = 59.32%, $P < 0.0002$; PC2 inertia = 16.80%, $P = 0.1998$). (C) Only the Atlantic kittiwake populations (PC1 inertia = 20.67%, $P = 0.516$; PC2 inertia = 18.29%, $P = 0.0598$). (D) Only the Atlantic tick populations (PC1 inertia = 44.60%, $P < 0.002$; PC2 inertia = 17.55%, $P = 0.2042$). Populations are labelled by geographical region: ◇, MI; ◆, PL and HI; ▽, Newfoundland (NF); ▼, FT; ▲, CS; △, BJ and NK; □, Barents Sea (GJ, SF, RN, HN, EK); ■, Spitzbergen (KF, OS); ●, British Isles (CO, FI, FO, OK, RB, SH). Abbreviations refer to colony names given in Table 1.

the North Atlantic (Fig. 2D). In this analysis, the first two axes explained 62.16% of the variance in allele frequencies and separated populations into three main groups (Barents Sea, British Isles and Newfoundland). These groups were supported by assignment tests (85.34% of ticks were correctly assigned to their group of origin).

Overall differentiation among tick populations was higher than that for their hosts ($F_{ST} = 0.11 \pm 0.02$, $P < 0.0002$). Again, all pairwise F_{ST} estimates between MI and the Atlantic populations were highly significant (Table 2). However, the overall estimate of differentiation was still relatively high among the Atlantic populations ($F_{ST} = 0.048 \pm 0.011$, $P < 0.0002$). Significant pairwise estimates of F_{ST} were found between many of the populations and generally corresponded to the groupings found in the PCA analysis (Table 2).

Unlike for the kittiwake, strong isolation by distance was found for tick populations ($P < 0.00001$) (Fig. 3B). This result was the same regardless of how intercolony geographical distance was measured. Furthermore, the addition of the sampling year variable did not strongly affect this relationship (partial Mantel test: distance, $P = 0.0005$; difference in sample years, $P = 0.098$).

Host–parasite

Despite the fact that overall variability of the genetic markers was similar for kittiwakes and ticks (Wilcoxon

Table 2 Estimates of F_{ST} between all populations of kittiwakes (upper-half matrix) and ticks (lower-half matrix). Note that estimates less than 0.001 are marked as 0.000. Significance levels are indicated by the following: values at $P < 0.05$ are underlined, $P < 0.01$ are underlined and in bold, and values that are significant after Bonferroni correction are indicated by *

