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Climate change in the Arctic: Testing the poleward expansion of ticks and tick-borne diseases

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Abstract

Climate change is most strongly felt in the polar regions of the world, with significant impacts on the species that live there. The arrival of parasites and pathogens from more temperate areas may become a significant problem for these populations, but current observations of parasite presence often lack a historical reference of prior absence. Observations in the high Arctic of the seabird tick *Ixodes uriae* suggested that this species expanded poleward in the last two decades in relation to climate change. As this tick can have a direct impact on the breeding success of its seabird hosts and vectors several pathogens, including Lyme disease spirochaetes, understanding its invasion dynamics is essential for predicting its impact on polar seabird populations. Here, we use population genetic data and host serology to test the hypothesis that *I. uriae* recently expanded into Svalbard. Both black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) were sampled for ticks and blood in Kongsfjorden, Spitsbergen. Ticks were genotyped using microsatellite markers and population genetic analyses were performed using data from 14 reference populations from across the tick's northern distribution. In contrast to predictions, the Spitsbergen population showed high genetic diversity and significant differentiation from reference populations, suggesting long-term isolation. Host serology also demonstrated a high exposure rate to Lyme disease spirochaetes (Bbsl). Targeted PCR and sequencing confirmed the presence of *Borrelia garinii* in a Spitsbergen tick, demonstrating the presence of Lyme disease bacteria in the high Arctic for the first time. Taken together, results contradict the notion that *I. uriae* has recently expanded into the high Arctic. Rather, this tick has likely been present for some time, maintaining relatively high population sizes and an endemic transmission cycle of Bbsl. Close future observations of population infestation/infection rates will now be necessary to relate epidemiological changes to ongoing climate modifications.

KEYWORDS
Borrelia, colonial seabirds, invasion, *Ixodes uriae*, Ixodidae, Lyme disease, *Rissa tridactyla*, Svalbard, *Uria lomvia*

1 | INTRODUCTION

The climate is changing quickly and particularly so in the highly sensitive Arctic region where ice sheets are melting at an alarming rate and record high temperatures have become the norm (Box et al., 2019; Hoegh-Guldberg et al., 2018). As a consequence of such changes, animal and plant distributions in these regions are shifting with potential cascading effects along trophic chains (Descamps & Strøm, 2021; Fossheim et al., 2015; Nater et al., 2021). Species that were previously maladapted to survive under polar conditions may now be able to invade, including novel parasites and pathogens (Altizer et al., 2013; Kutz et al., 2009). However, while there is no doubt about the potential impacts of climate change, precaution is required before pronouncing the emergence of a parasite or pathogen. Solid baseline data that support its prior absence is necessary to support claims of recent invasion. These data are often lacking, particularly for isolated regions and populations where few historical observations exist.

Recent studies suggest that ticks and Lyme disease are emerging in more northern areas due to climate change (Léger et al., 2013; Jaenson et al., 2012) and becoming significant public health problems (e.g., Hvidsten et al., 2015). In polar regions, few tick species have been able to colonize, except those associated with colonial seabirds. These colonies represent particularly good environments for nidicolous ticks because host birds aggregate in high numbers to breed and return to the same nest site year after year in a very predictable manner (e.g., McCoy et al., 2016). However, at high latitudes, these ectoparasites also have to deal with harsh off-host conditions while waiting several months for their host to return for the next breeding season. Among tick species found in polar seabird colonies, the hard tick, *Ixodes uriae*, is the most widespread and abundant (Dietrich et al., 2011; Lynch et al., 2010; Muñoz-Leal & González-Acuña, 2015). *I. uriae* has evolved specific physiological and behavioural adaptations to deal with extreme conditions of temperature and humidity (Davies et al., 2021; Lee Jr. & Baust, 1987) but has been considered rare or absent in high polar seabird colonies until relatively recently. Indeed, ticks were noted for the first time in penguin colonies of the Antarctic peninsula in the early 2000s, where it was suggested that their numbers were increasing (Lynch et al., 2010). Population genetic studies indicated that these tick populations were not the result of recent colonisation or expansion events but rather had existed in the area for a long period of time unnoticed by ornithologists (McCoy et al., 2012). In the high Arctic (the zone where woodlike vegetation no longer grows), the presence of *I. uriae* was noted as early as 1999 in the Ossian Sarsfjellet colony of Spitsbergen (McCoy, 2001) on a black-legged kittiwake (*Rissa tridactyla*) chick, but at extremely low densities; only one larval tick was found on 67 captured birds, 61 kittiwakes and 6 thick-billed murres (*Uria lomvia*). In 2007, Coulson et al. (2009) observed ticks on thick-billed murres in two colonies of the same area (prevalence of 20%) but did not find them in smaller murre colonies, nor on black-legged kittiwakes. The authors suggested that *I. uriae* may have recently colonised the region or had undergone a population expansion due to milder winter conditions or to weaken seabird immune responses caused by pollution.

From this time onward, specific efforts to record the presence of *I. uriae* in Svalbard have been made; Descamps (2013) found a clear relationship between the prevalence of ticks and the average temperature of the previous winter, supporting the notion that the establishment and spread of this tick are linked to environmental changes that favour tick survival. However, the question still remains as to whether the presence of this tick in the high Arctic represents a recent phenomenon, with its establishment and spread since the late 1990s, or whether these populations have been present over longer periods of time but were unobserved.

Ixodes uriae is a known vector of several pathogenic infectious agents (Dietrich et al., 2011), the most significant from a human perspective being the bacteria responsible for Lyme disease, bacteria of the complex *Borrelia burgdorferi* sl (also referred to as *Borreliella burgdorferi* sl). Indeed, Olsen et al. (1993, 1995) showed early on that *B. garinii* spirochaetes could be found in *I. uriae* ticks sampled from temperate seabird colonies. Later serological studies demonstrated that colonial seabirds are frequently exposed to this infectious agent, particularly in North Atlantic colonies where the prevalence of seropositive birds averages almost 40% (Lobato et al., 2011; Staszewski et al., 2008). Seropositive individuals and infected ticks have also been found within sub-Arctic colonies of northern Norway and Iceland (Dietrich et al., 2008; Duneau et al., 2008; Gasparini et al., 2001; Larsson et al., 2007). Genetic analyses of infected ticks demonstrated that the most frequently encountered *Borrelia* species in these seabird colonies is *B. garinii*, but other genospecies, such as *B. burgdorferi* ss and *B. afzelii* also occur (Dietrich et al., 2008; Duneau et al., 2008). In the high Arctic, a PCR screening of ticks collected in Spitsbergen, Bjørnøya and Jan Mayen between 2008 and 2012, did not detect *Borrelia spirochaetes* (Elsterová et al., 2015), but sample sizes from Svalbard were extremely low (Spitsbergen = 9 ticks, Bjørnøya = 11 ticks). In the Southern hemisphere, studies have demonstrated the presence of *Borrelia* in association with King penguins in the subantarctic islands (Schramm et al., 2014) but have not detected *Borrelia* at higher latitudes (Barbosa & Palacios, 2009).

Here, we test the hypothesis that *I. uriae* has recently expanded into Spitsbergen, an Arctic island that has experienced severe temperature increases over the last three decades (Nordli et al., 2014). We use a population genetic approach to compare the genetic diversity and structure of ticks sampled on Spitsbergen with those from more southern locations in the Northern hemisphere. If the arrival and spread of *I. uriae* represents a recent phenomenon, we expected to see low diversity within the Spitsbergen tick population relative to the other locations due to a founder effect. Using the genetic signatures from the southern colonies, we then determined the potential origin of the Spitsbergen population using tests of population structure and individual multilocus assignments. If the establishment of *I. uriae* populations is recent, we also expected a low frequency of infectious agents in this population, as there should be a delay between the arrival of the vector and the arrival and spread of associated vector-borne agents (Juliano & Lounibos, 2005; Kada

et al., 2017; Van Riper III et al., 1986). We examined this prediction in two ways: by analyzing the exposure of seabirds in Spitsbergen to *Borrelia spirochaetes* using serology and by the direct detection of bacterial DNA in the sampled ticks.

