

Local adaptation of the ectoparasite *Ixodes uriae* to its seabird host

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ABSTRACT

In addition to reproductive rates and generation times, local parasite adaptation is predicted to be associated with relative host/parasite migration rates, parasite virulence and local resource levels. We tested for local parasite adaptation in a spatially structured natural host–parasite system with fluctuating host resources. Using a cross-fostering design replicated over 2 years, we exchanged chicks of the Black-legged kittiwake (*Rissa tridactyla*) between subpopulations of its ectoparasite, the tick *Ixodes uriae*. We found evidence that ticks were adapted to their local hosts; ticks had higher success (capacity to continue to the next life stage) and shorter engorgement times on sympatric birds than on allopatric birds. However, infestation levels were similar between the resident and non-resident chicks in a nest, implying that ticks are unable to distinguish between good and bad hosts and that selection acts during tick engorgement. Hosts appeared to be locally maladapted to their parasites; growth rates tended to be lower for sympatric birds in the presence of parasites. However, we found no effect of host group on the T-cell immune response of chicks. Overall, the results seemed to depend on the environmental quality. When resources were low, local maladaptation was expressed in the host, but adaptation was not shown by the parasite. In the higher quality year, evidence for local parasite adaptation was found, but the host seemed to be able to compensate for the pathogenic effects of ticks. This suggests that virulence (pathogenic effect on host) and the reciprocal effects of the interaction can fluctuate depending on host environmental conditions.

Keywords: co-evolution, host–parasite interactions, *Ixodes uriae*, *Rissa tridactyla*, tick, virulence.

INTRODUCTION

The antagonistic interaction between parasites and their hosts has gained considerable recognition recently as an important force shaping the evolutionary and ecological dynamics of species in space and time (Grenfell and Dobson, 1995; Thompson, 1999). Parasites are typically thought to ‘win’ the arm’s race between exploiter and victim because

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of shorter generation times, higher reproductive rates and higher mutation/recombination rates. Thus, parasites should be able to adapt locally to their hosts such that they infect sympatric host populations more efficiently than allopatric host populations (Ebert, 1994; Ebert and Hamilton, 1996). While several studies have supported this idea (e.g. Koskela *et al.*, 2000), others have found no such relationship (e.g. Mutikainen *et al.*, 2000; see references in Kaltz and Shykoff, 1998) or, indeed, the reverse pattern where parasites are maladapted to their local hosts (Kaltz *et al.*, 1999; Oppliger *et al.*, 1999).

In parallel with these variable experimental results, several theoretical studies have been carried out to help us to understand and predict patterns of co-evolution. Gandon *et al.* (1996) suggest that the capacity for a parasite to become locally adapted depends, in part, on relative host/parasite migration rates; parasites that migrate more than their hosts should be able to locally adapt to their host due to the potential availability of novel alleles. A model of antagonistic interactions over productivity gradients found that such interactions should depend on local resource availability with the intensity of reciprocal selective forces increasing with resources (Hochberg and van Baalen, 1998). Lively (1999) has shown theoretically that local parasite adaptation should increase with increasing virulence (or the pathogenic effect of the parasite) if parasite migration rates are reasonably low. In addition to such factors, adaptation can take place at many spatial scales – from individuals to regions – and, as such, patterns of local adaptation will depend on the scale considered for a given system (Kaltz and Shykoff, 1998). Thus, the co-evolutionary interactions between parasites and hosts are complex processes that should depend on the interplay between multiple factors. Here, we test for local adaptation in a host–parasite system involving the ectoparasite *Ixodes uriae* and one of its host species, the Black-legged kittiwake, *Rissa tridactyla*. As this interaction is strongly spatially structured and shows a clear dependence on host resource availability and breeding success, it provides an ideal system to consider the influence of different factors on the evolution of local adaptation.

Ixodes uriae (family Ixodidae) is a common ectoparasite of seabirds in the circumpolar areas of both hemispheres (Guiguen, 1988). This tick typically has a 4 year life cycle consisting of three active stages – larva, nymph and adult – and is only found in association with the host for a short period each year (4–10 days) when it takes a single, long blood meal that enables it to continue to the next life stage. As adults, male ticks do not feed and engorged females lay a single clutch of several hundred eggs before dying (Eveleigh and Threlfall, 1974). During the long off-host period, the tick lives in the area surrounding the host nest (Eveleigh and Threlfall, 1974). Independent migration abilities are considered to be limited for ticks (e.g. Falco and Fish, 1991) and dispersal among host (sub)populations relies on host movement (Danchin, 1992; McCoy *et al.*, 1999). Recent results have shown that there is low neutral genetic structure of tick populations between nearby host subpopulations, suggesting that dispersal through the intra-colony movements of birds does occur (McCoy *et al.*, 2001).