	MI	CO	CS	WF	HI	RB	FT	NF	BJ	EK	GJ	HN	NK	RN	SF	PL	OK	FI	FO	SH	KF	OS
MI		**0.101***	**0.127***	**0.129***	**0.081***	**0.128***	**0.071***	**0.104***	**0.108***	**0.104***	**0.096***	**0.099***	**0.084***	**0.078***	**0.092***	**0.093***	**0.097***	**0.088***	**0.101***	**0.104***	**0.121***	**0.094***
CO	—		0.003	0.000	0.001	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.007	0.004	0.000	0.000	0.000	0.000	0.018	0.000
CS	**0.307***	—		0.009	0.002	0.002	0.017	0.009	0.007	0.009	0.006	**0.010**	0.000	0.016	0.020	**0.026**	0.005	**0.014**	0.001	0.008	**0.030***	**0.011**
WF	**0.368***	—	**0.037***		0.016	0.000	0.017	0.015	0.022	0.000	0.008	0.011	0.007	**0.026**	0.012	0.018	0.002	0.022	0.007	0.017	**0.039**	0.001
HI	—	—	—	—		0.006	0.007	0.000	0.000	0.001	0.001	0.004	0.000	0.007	0.018	0.000	0.003	0.008	0.000	0.001	**0.027**	0.011
RB	—	—	—	—	—		**0.021**	0.006	0.005	0.002	0.003	**0.011**	0.007	0.017	0.019	0.017	0.000	0.010	0.002	0.008	0.014	**0.012***
FT	—	—	—	—	—	—		0.011	0.028	0.004	0.005	0.011	0.002	0.000	0.000	0.011	0.006	0.007	0.005	0.010	**0.035**	0.005
NF	**0.366***	—	**0.093***	**0.053***	—	—	—		0.018	0.010	0.000	0.000	0.006	0.013	0.010	0.000	0.001	0.011	0.000	0.011	**0.024**	0.011
BJ	—	—	—	—	—	—	—	—		0.009	0.004	0.012	0.001	0.008	0.023	0.025	0.001	0.003	0.000	0.000	0.012	0.005
EK	**0.293***	—	**0.066***	**0.079***	—	—	—	**0.107***	—		0.000	0.004	0.005	0.003	0.000	0.011	0.002	0.004	0.000	0.000	0.025	0.000
GJ	**0.251***	—	**0.058***	**0.092***	—	—	—	**0.087***	—	0.001		0.000	0.000	0.000	0.002	0.004	0.000	0.000	0.000	0.000	0.012	0.000
HN	**0.288***	—	**0.063***	**0.072***	—	—	—	**0.084***	—	0.000	0.001		0.000	0.004	0.003	0.000	0.000	0.003	0.000	0.003	**0.023**	0.000
NK	**0.324***	—	**0.046***	**0.039***	—	—	—	**0.074***	—	**0.061***	**0.054***	**0.057***		0.003	0.005	0.000	0.000	0.000	0.000	0.002	0.016	0.000
RN	**0.295***	—	**0.056***	**0.063***	—	—	—	**0.085***	—	0.001	0.002	0.000	**0.058***		0.000	0.006	0.001	0.000	0.001	0.001	0.020	0.002
SF	**0.245***	—	**0.068***	**0.082***	—	—	—	**0.108***	—	0.010	0.004	0.003	**0.043***	0.009		0.000	0.006	0.008	0.004	0.010	**0.037**	0.000
PL	—	—	–	–	—	—	—	—	—	—	—	—	—	—	—		0.000	0.016	0.005	0.009	**0.040**	**0.012**
OK	**0.344***	—	**0.047***	**0.000**	—	—	—	**0.057***	—	**0.083***	**0.093***	**0.076***	**0.056***	**0.063***	**0.082***	—		0.000	0.000	0.001	0.007	0.000
FI	**0.321***	—	**0.024***	**0.002**	—	—	—	**0.046***	—	**0.066***	**0.063***	**0.060***	**0.036***	**0.046***	**0.066***	—	**0.003**		0.000	0.001	0.004	0.003
FO	**0.331***	—	**0.034***	0.007	—	—	—	**0.060***	—	**0.067***	**0.066**	**0.059***	0.023	**0.048***	**0.059***	—	0.006	0.003		0.000	0.012	0.000
SH	**0.334***	—	**0.030***	0.005	—	—	—	**0.038***	—	**0.071***	**0.063***	**0.055***	**0.029***	**0.047***	**0.064***	—	**0.007**	0.000	0.000		**0.031**	0.001
KF	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		**0.030**
OS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