2 | MATERIALS AND METHODS

2.1 | Study site, species, and collections

Adults of two seabird species, the thick-billed murre (*U. lomvia*) and the black-legged kittiwake (*R. tridactyla*) were captured during reproduction at the Ossian Sarsfjellet colony, Kongsfjorden, Spitsbergen, Norway (78°55′ N 12°26′ E) using a noose pole in 2012 and 2014. Both species have large colonies in the reserve, divided among several distinct cliffs where breeding takes place from May until August each year (i.e., Kongsfjorden population estimates in 2011 of 1150 pairs of thick-billed murre and 3700 pairs of black-legged kittiwake, S. Descamps, unpublished). Whereas kittiwakes breed in individual nests built on vertical cliff areas, murres aggregate and breed directly on cliff ledges. These birds are long-lived and highly faithful to both their breeding partner and breeding site among years (Mercier et al., 2021). During capture, birds were searched for ticks and a blood sample (1 mL) was taken from the ulnar vein for serological analyses. This blood was centrifuged after sampling for approximately 10 min at 5000 rpm and the plasma was extracted and stored at −20°C until immunological assays. All work was carried out in accordance with standard animal care protocols and approved by the Ethical Committee of the French Polar Institute (France) and the Norwegian Animal Research Authority.

Ixodes uriae (Family Ixodidae) is a colonial seabird specialist tick that occurs in polar regions of both hemispheres. Like other ixodid ticks, it has three developmental stages (larvae, nymph, and adult), but a relatively long life cycle (~3–4 years) because of colder environmental conditions and limited host access (i.e., only during the relatively short breeding season). Larvae and nymphs of both sexes attach to the bird for a single blood meal that lasts from 3 to 8 days, after which they return to host nesting environment to moult and overwinter. As adults, only female ticks feed on the host (c. 10 days) before laying a single clutch of several hundred eggs and dying (Barton et al., 1996; McCoy et al., 2002). Mating typically occurs prior to the female blood meal in the nesting environment (McCoy & Tirard, 2002). In the present study, all captured birds were searched for ticks, and any found were removed and conserved in 70% ethanol until analyses.

2.2 | Population genetic analyses

For ticks collected in the Ossian Sarsfjellet colony, DNA from each tick was extracted individually following the protocol of Kempf et al. (2009). These samples were then genotyped at eight independent microsatellite markers developed specifically for this tick species (McCoy & Tirard, 2000). Microsatellite PCR amplification and allele size determination were performed as described in Kempf et al. (2009). Genotypes were visualized using an ABI PRISM 3130xl Genetic Analyser and allele sizes were assigned using GeneMapper v.4 (Applied Biosystems). The final corrected genotype data can be found here: https://doi.org/10.5281/zenodo.7547277.

For the other tick populations included in statistical analyses, we used the microsatellite data previously published by Dietrich et al. (2012, 2014), along with two new population locations sampled in 2016 from Grimsey, Iceland, and from Gull Island, Newfoundland, Canada (Figure 1). These locations were chosen to cover representative populations from the different possible source locations for ticks of the Ossian Sarsfjellet colony. In all locations, ticks were sampled from available host species, but ticks from different sympatric seabird species were treated as independent populations for the analysis based on results of previous work that demonstrated the presence of host-specific tick races within colonies (Dietrich et al., 2012; McCoy et al., 2001, 2003, 2005). The three additional tick populations were genotyped as described above for the Ossian Sarsfjellet ticks, and control ticks from previously analysed populations were included to calibrate genotypes among data sets. The final data set used for analyzing the diversity and structure of the Svalbard population was, therefore, composed of 15 populations from six locations (Table 1). Although the included populations were sampled over a 5-year period, we did not expect this to alter our biological inferences on population structure. The generation time of *I. uriae* is long (3–4 years) and therefore, at most, we have included data from two tick generations. Likewise, tick population sizes are typically large in most colonies and, therefore, resistant to rapid genetic drift. Indeed, here, we combined two different years for the Svalbard population, 2012 and 2014 (Table 1) but found no suggestion of between-year population structure (i.e., no heterozygote deficit suggested by the estimated F_{IS}; see below and Table S1).

Genetic diversity in each colony was estimated by calculating allelic richness using a rarefaction method, and Nei's unbiased gene diversity (H_S). Within-population departures from Hardy–Weinberg (HW) proportions were investigated by estimating the inbreeding coefficient (F_{IS}). The significance of this estimator was assessed by randomizing alleles among individuals within samples (2400 permutations). These basic analyses were all carried out using FSTAT (Goudet, 2003).

To examine population isolation, pairwise F_{ST} estimates were calculated from microsatellite data according to Weir and Cockerham (1984). Significance was assessed by permuting multilocus genotypes among populations using FSTAT (Goudet, 2003), with 2100 permutations and a significance level of 5%, corrected using the standard Bonferroni method for multiple tests.

Population genetic structure was also inferred using a Bayesian clustering approach implemented in the program STRUCTURE 2.3.4 (Pritchard et al., 2000). The program was run with five independent runs, using the admixture model with correlated allelic frequencies and the LOCPRIOR model developed by Hubisz et al. (2009) to take into account the sampling location of each individual. All simulations used 100,000 iterations in the burn-in phase and 100,000 generations in the data collection phase. Selection of the number of distinct clusters (k) was based on Evanno's DeltaK (Evanno et al., 2005) using the