The Black-legged kittiwake is a long-lived seabird that nests in dense colonies, typically containing from a few hundred to several thousand breeding pairs. These large colonies are often divided into discrete breeding cliffs (i.e. subpopulations). After reaching adulthood, individuals can reproduce for more than 10 years, producing 0 to 3 chicks each year (e.g. Erikstad *et al.*, 1995). Although there is at present no data on the genetic structure of kittiwake populations, observational work has indicated that high levels of breeding and natal philopatry occur in this species (Coulson and Nève de Mévergnies, 1992). For example, in a flourishing colony in Brittany, France, studied over a 10 year period, breeding

and natal philopatry were estimated to be 98 and 56%, respectively (Danchin and Monnat, 1992). Given this, it is likely that tick dispersal rates are higher at a local scale (between host subpopulations) than that of their hosts.

Tick parasitism can negatively impact hosts through several direct mechanisms: blood loss leading to anaemia, injection of toxins that can paralyse the host, or irritation that may modify host behaviour (Lehmann, 1993). Similarly, these ectoparasites may indirectly impact their host by vectoring different micropathogens (Chastel, 1988). For example, *Borrelia burgdorferi* s.l., the spirochete responsible for Lyme disease, is transmitted to seabirds via *Ixodes uriae* (Olsen *et al.*, 1995). Hosts can resist tick parasitism using both innate and acquired components of the immune system involving, among other bioactive molecules, antibodies, complement, antigen-presenting cells and T-lymphocytes (Wikel, 1996). For kittiwakes, it has been shown that females can transfer antibodies against local parasites to their offspring via the egg (Gasparini *et al.*, 2001). The expression of host resistance can impair tick engorgement, ova production and viability (Wikel, 1996). Ticks modulate host responses by injecting different molecules with the saliva that can inhibit complement activity linked with innate responses (Lawrie *et al.*, 1999) and that can block the activation and proliferation of T-lymphocytes, and thus retard stimulation of directed immune responses (Wikel, 1996).

Based on the potential force of reciprocal selection in this system and predicted relative dispersal rates, combined with the difference in generation times and reproductive rates between the parasite and its host, we expected *I. uriae* to be adapted to its local seabird hosts. We examined this hypothesis using a cross-fostering experiment in which host individuals were exchanged among parasite subpopulations and where the relative fitness of both the host and parasite were assessed. If ticks are locally adapted to their hosts, we expected that they should have relatively higher fitness on sympatric hosts than on allopatric hosts. If hosts are locally maladapted, sympatric birds should have reduced fitness compared with allopatric birds in the presence of the parasite. As patterns of adaptation depend on the reciprocal nature of the interaction, it is possible to find local parasite adaptation and no host maladaptation (or the reverse).

MATERIALS AND METHODS

Experimental protocol

Although *Ixodes uriae* is known to parasitize many seabird species (Guiguen, 1988), we restricted our experiment to the Black-legged kittiwake (*Rissa tridactyla*). We chose this species because chicks remain at the nest site (nests are on vertical cliffs) until fledging (approximately 43 days; Coulson and White, 1958) and this species is tolerant to disturbance (Sandvik and Barrett, 2001). Furthermore, transplanted chicks are readily accepted for the first 4 weeks of the chick-rearing period due to low parent–offspring recognition in this species (Storey *et al.*, 1992).

The study took place on Hornøya, Norway (70°22' N, 31°10' E) in June and July of 1998 and 1999. The kittiwake population on Hornøya consists of about 21,000 breeding pairs (Lorentsen, 1998) divided among several isolated cliffs. Breeding cliffs were chosen for the experiment based on accessibility (Table 1). The distance between these cliffs varied from a minimum of 50 m to a maximum of 800 m. The estimated level of tick infestation could not be determined before the first year of study because infestation can only be assessed by

the examination of chicks. This meant that one cliff was later found not to be infested by ticks (cliff K7) and was not used in the second year of the experiment. Overall, infestation of cliffs varied from 0.06 ± 0.06 to 28.01 ± 7.11 ticks per chick per nest (mean $\pm$ standard error; Table 1).

For each breeding cliff, all nest sites were monitored to determine hatching dates. Nests with the same hatching dates (within 1 day) and containing at least two chicks were paired. Chicks with matching weights were transferred between nests when they were 5 days old. At the time of the exchange, both chicks in each nest were ringed for identification and the condition of the chick (weight, infestation level) was recorded. On this day, chicks were exhaustively searched for ticks using standard techniques of visual search and skin palpation (Danchin, 1992). All ticks were removed from both the sympatric and allopatric chick such that both started the experiment uninfested.