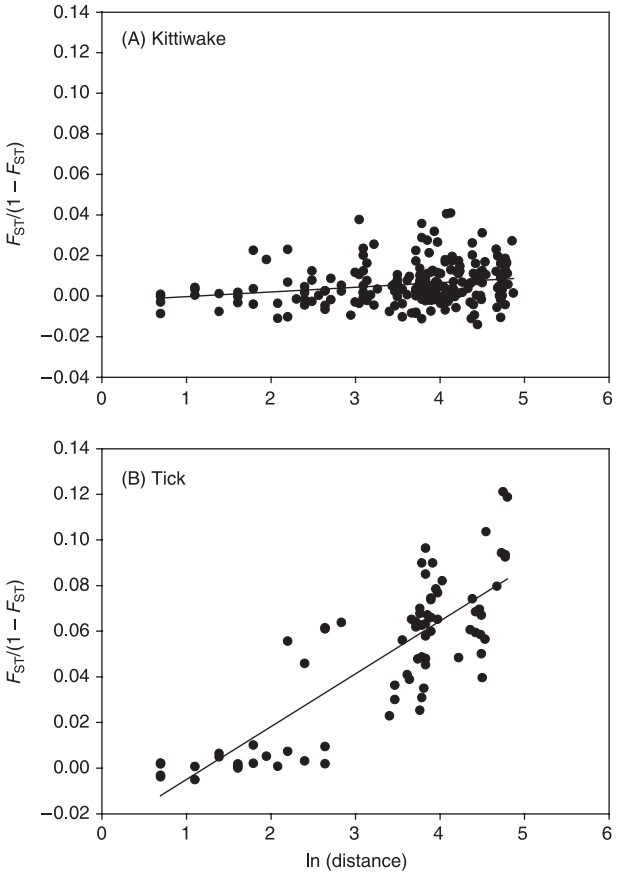

Fig. 3 Pairwise genetic distance ($F_{ST}/1 - F_{ST}$) and geographical distance between kittiwake (A) and tick (B) populations. Geographical distances are measured as the shortest distance by sea. Only Atlantic populations and those greater than 5 km apart are included in the analyses. Both host and parasite showed significant patterns of isolation by distance [kittiwake: $F_{ST}/(1 - F_{ST}) = -0.0025 + 0.0023$ (ln distance), $P = 0.0477$; tick: $F_{ST}/(1 - F_{ST}) = -0.028 + 0.024$ (ln distance), $P < 0.0001$].

2-sample test: gene diversity, $z = 0.1736$, $P = 0.862$; observed heterozygosity, $z = 0.405$, $P = 0.685$), tick populations tended to be more structured than those of their hosts. When all populations were considered, there was a significant correlation between estimates of genetic distance of the two species ($P = 0.007$). However, when the Pacific population (MI) was removed, this correlation largely disappeared and there was little correspondence between the genetic structures of the interacting species ($P = 0.108$) (Fig. 4). When the geographical distance between colonies is mapped onto this correlation, we see that this result was largely due to variation in the estimated genetic differentiation of the host (Fig. 4). Under distances of 500 km, both host and parasite show little population structure. However, at greater distances, the parasite starts to show significant structure, whereas the pattern in the host remains low and variable.

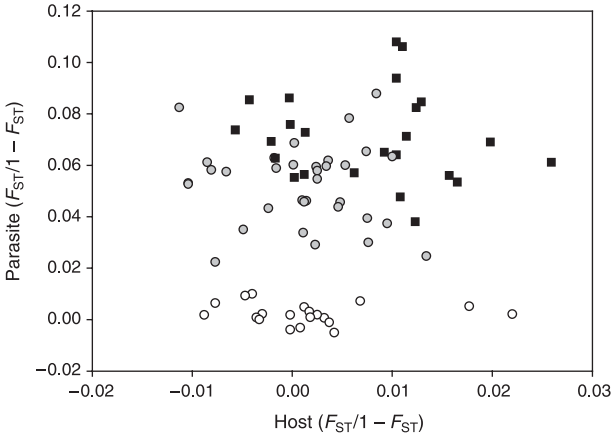

Fig. 4 Pairwise genetic distance ($F_{ST}/1 - F_{ST}$) estimates between populations of hosts and parasites ($n = 14$ populations). Symbols refer to the geographical distance between colonies (open circles, less than 500 km; grey circles, between 500 and 3000 km; black squares, greater than 3000 km). At distances greater than 500 km, the parasite shows significant genetic structure, but the host does not.

Discussion

Much can be learned through the comparison of the population genetic structures of interacting species. In particular, contrasting host and parasite will not only inform us about the population ecology of each species, but also about the factors influencing the co-evolutionary interaction. Here, we examined the population genetic structure of the black-legged kittiwake using hypervariable microsatellite markers and compared results to those of its parasite, the tick *Ixodes uriae*. This parasite is involved in an intimate interaction with this seabird host, depending on it for its local survival and dispersal.