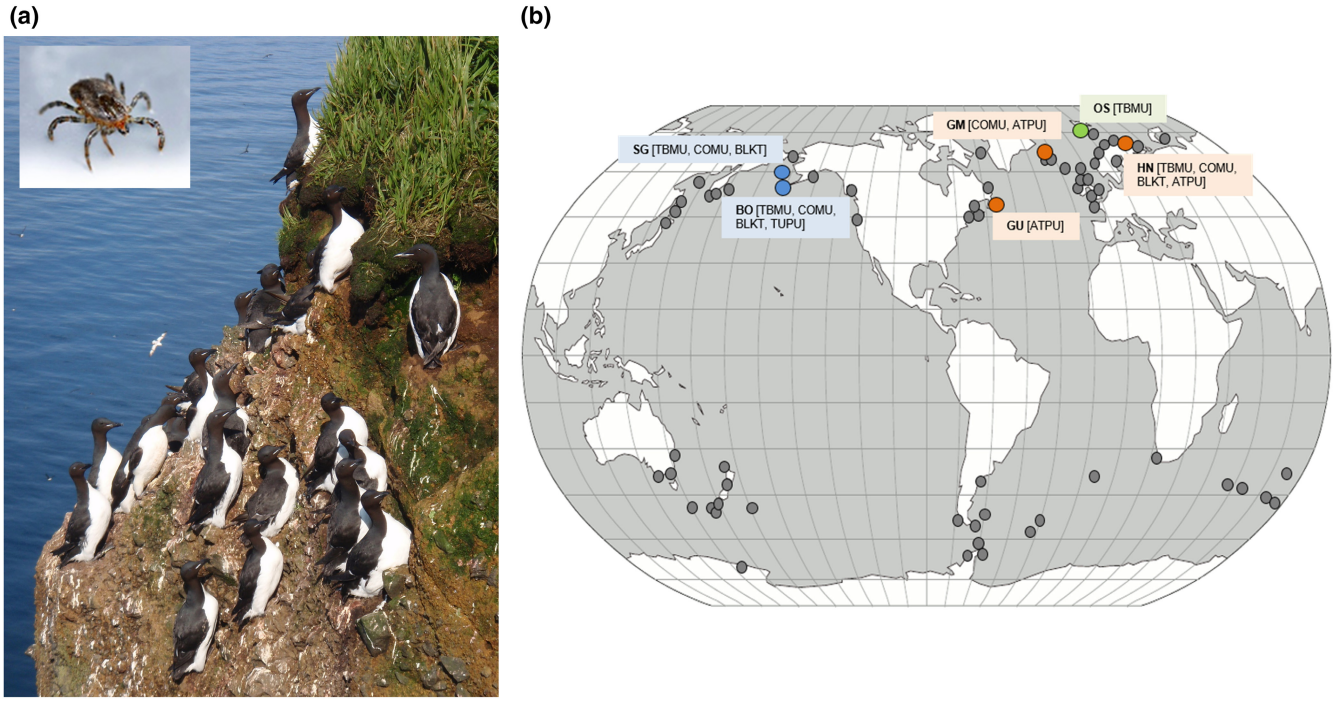

FIGURE 1 Hosts of *Ixodes uriae* ticks and sample locations. (a) *I. uriae* (inset) exploits seabird species such as thick-billed murres *Uria lomvia* across the polar regions of both hemispheres. (b) The known worldwide distribution of *I. uriae*, with locations where the tick has been directly observed indicated by grey points (after Dietrich et al., 2011; Muñoz-Leal & González-Acuña, 2015). The central study population in Ossian Sarsfjellet, Svalbard is indicated by a green point and the five additional locations used for comparative population genetic analyses are indicated in blue (North Pacific locations) and orange (North Atlantic locations) with seabird host species sampled for ticks indicated for each location. Acronyms for locations and seabird species are given in Table 1. Photo credits: P. Landmann (*I. uriae*); K.D. McCoy (*U. lomvia*).

Harvester software (Earl & vonHoldt, 2012). STRUCTURE analyses were conducted on two partitions of the data: (i) the entire data set to identify those populations that were most related to the tick population on Spitsbergen ($n = 418$ ticks from 15 populations, testing $k = 1$–15) and (ii) the three most closely related populations to examine finer scale structure ($n = 135$ ticks from four populations, testing $k = 1$–5).

2.3 | Immunological assays

Plasma from 19 black-legged kittiwakes and 16 thick-billed murres sampled in 2014 from Ossian Sarsfjellet were screened for antibodies directed against three subspecies of *B. burgdorferi* sensu lato (Bbsl; *B. garinii*, *B. afzelii*, and *B. burgdorferi* ss) using a commercially available enzyme-linked immunosorbent assay (ELISA) kit (Borrelia + VlsE IgG ELISA; IBL International). This kit was slightly modified for use on seabirds (as per Staszewski et al., 2008). Briefly, we replaced the secondary (anti-IgG) antibody of the kit by an anti-chicken IgY antibody conjugated with peroxidase (Sigma A-9046; Sigma-Aldrich) diluted to 1:750 and then followed the kit manufacturer's instructions. Each sample was run in duplicate and anti-Bbsl antibody levels were quantified as the mean optical density (OD) of the resulting solution read at 450 nm in a spectrophotometer (Victor 1420; Perkin Elmer). We used the method described by Garnier et al. (2017) to determine negative and positive exposure thresholds (for details, see Figure S2 and https://doi.org/10.5281/zenodo.7538438). As anti-Bbsl antibodies are known to persist for several years in seabirds (Staszewski et al., 2007), a seropositive status reflects an exposure event that occurred at an unknown time prior to sampling.

2.4 | *Borrelia* detection in ticks

We applied a highly sensitive target-specific qPCR procedure to detect the presence of *Borrelia* infection in ticks collected from the Ossian Sarsfjellet population following Gómez-Díaz et al. (2010). We used DNA from cultured *B. garinii* (20047) as a positive control and purified water as a negative control. Any positive samples were reamplified using the nested PCR procedure described in Duneau et al. (2008) and were sent for direct sequencing (Eurofins). Sequences were cleaned and aligned using the ClustalW algorithm implemented in MEGA v7 (Kumar et al., 2016), and a blastn search was carried out to determine species identity.

3 | RESULTS

3.1 | Tick genetic diversity

Genetic diversity was relatively high in all populations, varying from 3.88 (±2.15) to 5.42 (±2.72) in AR and from 0.50 (±0.37) to 0.67 (±0.19) in gene diversity; the Svalbard tick population fell

TABLE 1 Tick populations used in genetic analyses and diversity measures across loci.

Colony location	Year sampled	Seabird species	No. ticks (No. hosts)	Avg allelic richness (±SE)[a]	Avg gene diversity (±SE)
Hornøya (HN), Norway	2010	TBMU	35 (21)	3.88 (±2.15)	0.52 (±0.26)
	2009	COMU	33 (off[b])	4.66 (±2.44)	0.59 (±0.26)
	2009	BLKT	35 (–[c])	4.85 (±1.76)	0.66 (±0.21)
	2009	ATPU	35 (off[b])	4.90 (±2.85)	0.57 (±0.32)
Grimsey (GM), Iceland	2016	COMU	30 (off[b])	4.81 (±1.82)	0.65 (±0.22)
	2016	ATPU	28 (off[b])	4.31 (±2.71)	0.50 (±0.37)
Gull Island (GU), Canada	2016	ATPU	19 (off[b])	4.92 (±3.14)	0.61 (±0.32)
St. George (SG), Alaska	2009	TBMU	20 (20)	5.15 (±2.82)	0.63 (±0.29)
	2009	COMU	31 (20)	5.32 (±2.94)	0.64 (±0.24)
	2009	BLKT	17 (14)	4.42 (±2.12)	0.58 (±0.27)
Bogoslof (BO), Alaska	2009	TBMU	28 (13)	5.39 (±2.81)	0.63 (±0.28)
	2009	COMU	27 (12)	5.42 (±2.72)	0.65 (±0.27)
	2009	BLKT	27 (11)	5.27 (±2.91)	0.66 (±0.20)
	2009	TUPU	16 (>2[d])	4.74 (±2.08)	0.67 (±0.19)
Ossian Sarsfjellet (OS), Svalbard	2012/14	TBMU	37 (37)	4.06 (±1.70)	0.57 (±0.20)

Note: The colonies from the North Atlantic are indicated in orange, those from the North Pacific are in blue and those from Spitsbergen (Svalbard) are in green. Raw genotype data are available in Table S3.

Abbreviations: ATPU, Atlantic puffin (Atlantic Ocean only); BLKT, black-legged kittiwake; COMU, common murre; TBMU, thick-billed murre; TUPU, tufted puffin (Pacific Ocean only).

[a]Based on eight randomly sampled tick individuals in each population.

[b]Off: all ticks sampled off-host from around the nest.

[c]Gorged ticks were collected from over 50 birds, but ticks were pooled after collection and, thus, the true number of sampled host birds is not available.

[d]One tick collected on-host, all others from the off-host environment.

within the middle ranges of both estimates (Table 1). Tests of HW indicated that several tick populations did not conform to expectations (Table S1). In North Pacific populations, this was largely due to heterozygote deficits at locus T44. Previous studies have suggested that this locus may be linked to a gene under host-associated selection (Dietrich et al., 2012; McCoy et al., 2005). When this locus was removed, all populations except ATPU-GU were shown to respect HW proportions. In the ATPU-GU population, the overall deficit was due to locus T39 and is likely linked to a combination of genotyping errors and low sample size (Table S1). However, to account for potential non-independence in the data, tests for population differentiation did not assume HW equilibrium. In addition, STRUCTURE analyses were run with and without T44. As results were similar in both cases, only results that include all eight loci are presented below.

3.2 | Tick population genetic structure

Pairwise tests of population structure showed that the Spitsbergen population differs strongly and significantly from all other tick populations, with F_{ST} estimates varying from 0.0853 to 0.3843 (Table 2). These distances were lower overall than those between North Atlantic and North Pacific populations but higher than those within the North Pacific and of similar magnitude as those within the North Atlantic (Table 2).