After transfer, the chicks were not disturbed for 48 h. Thereafter, they were monitored every 24 h until they were 20 days old (~ 2 weeks). Chick weights (to nearest 1 g) were taken every other day in 1998 and at ages 5, 10 and 20 days in 1999. Tick infestation of chicks was assessed at each visit. To help standardize this measure, we counted the number of ticks of each life stage over the entire body of the chick a single time in a systematic fashion. Newly feeding nymphal or adult ticks (attached, but non-engorged) were marked with coloured permanent markers. The colour and location on the bird were noted for each tick so that its presence or absence could be recorded at each visit. After approximately 4 days on the host, the semi-engorged tick was attached by a small piece of grey duct tape ($\sim 0.5 \times 0.5$ cm) to a few of the surrounding feathers. This was done to help try to prevent ticks from dropping off into the nest substrate when engorgement was complete and enabled the collection of 40% of followed individuals. There was no apparent effect of the tape on the birds. In most cases, even if the tick was not successfully collected, the piece of tape was recovered.

The method we used to monitor feeding ticks did not allow for a fine-scale assessment of engorgement time (i.e. hours or minutes); however, as differences in the duration of

Table 1. Infestation levels (mean $\pm$ standard error) of kittiwake breeding cliffs by *Ixodes uriae* and the number of nests used in the 2 years of study

Cliff	1998		1999	
	No. of nests	Mean infestation	No. of nests	Mean infestation
K1	6	0.66 ± 0.12	5	0.93 ± 0.49
K2	5	14.00 ± 5.65	11	7.90 ± 1.83
K3	2	9.04 ± 9.04	3	1.36 ± 1.29
K4	2	0.36 ± 0.19	2	2.09 ± 1.19
K6	3	8.04 ± 6.78	2	6.88 ± 5.38
K7	2	0	—	—
K8	4	10.65 ± 3.00	7	28.01 ± 7.11
K9	2	0.06 ± 0.06	2	0.53 ± 0.43
Total	26		32	

Note: Mean infestation was calculated as the number of ticks per chick per nest.

engorgement for *I. uriae* vary between 4 and 9 days (e.g. Barton *et al.*, 1995), we expected a difference between engorgement times on sympatric and allopatric chicks to be detectable if it existed and was impacting tick fitness. This method also enabled us to assess whether ticks survived the entire feeding period; Barton *et al.* (1995) found that only 74% of nymphal *I. uriae* survived to complete engorgement. If collected, engorged ticks were maintained in the laboratory so that the egg-laying success of females and moulting success of nymphs could be monitored.

When the chick was 20 days old, a measure of the T-cell-mediated immune response was taken. This measure of the competence of the cell-mediated immune system is correlated with chick condition (Saino *et al.*, 1997) and is considered to be positively related to the survival of young chicks (Wikel, 1996; Saino *et al.*, 1997). Each chick was injected in the centre of the right wing-web (the skin in the joint between carpometatarsus and ulna/radius) with 0.05 ml of PHA (Phytohaemagglutinin-P; Sigma L8754) mixed with physiological saline (concentration of $5 \text{ mg} \cdot \text{ml}^{-1}$). In the left wing-web, a control of 0.05 ml of saline was injected. The thickness of the wing-web was measured to the nearest 0.01 mm using a spessimeter (Teclock Co., Japan). To help minimize measurement errors, wing-webs were measured three times and the average of these values was used as the measured thickness. Measures of wing-web thickness before injection and after 24 h for both the PHA-injected and control wings allowed us to calculate the T-cell-mediated immune response of chicks to this novel immunogen.

Predictions and statistical analyses

Local adaptation may occur at different spatial scales and determining the appropriate scale for tests will depend on the characteristics of the system under consideration (Kaltz and Shykoff, 1998). Although there is spatial variation in tick infestation among breeding cliffs (Table 1), there is also strong aggregation of ticks among nests (Boulinier *et al.*, 1996; McCoy *et al.*, 1999). Given that kittiwakes are long-lived and nest-site faithful, we felt that the nest level was the appropriate scale to test for local adaptation in this system. We examined this assumption by including 'cliff' in the statistical models; cliff was unable to explain significant variation for any of the response variables considered when nest was included in the model.

All statistical analyses were performed using the SAS statistical package (SAS Institute, 1990). When clear predictions were made regarding the direction of tests, we used directed tests for determining significance rather than one-tailed tests (Rice and Gaines, 1994). Directed tests are more conservative than one-tailed tests, but allow one to perform a more powerful test when deviations from the null hypothesis are in the anticipated direction. To calculate directed *P*-values, one-tailed values are adjusted to take into account asymmetrical critical regions in the two tails of the test statistic distribution. For all directed tests, we considered significance at the γ/α level of 0.8 (i.e. 80% of type I error in the predicted direction), as suggested by Rice and Gaines (1994).