Kittiwake population structure

The seven microsatellite markers used in this study showed levels of variability comparable to those found for other seabirds (Burg & Croxall 2001, 2004; Roeder *et al*. 2001; Abbott & Double 2003; Riffaut *et al*. 2005). Nonetheless, there was only weak evidence of population structuring in this species across its range and most differentiation was found between the Pacific population (MI) and those in the North Atlantic. This last result matches that found at a mitochondrial locus (Patirana 2000) and corresponds to the subspecies status given to kittiwakes of each ocean basin. As kittiwake colonies extend across the Arctic coast of Asia towards the North Pacific, it is unclear where the transition between the two subspecies occurs and whether there is complete separation of their distributions (Coulson 2002). Samples would be required from these populations to determine the amount

of mixing that occurs and whether there is any hybridization between the two groups.

In contrast to population genetic subdivision between the ocean basins, there was no evidence of structuring among kittiwake populations of the North Atlantic. No regional groups were identifiable from the PCA and only weak evidence for isolation by distance was detected among populations. These results correspond to low overall estimates of differentiation ($F_{ST} = 0.006 \pm 0.003$) and generally nonsignificant pairwise population structures (Table 2). The fact that kittiwakes were sampled over a 10-year period did not seem to affect results, which is not surprising given that this period likely falls within a single kittiwake generation. Overall, the results suggest that either (i) kittiwakes are generally panmictic across the North Atlantic and follow an island model of dispersal (i.e. if they decide to disperse there is an equal probability that they may go to any colony within the ocean basin) or (ii) dispersal occurs frequently enough to mask the genetic structure of regional population groups.

These results contrast those found for morphological and mitochondrial markers (Patirana 2000; Chardine 2002). A study of geographical variation in wingtip plumage across the circumpolar range of the kittiwake indicated two morphologically distinguishable groups in the North Atlantic: one in the Canadian Arctic–west Greenland and one including Newfoundland, the British Isles and the Barents Sea (Chardine 2002). Assuming a genetic basis for wingtip patterns, this second large group was attributed to the occurrence of long-distance dispersal by immature birds from the west Atlantic that remain in southwest Greenland and Newfoundland after the overwinter period (Coulson & Nève de Mévergnies 1992; Nikolaeva *et al*. 1997). Mitochondrial control region sequences also suggested that kittiwakes show significant structure across the North Atlantic, with the formation of five regional population groups: northeast Atlantic (British Isles, France), Barents, Svalbard, Newfoundland, and Arctic Canada (Patirana 2000). These results were attributed to low historical population sizes and limited gene flow.

Morphological characters may be influenced by either environmental effects or selection, but differences between neutral markers of the nuclear and mitochondrial genomes are more difficult to explain. Higher structure in the mitochondrial genome is often explained by the occurrence of male-biased dispersal (females show higher levels of philopatry resulting in structure at mitochondrial markers; Prugnolle & De Meeus 2002). However, ringing data suggest that male kittiwakes are more philopatric than females (Coulson & Nève de Mévergnies 1992; Coulson 2002). One potential explanation may be that despite higher natal philopatry, males still show greater long-distance dispersal than females (i.e. when they decide to disperse, they disperse greater distances than females). Genetic studies using male sex-linked markers would enable a test of this hypothesis. Another explanation may be linked to the nature of the markers themselves. The greater the effective population size, the longer it takes for populations to reach genetic equilibrium. As mitochondrial DNA is transmitted maternally, its theoretical effective population size is one-fourth that of nuclear markers and variation at these markers should therefore reach equilibrium before nuclear markers. As the kittiwake populations of the North Atlantic have only been established during the last 10 000 years (Stein *et al*. 1994), there may not yet have been sufficient time for complete lineage sorting to occur. In this way, variation at microsatellite loci may reflect historical population structure more closely than highly variable mitochondrial markers.