Results from the STRUCTURE analysis mirrored tests of pairwise population structure. When all 15 populations were included in the analysis, two major clusters were identified according to the deltaK (Figure S1), one in the Pacific, which included Atlantic murre ticks, and the other with the remaining Atlantic tick populations. The selection of $k = 2$ is not surprising given the strong differentiation between ticks from different ocean basins (Dietrich et al., 2012, 2014) (Table 2). However, small peaks in deltaK values were also seen at $k = 3$ and $k = 5$ (Figure S1). When these clusters are examined in more detail, isolation of the Spitsbergen population becomes more apparent; when $k = 3$, the Spitsbergen population groups with other murre ticks from the North Atlantic and when $k = 5$, isolation of the Spitsbergen population becomes evident (Figure 2a). When STRUCTURE was run a second time, but including only the three most closely related murre tick populations from the North Atlantic, the optimal number of clusters was 3 (Figure S1). In this case, the Spitsbergen tick population was clearly isolated from the murre tick populations on Hornøya (Norway) and Grimsey (Iceland); no misassignments that might indicate recent gene flow are evident (Figure 2b).

TABLE 2 Pairwise population genetic structure among tick populations ($n = 15$ populations).

	TBMU-SG	TBMU-BO	BLKT-SG	BLKT-BO	COMU-SG	COMU-BO	TUPU-BO	ATPU-GU	TBMU-HN	BLKT-HN	COMU-HN	ATPU-HN	COMU-GM	ATPU-GM	TBMU-OS
TBMU-SG		0.0032	0.0022	0.0150	−0.0068	0.0202	**0.0522**	**0.2923**	**0.1647**	**0.2615**	**0.1425**	**0.3458**	**0.1471**	**0.3523**	**0.1146**
TBMU-BO	NS		0.0124	0.0113	0.0035	0.0042	**0.0522**	**0.3018**	**0.1667**	**0.2527**	**0.1441**	**0.3416**	**0.1383**	**0.3527**	**0.0923**
BLKT-SG	NS	NS		0.0038	0.0090	0.0163	**0.0581**	0.3088	**0.1690**	**0.2675**	**0.1408**	**0.3684**	**0.1396**	0.3759	**0.1039**
BLKT-BO	*	*	NS		0.0133	0.0165	**0.0497**	**0.2578**	**0.1564**	**0.2213**	**0.1256**	**0.3112**	**0.1201**	**0.3137**	**0.0920**
COMU-SG	NS	NS	*	*		0.0193	**0.0516**	**0.2892**	**0.1496**	**0.2539**	**0.1271**	**0.3386**	**0.1341**	**0.3408**	**0.1039**
COMU-BO	*	NS	NS	*	*		0.0319	**0.2691**	**0.1427**	**0.2253**	**0.1171**	**0.3172**	**0.1140**	**0.3150**	**0.0853**
TUPU-BO	***	***	***	***	***	**		**0.2703**	**0.1760**	**0.2352**	**0.1392**	**0.3220**	**0.1439**	**0.3365**	**0.1085**
ATPU-GU	***	***	**	***	***	***	***		**0.3449**	**0.1390**	**0.2895**	0.1428	0.2408	0.0993	**0.3432**
TBMU-HN	***	***	***	***	***	***	***	***		**0.2540**	0.0022	**0.3716**	**0.1152**	**0.3771**	**0.1057**
BLKT-HN	***	***	***	***	***	***	***	***	***		**0.2036**	**0.0797**	**0.1785**	**0.1027**	**0.2620**
COMU-HN	***	***	***	***	***	***	***	***	NS	***		**0.3222**	**0.0838**	**0.3240**	**0.1014**
ATPU-HN	***	***	***	***	***	***	***	**	***	***	***		**0.2877**	**0.0847**	**0.3843**
COMU-GM	***	***	***	***	***	***	***	**	***	***	***	***		0.2714	**0.1272**
ATPU-GM	***	***	**	***	***	***	***	*	***	***	***	***	*		**0.3797**
TBMU-OS	***	***	***	***	***	***	***	***	***	***	***	***	***	***	

Note: Comparisons within and among ocean basins are highlighted in different colors (orange = North Atlantic seabird colonies, blue = North Pacific colonies, grey = North Atlantic vs. North Pacific) and comparisons with the Spitsbergen population are shown in green. Estimates of F_{ST} are shown above the diagonal, with the associated significance levels below the diagonal. F_{ST} values in bold are those considered significant at the adjusted nominal level of 5% after accounting for multiple comparisons ($p < .0005$). The significance levels below the diagonal are as follows: ***$p < .0005$, **$p < .001$, *$p < .05$, NS $p > .05$. Populations are identified by acronyms that indicate the seabird host species and the geographic location as outlined in Table 1.

Abbreviations: ATPU, Atlantic puffin (Atlantic Ocean only); BLKT, black-legged kittiwake; COMU, common murre; TBMU, thick-billed murre; TUPU, tufted puffin (Pacific Ocean only).

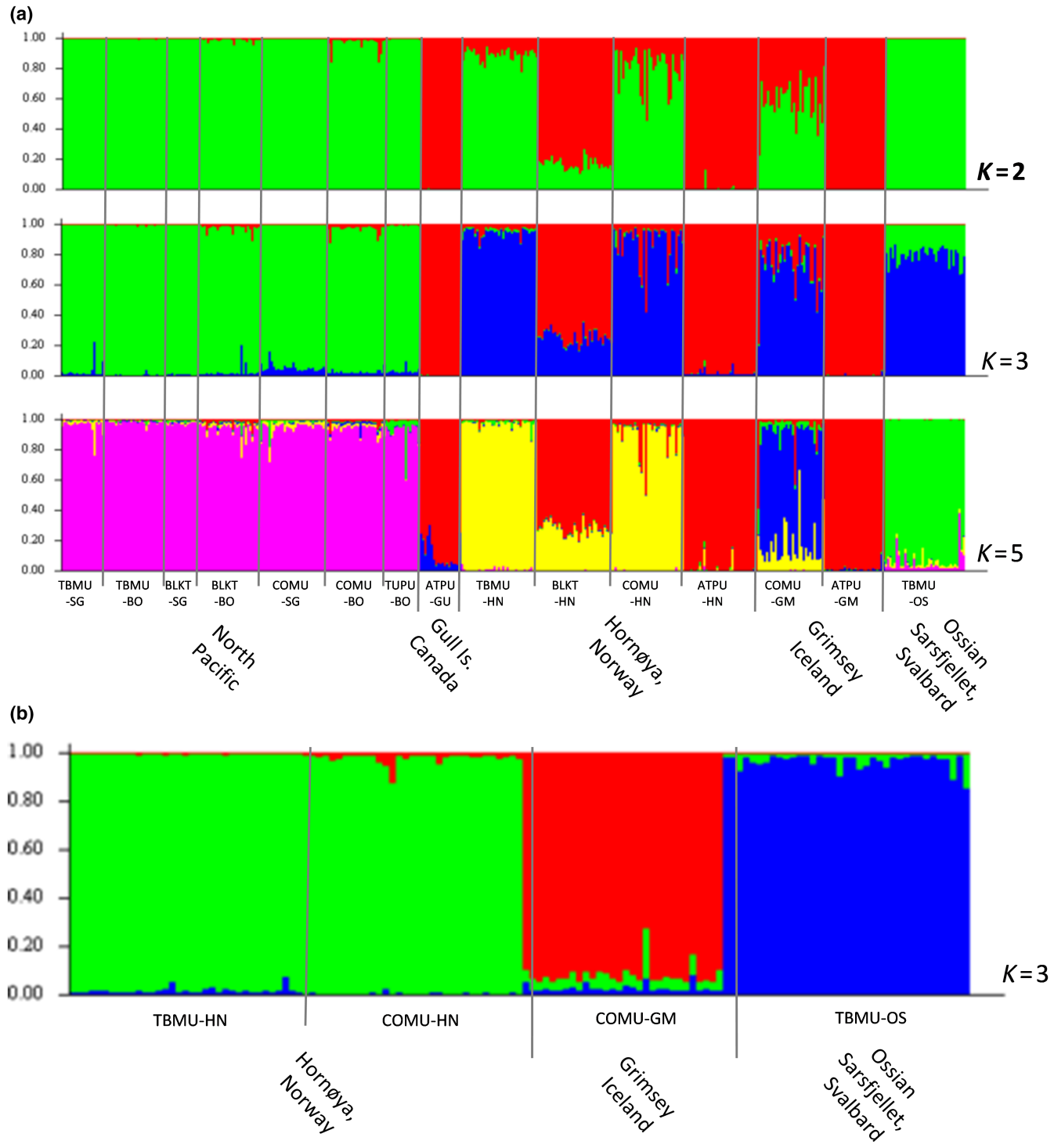

FIGURE 2 Genetic groupings of *Ixodes uriae* according to STRUCTURE (a) Multilocus assignments of ticks to population groups when considering the 15 analysed tick populations and an increasing number of defined clusters ($k = 2$, 3 and 5). Each individual bar represents the probability that a tick belongs to a cluster of a given color. The Ossian Sarsfjellet tick population groups with other ticks exploiting murres in the North Atlantic when $K = 2$ (optimal number of clusters as defined by the deltaK: see text) but becomes more isolated as the number of defined clusters increases. (b) Results when only the three more closely related tick populations to the Ossian Sarsfjellet colony are considered in the analysis. In this case, the optimal number of defined clusters was 3, with no indication of any recent tick migrations into the Ossian Sarsfjellet colony (i.e., misassignments).

3.3 | Immunological assays

The plasma of 19 black-legged kittiwakes and 16 thick-billed murres were screened for Bbsl antibodies. The distribution of mean OD values based on the reference sample was bimodal for both species (Figure S2), with high OD values corresponding to seropositive plasma samples and low OD values to seronegative samples. Based on defined threshold values for positive and negative tests

(Table S2), 63% of sampled black-legged kittiwakes were seropositive (12/19), with one ambiguous status, whereas all thick-billed murres were seropositive (Figure S2).

3.4 | *Borrelia* detection

Of the 37 tick DNA extracts tested by qPCR, one was found positive for Bbsl infection. After reamplification and Sanger sequencing, we obtained a 379 bp fragment that was used in the blastn search (Genbank accession number ON979421). The top 100 sequences identified in the blast search all corresponded to *B. garinii* (or a non-identified *Borrelia*) with more than 98.42% identity.

4 | DISCUSSION

Climate change is rapidly altering polar environments, opening the door to invasive species, including novel parasites and pathogens (Khan et al., 2019). It was hypothesized that *I. uriae* expanded into the Svalbard archipelago over the last two decades due to these changing climatic conditions (Coulson et al., 2009). Here, we examined the hypothesis of a recent expansion using a population genetic approach and explore the possible concomitant presence of Lyme disease spirochaetes at very high latitudes. The first documented observation of *I. uriae* in Svalbard to our knowledge is from 1999 when a single larval tick was found on a nestling in Kongfjorden (McCoy, 2001). If this observation was due to the recent establishment of the tick, we would expect to see a strong founder effect signal a decade or so later (i.e., after roughly three tick generations), when sampling for our study took place. This was not the case. Here, we found that genetic diversity within the Spitsbergen tick population was equal to or higher than that of more southern populations. We also found that although this population was most closely related to that of the same seabird host species from populations of Norway and Iceland (i.e., murre hosts), it was still significantly isolated from these other populations, suggesting limited ongoing gene flow.

The presence of *I. uriae* in a seabird colony depends on three factors: the availability of a suitable host for the bloodmeal, an appropriate off-host environment for moulting and overwintering, and a means of transportation to colonise the location. Although considered a seabird generalist, *I. uriae* has been shown to repeatedly form host-associated races throughout its distribution (Dietrich et al., 2014; Kempf et al., 2009; McCoy et al., 2001, 2005). Therefore, the exploitation of one seabird species within a colony can be independent of that of other sympatric bird species and depends on spillover dynamics (Dietrich et al., 2014). We can see in our results that only ticks collected from the closely related thick-billed and common murres showed no structure within colonies (Table 2), but some introgression among local host-associated tick populations is evident, demonstrating that host switching can occur (Figure 2). Thus, as several suitable avian host species breed in large numbers within the Svalbard archipelago, it is unlikely that the host per se represents a barrier to tick colonisation in this part of the world. Indeed, our results show that both thick-billed murres and black-legged kittiwakes in the Ossian Sarsfjellet colony are exposed to enough ticks and for a sufficient amount of time to be exposed to *Borrelia spirochaetes* (see below). If the requirement for suitable hosts is met, the other two factors required for tick establishment are less evident.

In terms of the off-host environment, it was previously suspected that the cold, dry winters of the high latitudes were likely unsuitable for overwintering ticks (Coulson et al., 2009; McCoy, 2001). A recent experimental study of tick physiology demonstrated that temperature and humidity interact to determine *I. uriae* survival and that different life stages and physiological states are more or less susceptible to low temperatures (Davies et al., 2021). A regular survey of murres in the Kongsfjorden area started in 2005, with between 10 and 100 adult birds captured per year. *I. uriae* was first noted in 2007 (Coulson et al., 2009) and targeted screening for ticks on captured birds started after this point. Prevalence in captured adult birds varied between 0% and 35% over the following 6 years of study. A correlation between the average temperature the previous winter and tick prevalence the following summer was highly significant, with winter temperature explaining almost 90% of the variance in tick prevalence over time. This correlation translated into a 5% increase in prevalence for every 1°C increase in winter temperature. However, no overall increasing trends in tick prevalence or temperature were evident across the 6 years (Descamps, 2013). It is, therefore, probable that tick population sizes increase with increasingly mild winters, and that the high Arctic is becoming more suitable for this tick. Indeed, surveys in a murre colony of Isfjorden (Diabasodden) recorded the presence of *I. uriae* for the first time in 2020 (S. Descamps, unpublished data). However, long-term trends in tick abundance remain difficult to predict as extreme events may have a major impact on tick survival (Davies et al., 2021). What is surprising and important in our results is that tick genetic diversity within the Ossian Sarsfjellet colony was similar to that found at lower latitudes. This means that, even if fluctuating winter conditions alter tick survival probability, enough ticks survive each year to maintain high local diversity. A prolonged life cycle that includes years of dormancy, when ticks do not attempt to feed and remain protected within the cliff environment, may help explain these patterns (Belozerov, 2009); changes in climatic conditions in certain years may then favour tick reactivation.

Finally, to colonize a new location, ticks must arrive at the site. As seen in the overall population genetic analyses presented here, the structure tends to be high among populations in different locations but depends on the tick host race. Indeed, dispersal in *I. uriae* is considered a relatively rare event because it depends on the movement of infested birds between breeding locations at a time when few birds move (Boulinier et al., 2016). It has, therefore, been suggested to occur during prospecting, when failed breeders or juvenile birds visit new colonies in late reproduction to choose a future breeding site (Boulinier et al., 2016; Danchin, 1992). The probability of dispersing ticks during such visits depends on the behaviour of the different seabird species within the colony (McCoy et al., 2003).