Ring recoveries are in line with large scale dispersal in kittiwakes and suggest movement over great distances (> 500 km). However, it is often not known whether recovered birds were actually breeding in the areas they were found making inferences about the frequency of effective dispersal at large spatial scales difficult. Although no birds from the eastern Atlantic are known to have dispersed to western Atlantic colonies (Coulson 2002), ringing data suggest a westward migration of kittiwakes for the winter period at sea (Barrett & Bakken 1997; Nikolaeva *et al*. 1997). These migrational tendencies may result in the recruitment of birds to distant colonies after the overwinter period (i.e. birds never return to the natal colony). Such dispersal events may be accidental (i.e. birds are unable to return to the natal area) or may reflect behavioural variation in philopatry among individuals (Weatherhead & Forbes 1994). The tendency for birds to disperse may also be linked to the conditions in the natal colony the year they were borne and to the local dynamics of the colonies that they recruit to (see discussion in the next section). Such long-distance dispersal events may be sufficient to eliminate the traces of regional structure among populations.

Parasite population structure and host ecology

We found that ticks were more strongly structured than their hosts. Kittiwake ticks were highly differentiated between ocean basins, matching the structure found in their hosts, but patterns within the North Atlantic were quite different. Whereas kittiwakes showed little population subdivision, ticks sampled in the same colonies formed clear population groups. Among the sampled populations, we see the presence of at least three regional groups: Barents Sea, British Isles (including populations from France and central Norway) and Newfoundland (Fig. 2D). Within the British Isles group, many tick populations were significantly differentiated suggesting that this group is not panmictic. As no one tick population showed reduced levels of genetic diversity (indicative of a possible past bottleneck), population differentiation may

be better explained by dispersal than by patterns of recent colonization (Hedrick 2000). Indeed, in contrast to their hosts, strong patterns of isolation by distance were detected for kittiwake ticks (Fig. 3B). This suggests that ticks are dispersed among kittiwake colonies in a stepping-stone manner (i.e. there is a higher probability of ticks being dispersed to a nearby colony than to a distant colony). Similar results for kittiwake ticks were found in an earlier study, where, despite the inclusion of different populations, the same three regional groups and dispersal patterns were identified (McCoy *et al*. 2003). Although different patterns of genetic structure were found for the kittiwake depending on the type of marker employed (see above), we do not necessarily expect this to occur for ticks. While hypervariable mitochondrial markers have reduced effective population sizes, this may be compensated for by higher dispersal rates; male ticks of this species do not feed during the adult stage (i.e. they are not in contact with the seabird host). This means that female ticks should on average show higher levels of dispersal than males because they have an additional chance of being dispersed at each generation. Nonetheless, future studies using mitochondrial markers (particularly, those with relatively slow mutation rates) would enable us to test this prediction and could provide important information on the history of the colonization process.

The only way for ticks to disperse between discrete host patches is through host movement. Due to the constraints imposed by the host's life history, this is only likely to occur during the limited part of the year that the seabird is associated with land (i.e. during the breeding season). The dispersal of the parasite is thus an indirect measure of kittiwake activity during this most important period of the host life cycle. Young kittiwakes can visit colonies in the weeks just after fledging (Danchin 1992), but typically do not start to prospect in different colonies until at least 2 years of age (Cadiou *et al*. 1994). As birds approach breeding age, they tend to remain closer to the natal colony (Coulson 2002) and may engage in active prospecting (landing on unused or temporarily unoccupied nest sites, Cadiou *et al*. 1994). Not all colonies are equally appealing to new breeders. Smaller colonies are thought to be more attractive to recruits than large ones (Coulson & Nève de Mévergnies 1992) and flourishing colonies typically have more young birds visiting than declining colonies (Danchin & Monnat 1992). These patterns are thought to be linked to habitat selection behaviours; birds visit colonies as a way to evaluate their potential reproductive quality (breeding-habitat selection based on public information; Boulinier *et al*. 1996; Danchin *et al*. 1998). The prospecting of young birds and failed breeders may result in the dispersal of ticks among colonies (Danchin 1992). Patterns of parasite population structure may thus be used to measure the spatial extent of these behaviours.