For example, the geographic structure among puffin tick populations within the North Atlantic is very weak compared with that in ticks associated with other species (McCoy et al., 2001, 2005; this study). Puffins nest in burrows or rock piles on cliff slopes and spend a good proportion of their time interacting outside the nest site (Harris, 1984). Visiting birds may land on a puffin slope without aggression and can, therefore, pick up or leave ticks behind relatively easily. This is less the case for highly territorial species such as murres, where visiting birds must remain at the outskirts of breeding ledges or suffer attacks from nesting individuals. This territorial behaviour should reduce the probability of tick dispersal among sites. In addition, murre populations in Svalbard have been declining since the 1990s (Descamps & Ramírez, 2021), which may reduce prospecting in these colonies (Boulinier et al., 1996) and, therefore, the probability of birds carrying ticks into the area. In agreement with these observations, our genetic results suggest that ticks of the Ossian Sarsfjellet colony have been isolated for some time, with little current gene flow from other colonies.

Additional results from our study support the long-term presence of *I. uriae* in Svalbard and, in particular, the high prevalence of exposure to a tick-transmitted infectious agent, Lyme disease bacteria. Indeed, if the arrival of this tick was a relatively recent event, we would expect a lag in the arrival and spread of tick-borne pathogens (Kada et al., 2017). *I. uriae* is a known vector of Lyme disease spirochaetes, and populations frequently show high prevalence [e.g., 11% in kittiwake ticks (Dietrich et al., 2008)]. Correspondingly high exposure rates in diverse seabird species have also been observed [40% on average in North Atlantic colonies (Staszewski et al., 2008); up to 18% in North Pacific colonies (Lobato et al., 2011)]. Here, we found that all tested thick-billed murres of Ossian Sarsfjellet were seropositive, demonstrating that birds are exposed to enough ticks to eventually become infected and mount a humoral immune response. Exposure rates in kittiwakes of this same colony were lower (63%), showing that kittiwakes are also exposed to ticks within this colony. These data, combined with the high diversity and isolation of the tick vectors, suggest that *Borrelia* is maintained in an enzootic cycle in the Ossian Sarsfjellet seabird community.

To verify the presence of Lyme disease spirochetes in ticks from Spitsbergen, we carried out targeted searches for *Borrelia* in tick DNA extracts and demonstrated the presence of a *B. garinii* isolate. Despite previous attempts (Elsterová et al., 2015), this is the first demonstration of Lyme disease spirochetes in the high Arctic. Only one tick of 37 tested was found to be positive using our qPCR protocol (i.e., prevalence <3%). This prevalence, combined with relatively low observed infestation levels, renders high seroprevalence in the birds difficult to explain. The apparent contrast may arise from several sources. First, ticks were extracted and tested after several years of storage in ethanol, potentially reducing the ability to detect harboured pathogens. In addition, a previous study showed that *Borrelia* spp. detection probability was lower in murre ticks compared with ticks from other host races due to lower infection intensities (Gómez-Díaz et al., 2010). The estimated prevalence of *Borrelia* in ticks may, therefore, be underestimated. Second, seropositivity reflects an exposure event at an unknown time in the past because antibodies are maintained over several years (Staszewski et al., 2007). Among seabird species, *Borrelia* seroprevalence of murres has been found to be higher than in other sympatric species, suggesting that these birds may react more strongly to infection and/or maintain specific antibodies for longer periods of time (Lobato et al., 2011; Staszewski et al., 2008). Indeed, here we found that optic density values (a proxy of antibody levels) in seropositive individuals covered a range of values, suggesting a mixture of recent and past exposure to *Borrelia* (Figure S2). Finally, there can be high heterogeneity in the presence of infected ticks at the colony scale (Dietrich et al., 2008); in our study, ticks were mostly sampled in 2012, whereas serology was carried out on birds captured in 2014. Samples may, therefore, have come from slightly different parts of the breeding colony.

Polar environments are changing quickly, with important consequences for the species that live there. As the poles warm, new species can invade, potentially adding stress to populations that are already dealing with changes in food resources, breeding habitats and increasing pollution. The invasion of novel parasites and pathogens is particularly important to survey in this respect. We show here that contrary to previous suggestions, *I. uriae*, and at least one of its associated pathogens, do not seem to be new additions to high Arctic parasite fauna. However, if infestation levels have been relatively benign in the past, climate change may alter this. Increasing temperatures may enable higher tick survival, and thus result in higher parasite pressure on breeding birds and their young and higher exposure rates to tick-borne pathogens. A warmer Arctic may advance the timing of breeding and, thus, may alter the nature of tick exploitation in terms of the avian species or the life stages (adult or chick) being exploited, as seen in other systems (Cohen et al., 2020; Paull & Johnson, 2014). Additional parasites and pathogens may also be introduced and act in synergy with ticks. Extreme climate events may limit some of these effects by periodically lowering parasite survival in the environment. Only continued monitoring of these polar populations will enable us to evaluate these different possibilities and to better relate ongoing epidemiological patterns to climate change.

AUTHOR CONTRIBUTIONS

Karen D. McCoy and Thierry Boulinier conceived the study. Karen D. McCoy, Thierry Boulinier, and Sébastien Descamps acquired funding and permits. Jérémy Tornos, Marlène Dupraz, Sébastien Descamps, Karen D. McCoy, and Thierry Boulinier performed field sampling. Céline Toty and Marlène Dupraz performed molecular assays. Amandine Gamble and Romain Garnier performed serological analyses. Karen D. McCoy carried out population genetic analyses and wrote the manuscript. All authors provided input for manuscript revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available. Microsatellie genotype data are provided in the Supporting Information files (Table S3) and at https://doi.org/10.5281/zenodo.7547277. Sequence data has been deposited in the NCBI database (accession number: ON979421). Host serology data and code is available at https://doi.org/10.5281/zenodo.7538438.

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REFERENCES

Altizer, S., Ostfeld, R. S., Johnson, P. T. J., Kutz, S., & Harvell, C. D. (2013). Climate change and infectious diseases: From evidence to a predictive framework. *Science*, *341*(6145), 514–519. https://doi.org/10.1126/science.1239401

Barbosa, A., & Palacios, M. J. (2009). Health of Antarctic birds: A review of their parasites, pathogens and diseases. *Polar Biology*, *32*(8), 1095–1115. https://doi.org/10.1007/s00300-009-0640-3

Barton, T. R., Harris, M. P., Wanless, S., & Elston, D. A. (1996). The activity periods and life cycle of the tick *Ixodes uriae* (Acari: Ixodidae) in relation to host breeding strategies. *Parasitology*, *112*, 571–580. https://doi.org/10.1017/S0031182000066154

Belozerov, V. N. (2009). Diapause and quiescence as two main kinds of dormancy and their significance in life cycles of mites and ticks (Chelicerata: Arachnida: Acari). Part 2. Parasitiformes. *Acarina*, *17*(1), 3–32.

Boulinier, T., Danchin, E., Monnat, J.-Y., Doutrelant, C., & Cadiou, B. (1996). Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology*, *27*(3), 252–256. https://doi.org/10.2307/3677230

Boulinier, T., Kada, S., Ponchon, A., Dupraz, M., Dietrich, M., Gamble, A., Bourret, V., Duriez, O., Bazire, R., Tornos, J., & McCoy, K. D. (2016). Migration, prospecting, dispersal? What host movement matters for infectious agent circulation? *Integrative and Comparative Biology*, *56*(2), 330–342. https://doi.org/10.1093/icb/icw015

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F.-J. W., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V. E., Walsh, J. E., Overland, J. E., Wang, M., Corell, R. W., Meier, W. N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., & Olsen, M. S. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, *14*(4), 045010. https://doi.org/10.1088/1748-9326/aafc1b

Cohen, J. M., Sauer, E. L., Santiago, O., Spencer, S., & Rohr, J. R. (2020). Divergent impacts of warming weather on wildlife disease risk across climates. *Science*, *370*(6519), eabb1702. https://doi.org/10.1126/science.abb1702

Coulson, S. J., Lorentzen, E., Strom, H., & Gabrielsen, G. W. (2009). The parasitic tick *Ixodes uriae* (Acari: Ixodidae) on seabirds from Spitsbergen, Svalbard. *Polar Research*, *28*(3), 399–402. https://doi.org/10.1111/j.1751-8369.2009.00117.x

Danchin, E. (1992). The incidence of the tick parasite *Ixodes uriae* in kittiwake *Rissa tridactyla* colonies in relation to the age of the colony and the mechanism of infecting new colonies. *Ibis*, *134*, 134–141.

Davies, B., Rosendale, A. J., Gantz, J. D., Lee, R. E., Denlinger, D. L., & Benoit, J. B. (2021). Cross-tolerance and transcriptional shifts underlying abiotic stress in the seabird tick, *Ixodes uriae*. *Polar Biology*, *44*(7), 1379–1389. https://doi.org/10.1007/s00300-021-02887-4

Descamps, S. (2013). Winter temperature affects the prevalence of ticks in an Arctic seabird. *PLoS One*, *8*(6), e65374. https://doi.org/10.1371/journal.pone.0065374

Descamps, S., & Ramírez, F. (2021). Species and spatial variation in the effects of sea ice on Arctic seabird populations. *Diversity and Distributions*, *27*(11), 2204–2217. https://doi.org/10.1111/ddi.13389

Descamps, S., & Strøm, H. (2021). As the Arctic becomes boreal: Ongoing shifts in a high-Arctic seabird community. *Ecology*, *102*(11), e03485. https://doi.org/10.1002/ecy.3485

Dietrich, M., Gomez-Diaz, E., Boulinier, T., & McCoy, K. D. (2008). Local distribution and genetic structure of tick-borne pathogens: An example involving the marine cycle of Lyme disease. In M. Bertrand, S. Kreiter, M. S. Tixier, M. Navajas, A. Migeon, K. D. McCoy, & L. Vial (Eds.), *Integrative acarology, proceedings of the 6th European congress of the European Association of Acarologists* (pp. 33–41). EURAAC.

Dietrich, M., Gomez-Diaz, E., & McCoy, K. D. (2011). Worldwide distribution and diversity of seabird ticks: Implications for the ecology and epidemiology of tick-borne pathogens. *Vector-Borne and Zoonotic Diseases*, *11*(5), 453–470. https://doi.org/10.1089/vbz.2010.0009

Dietrich, M., Kempf, F., Boulinier, T., & McCoy, K. D. (2014). Tracing the colonization and diversification of the worldwide seabird ectoparasite *Ixodes uriae*. *Molecular Ecology*, *23*(13), 3292–3305. https://doi.org/10.1111/mec.12815

Dietrich, M., Kempf, F., Gómez-Díaz, E., Kitaysky, A. S., Hipfner, J. M., Boulinier, T., & McCoy, K. D. (2012). Inter-oceanic variation in patterns of host-associated divergence in a seabird ectoparasite. *Journal of Biogeography*, *39*, 545–555. https://doi.org/10.1111/j.1365-2699.2011.02620.x

Duneau, D., Boulinier, T., Gomez-Diaz, E., Peterson, A., Tveraa, T., Barrett, R. T., & McCoy, K. D. (2008). Prevalence and diversity of *Lyme borreliosis* bacteria in marine birds. *Infection, Genetics and Evolution*, *8*, 352–359. https://doi.org/10.1016/j.meegid.2008.02.006

Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, *4*(2), 359–361. https://doi.org/10.1007/s12686-011-9548-7

Elsterová, J., Černý, J., Müllerová, J., Šíma, R., Coulson, S. J., Lorentzen, E., Strøm, H., & Grubhoffer, L. (2015). Search for tick-borne pathogens in the Svalbard Archipelago and Jan Mayen. *Polar Research*, *34*(1), 27466. https://doi.org/10.3402/polar.v34.27466

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A

simulation study. *Molecular Ecology*, *14*(8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*(7), 673–677. https://doi.org/10.1038/nclimate2647

Garnier, R., Ramos, R., Sanz-Aguilar, A., Poisbleau, M., Weimerskirch, H., Burthe, S., Tornos, J., & Boulinier, T. (2017). Interpreting ELISA analyses from wild animal samples: Some recurrent issues and solutions. *Functional Ecology*, *31*, 2255–2262. https://doi.org/10.1111/1365-2435.12942

Gasparini, J., McCoy, K. D., Haussy, C., Tveraa, T., & Boulinier, T. (2001). Induced maternal response to the Lyme disease spirochaete *Borrelia burgdorferi* sensu lato in a colonial seabird, the kittiwake *Rissa tridactyla*. *Proceedings of the Royal Society of London Series B*, *268*, 647–650. https://doi.org/10.1098/rspb.2000.1411

Gómez-Díaz, E., Doherty, P. F., Jr., Duneau, D., & McCoy, K. D. (2010). Cryptic vector divergence masks vector-specific patterns of infection: An example from the marine cycle of *Lyme borreliosis*. *Evolutionary Applications*, *3*(4), 391–401. https://doi.org/10.1111/j.1752-4571.2010.00127.x

Goudet, J. (2003). *Fstat (ver. 2.9.4), a program to estimate and test population genetics parameters*. http://www.unil.ch/izea/softwares/fstat.html. Updated from Goudet [1995] (2.9.4)

Harris, M. P. (1984). *The puffin*. T & AD Poyser Ltd.

Hoegh-Guldberg, O., Jacob, D., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F., Guiot, J., Hijioka, Y., Mehrotra, S., Payne, A., Seneviratne, S. I., Thomas, A., Warren, R., Zhou, G., Halim, S. A., Achlatis, M., … Zougmoré, R. B. (2018). *Impacts of 1.5°C global warming on natural and human systems*. IPCC Secretariat. http://hdl.handle.net/10138/311749

Hubisz, M. J., Falush, D., Stephens, M., & Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, *9*(5), 1322–1332. https://doi.org/10.1111/j.1755-0998.2009.02591.x

Hvidsten, D., Stordal, F., Lager, M., Rognerud, B., Kristiansen, B. E., Matussek, A., Gray, J., & Stuen, S. (2015). *Borrelia burgdorferi* sensu lato-infected *Ixodes ricinus* collected from vegetation near the Arctic Circle. *Ticks and Tick-Borne Diseases*, *6*(6), 768–773. https://doi.org/10.1016/j.ttbdis.2015.07.002

Jaenson, T. G. T., Jaenson, D. G. E., Eisen, L., Petersson, E., & Lindgren, E. (2012). Changes in the geographical distribution and abundance of the tick *Ixodes ricinus* during the past 30 years in Sweden. *Parasites & Vectors*, *5*, 8. https://doi.org/10.1186/1756-3305-5-8

Juliano, S. A., & Lounibos, L. P. (2005). Ecology of invasive mosquitoes: Effects on resident species and on human health. *Ecology Letters*, *8*(5), 558–574. https://doi.org/10.1111/j.1461-0248.2005.00755.x

Kada, S., McCoy, K. D., & Boulinier, T. (2017). Impact of life stage-dependent dispersal on the colonization dynamics of host patches by ticks and tick-borne infectious agents. *Parasites & Vectors*, *10*(1), 375. https://doi.org/10.1186/s13071-017-2261-y

Kempf, F., Boulinier, T., De Meeus, T., Arnathau, C., & McCoy, K. D. (2009). Recent evolution of host-associated divergence in the seabird tick *Ixodes uriae*. *Molecular Ecology*, *18*(21), 4450–4462. https://doi.org/10.1111/j.1365-294X.2009.04356.x

Khan, J. S., Provencher, J. F., Forbes, M. R., Mallory, M. L., Lebarbenchon, C., & McCoy, K. D. (2019). Parasites of seabirds: A survey of effects and ecological implications. *Advances in Marine Biology*, *82*, 1. https://doi.org/10.1016/bs.amb.2019.02.001

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, *33*(7), 1870–1874. https://doi.org/10.1093/molbev/msw054