The population structures of host and parasite were not correlated. When the geographical distance between populations was mapped onto this relationship, we saw that discordant patterns were largely due to a lack of population structure at intermediate distances in the host. Neither host nor parasite populations were structured at small scales, but tick populations were significantly differentiated at distances greater than 200 km. Although patterns of tick population structure do not match those found for the host using the same markers, they do globally correspond to the regional kittiwake groups identified by mitochondrial control region sequences (Patirana 2000). It is therefore possible that differences between host and parasite population structures in the present study are due to differences in the evolutionary rates of kittiwakes and ticks; these species have different generation times (kittiwakes, up to 20 years; ticks, 4 years) and may have different effective population sizes. In addition, mutation rates at microsatellites could differ between them (e.g. Sainudiin *et al*. 2004; but see Hafner *et al*. 1994). If parasites have higher evolutionary rates than their hosts, differentiation may build up more quickly in ticks than in seabirds. In this case, the information stored in the parasite genome may provide more pertinent information on the host than studies of the host itself. Indeed, information provided by the tick shows that kittiwake populations do in fact function at regional scales within the breeding season and that prospecting behaviour may be largely constrained to distances of 200 km. It further suggests that certain genetic markers may be limited in their ability to identify present-day population subdivisions, either due to historical effects or to male-biased long-distance dispersal.

Relative host–parasite population structure and co-evolutionary potential

The comparison of host–parasite population structures provides essential elements for predicting the outcome of local co-evolutionary interactions. First, the population structure of each species informs us about the geographical scale at which interactions evolve. Incongruencies in population structure can lead to the formation of a geographical mosaic in traits under selection and linked to the antagonistic interaction (Thompson 1994). Moreover, theory suggests that host–parasite gene flow is a key feature that affects the potential of species to locally adapt (Gandon *et al*. 1996; Gandon & Michalakis 2002). The species with higher gene flow will receive novel alleles that will enable it to counter evolution in the antagonist. Comparing population structures can therefore help us to understand how the interplay between selection and gene flow determines the distribution of traits across broad geographical scales.

Here, we found that ticks were more strongly structured at large scales than their hosts. If this structure reflects

current population functioning, it would suggest that kittiwakes disperse more frequently than their parasites and thus should readily adapt to local parasites. However, an experimental study suggested that ticks are adapted to local kittiwake subpopulations (McCoy *et al*. 2002). Although this study could not identify the precise spatial scale of the adaptation (subpopulation or nest), it suggested that gene flow was higher in the parasite at small spatial scales. Taken together, these studies imply that respective levels of gene flow are scale dependent; gene flow is similar or higher in the parasite at regional scales (i.e. not all seabird movement reflects dispersal), but lower than the host at larger spatial scales (i.e. birds do not disperse ticks between breeding seasons). As local adaptation and the co-evolutionary process depend on interactions occurring at several spatial scales (Thompson 1994), we may expect different patterns of local adaptation at different spatial scales. In addition, as *I. uriae* transmits microparasites, such as the bacterium *Borrelia burgdorferi sensu lato* (Olsen *et al*. 1993), relative gene flow and co-evolutionary outcomes will have important implications for disease epidemiology. Indeed, dispersal of both the kittiwake and the tick could result in the dissemination of the microparasite and its presence may interact in the process of local host–parasite adaptation.

Here, we used a comparative approach of host and parasite population structures to make inferences about the population functioning and dispersal of kittiwakes. Although kittiwake populations are only weakly structured at large spatial scales, the complementary results found in its parasitic tick suggest that this species functions at regional scales. In this way, the comparison of host and parasite gene flow has enabled us to disentangle the inter-colony movements of birds from that of true dispersal events (movement followed by reproduction). Future studies that combine comparable information from interacting species may be particularly useful for making ecological inferences in vertebrate animals and, as suggested here, may provide essential elements for predicting the outcome of co-evolutionary interactions at different spatial scales.

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This study is part of an ongoing research programme conducted by Karen McCoy and colleagues examining the interaction between *Ixodes uriae* and its different seabird hosts. Thierry Boulinier's research focuses on individual behaviour and spatial population dynamics. Claire Tirard specializes in the genetics of host–parasite systems.