Kutz, S. J., Jenkins, E. J., Veitch, A. M., Ducrocq, J., Polley, L., Elkin, B., & Lair, S. (2009). The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host-parasite interactions. *Veterinary Parasitology*, *163*(3), 217–228. https://doi.org/10.1016/j.vetpar.2009.06.008

Larsson, C., Comstedt, P., Olsen, B., & Bergstrom, S. (2007). First record of Lyme disease *Borrelia* in the Arctic. *Vector-Borne and Zoonotic Diseases*, *7*(3), 453–456. https://doi.org/10.1089/vbz.2006.0644

Lee, R. E., Jr., & Baust, J. G. (1987). Cold-hardiness in the Antarctic tick, *Ixodes uriae*. *Physiological Zoology*, *60*(4), 499–506. https://doi.org/10.1086/physzool.60.4.30157912

Léger, E., Vourc'h, G., Vial, L., Chevillon, C., & McCoy, K. D. (2013). Changing distributions of ticks: Causes and consequences. *Experimental and Applied Acarology*, *59*(1–2), 219–244. https://doi.org/10.1007/s10493-012-9615-0

Lobato, E., Pearce-Duvet, J., Staszewski, V., Gómez-Díaz, E., González-Solís, J., Kitaysky, A., McCoy, K. D., & Boulinier, T. (2011). Seabirds and the circulation of *Lyme borreliosis* bacteria in the North Pacific. *Vector-Borne and Zoonotic Diseases*, *11*, 1521–1527. https://doi.org/10.1089/vbz.2010.0267

Lynch, H. J., Fagan, W. F., & Naveen, R. (2010). Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic Peninsula. *Polar Biology*, *33*(4), 493–503. https://doi.org/10.1007/s00300-009-0726-y

McCoy, K. D. (2001). *Consequences of dispersal in host-parasite systems (population dynamics, genetic structure and local adaptation of a seabird parasite, the tick Ixodes uriae)* (Doctoral dissertation). University of Paris VI.

McCoy, K. D., Beis, P., Barbosa, A., Cuervo, J. J., Fraser, W. R., Gonzalez-Solis, J., Jourdain, E., Poisbleau, M., Quillfeldt, P., Leger, E., & Dietrich, M. (2012). Population genetic structure and colonisation of the western Antarctic Peninsula by the seabird tick *Ixodes uriae*. *Marine Ecology-Progress Series*, *459*, 109–120. https://doi.org/10.3354/meps09749

McCoy, K. D., Boulinier, T., Schjørring, S., & Michalakis, Y. (2002). Local adaptation of the ectoparasite *Ixodes uriae* to its seabird host. *Evolutionary Ecology Research*, *4*, 441–456.

McCoy, K. D., Boulinier, T., Tirard, C., & Michalakis, Y. (2001). Host specificity of a generalist parasite: Genetic evidence of sympatric host races in the seabird tick *Ixodes uriae*. *Journal of Evolutionary Biology*, *14*, 395–405. https://doi.org/10.1046/j.1420-9101.2001.00290.x

McCoy, K. D., Boulinier, T., Tirard, C., & Michalakis, Y. (2003). Host-dependent genetic structure of parasite populations: Differential dispersal of seabird tick host races. *Evolution*, *57*(2), 288–296. https://doi.org/10.1111/j.0014-3820.2003.tb00263.x

McCoy, K. D., Chapuis, E., Tirard, C., Boulinier, T., Michalakis, Y., Le Bohec, C., Le Maho, Y., & Gauthier-Clerc, M. (2005). Recurrent evolution of host-specialized races in a globally distributed parasite. *Proceedings of the Royal Society B-Biological Sciences*, *272*(1579), 2389–2395. https://doi.org/10.1098/rspb.2005.3230

McCoy, K. D., Dietrich, M., Jaeger, A., Wilkinson, D. A., Bastien, M., Lagadec, E., Boulinier, T., Pascalis, H., Tortosa, P., & Le Corre, M. (2016). The role of seabirds of the Iles Eparses as reservoirs and disseminators of parasites and pathogens. *Acta Oecologica*, *72*, 98–109. https://doi.org/10.1016/j.actao.2015.12.013

McCoy, K. D., & Tirard, C. (2000). Isolation and characterisation of microsatellites in the seabird ectoparasite *Ixodes uriae*. *Molecular Ecology*, *9*, 2213–2214. https://doi.org/10.1046/j.1365-294X.2000.105330.x

McCoy, K. D., & Tirard, C. (2002). Reproductive strategies of the seabird tick *Ixodes uriae* (Acari: Ixodidae). *Journal of Parasitology*, *88*(4), 813–816. https://doi.org/10.1645/0022-3395(2002)088[0813:RSOTST]2.0.CO;2

Mercier, G., Yoccoz, N. G., & Descamps, S. (2021). Influence of reproductive output on divorce rates in polar seabirds. *Ecology and Evolution*, *11*(19), 12989–13000. https://doi.org/10.1002/ece3.7775

Muñoz-Leal, S., & González-Acuña, D. (2015). The tick *Ixodes uriae* (Acari: Ixodidae): Hosts, geographical distribution, and vector roles. *Ticks*

and Tick-Borne Diseases, *6*(6), 843–868. https://doi.org/10.1016/j.ttbdis.2015.07.014

Nater, C. R., Eide, N. E., Pedersen, Å. Ø., Yoccoz, N. G., & Fuglei, E. (2021). Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate. *Ecosphere*, *12*(6), e03546. https://doi.org/10.1002/ecs2.3546

Nordli, Ø., Przybylak, R., Ogilvie, A. E. J., & Isaksen, K. (2014). Long-term temperature trends and variability on Spitsbergen: The extended Svalbard Airport temperature series, 1898–2012. *Polar Research*, *33*(1), 21349. https://doi.org/10.3402/polar.v33.21349

Olsen, B., Duffy, D. C., Jaenson, T. G. T., Gylfe, A., Bonnedahl, J., & Bergström, S. (1995). Transhemispheric exchange of Lyme disease spirochetes by seabirds. *Journal of Clinical Microbiology*, *33*, 3270–3274. https://doi.org/10.1128/jcm.33.12.3270-3274.1995

Olsen, B., Jaenson, T. G. T., Noppa, L., Bunikis, J., & Bergström, S. (1993). A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks. *Nature*, *362*, 340–342. https://doi.org/10.1038/362340a0

Paull, S. H., & Johnson, P. T. J. (2014). Experimental warming drives a seasonal shift in the timing of host-parasite dynamics with consequences for disease risk. *Ecology Letters*, *17*(4), 445–453. https://doi.org/10.1111/ele.12244

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959. https://doi.org/10.1534/genetics.116.195164

Schramm, F., Gauthier-Clerc, M., Fournier, J. C., McCoy, K. D., Barthel, C., Postic, D., Handrich, Y., Le Maho, Y., & Jaulhac, B. (2014). First detection of *Borrelia burgdorferi* sensu lato DNA in king penguins (*Aptenodytes patagonicus halli*). *Ticks and Tick-Borne Diseases*, *5*(6), 939–942. https://doi.org/10.1016/j.ttbdis.2014.07.013

Staszewski, V., McCoy, K. D., & Boulinier, T. (2008). Variable exposure and immunological response to Lyme disease *Borrelia* among North Atlantic seabird species. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1647), 2101–2109. https://doi.org/10.1098/rspb.2008.0515

Staszewski, V., McCoy, K. D., Tveraa, T., & Boulinier, T. (2007). Interannual dynamics of antibody levels in naturally infected long-lived colonial birds. *Ecology*, *88*, 3183–3191. https://doi.org/10.1890/07-0098.1

Van Riper, C., III, Van Riper, S. G., Goff, M. L., & Laird, M. (1986). The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs*, *56*(4), 327–344. https://doi.org/10.2307/1942550

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*(6), 1358–1370. https://doi.org/10.2307/2408641

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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