Tick success and engorgement time

If locally adapted to their hosts, ticks should have higher success on sympatric birds than on allopatric birds. Tick feeding success was quantified two ways: (1) by determining the number of ticks that remained on a bird for more than the minimum time required to successfully engorge (this minimum time was defined *a priori* based on previous studies; see

below); and (2) for individual ticks that were collected after engorgement, by whether they moulted to the next stage (for nymphs) or laid eggs (for adult females).

Barton *et al.* (1995) found that the minimum time required for nymphal ticks to feed successfully on kittiwakes was 4 days. We therefore considered any nymph that fed for 3 days or less to be unsuccessful. Finney *et al.* (1999) estimated the feeding range of adult ticks to be 5.22–9.51 days. Based on this, we considered the minimum time required for a female tick to feed successfully to be 5 days. The effect of the treatment on tick success was examined using the difference in average tick success (rank transformed) of the two birds in a nest (sympatric – allopatric). We tested whether this difference was significantly greater than zero using a *t*-test (Zar, 1996). Only nests where there were at least two observations for each chick were considered.

Direct measures of feeding success included observations of tick mortality on the host and moulting (for nymphs) or laying (for adults) success of collected, engorged ticks. As the number of ticks collected varied among chicks due to spatial variation in infestation and to the difficulty in collecting engorged ticks, we could not calculate the average success per bird. Instead, overall feeding success was compared between sympatric and allopatric chicks using a contingency table analysis (Zar, 1996).

The time a tick spends on the host for the blood meal imposes risks linked to host defences, such as specific immune responses or preening, and to the possibility of the parasite dropping off after engorgement in the wrong place (e.g. at sea). In addition, prolonged blood meals can be a direct result of host resistance (Wikel, 1996). Although there is a correlation between the blood volume taken by a female tick and the number of eggs produced (Sonenshine, 1991), we did not find a relationship between the length of the blood meal and the number of eggs produced ($F_{1,8} = 0.274$, $P = 0.61$). This suggests that females vary in the length of time required to fully engorge, but that longer engorgement times do not mean greater size. In this case, selection should favour ticks that can fully engorge in as short a time as possible. We therefore expected that successful ticks should have shorter average engorgement times on sympatric chicks than on allopatric chicks. Engorgement times of successful ticks (ticks that spent the minimum time required) were compared between ticks of sympatric and allopatric hosts using the average time ticks spent on an individual and considering only those nests where there was at least one observation per bird. We then tested if the difference in feeding times (sympatric – allopatric time) on the two birds in a nest was lower than zero using a *t*-test (Zar, 1996). In a second analysis, we considered only those ticks that were directly observed to be successful and compared relative times of ticks for sympatric and allopatric birds using two-sample tests (Zar, 1996).

Chick infestation, growth and immune response

Tick infestation levels of sympatric and allopatric chicks were compared using the difference in the number of ticks on each chick (sympatric – allopatric) at age 20 days old. From the hypothesis of local tick adaptation, we expected this difference to be significantly greater than zero (Zar, 1996). The infestation level at 20 days was strongly correlated with cumulative number of ticks infesting chicks over the entire experimental period (1998: $r = 0.87$, $n = 13$, $P < 0.001$; 1999: $r = 0.93$, $n = 39$, $P < 0.001$). Thus, we considered infestation at age 20 days to be a good estimate of the parasitic pressure experienced by chicks.

Growth rates of chicks were determined by linear regressions of chick weight on age. Although bird growth does not follow a linear path, the ages of the chicks considered here (between 5 and 20 days old) correspond to the linear part of the growth curve for kittiwakes

(Lance and Roby, 1998). As growth rates could have been affected by both the treatment (i.e. sympatric or allopatric) and by the level of tick infestation, we compared the growth of sympatric and allopatric chicks taking into account the infestation level. Based on the distribution of the frequency histogram of tick infestation on chicks, infestation levels were divided into two groups: low infestation (<5 ticks) and high infestation (≥ 5 ticks). The significance of effects on chick growth were determined using a two-way analysis of variance (ANOVA) including nest (GLM; SAS Institute, 1990). If birds are maladapted to their local tick population, we expected to see a significant treatment $\times$ infestation level interaction, indicating that at low infestation levels both chicks in a nest had similar growth rates, but at high levels the sympatric chick had a lower growth rate than the allopatric chick.

Based on our hypothesis, we also predicted that there should be a significant effect of the treatment on the T-cell immune response in the presence of ticks – that is, we expected a significant treatment $\times$ infestation level interaction. We tested for this interaction using a two-way ANOVA with treatment and infestation level (high or low) as factors and chick weight as a covariate (GLM; SAS Institute, 1990).

RESULTS

In the 2 years of this study, we exchanged kittiwake chicks between 58 nests spread over eight breeding cliffs (Table 1) and followed 116 chicks and 339 of their ticks. There was a significant difference in quality between the 2 years. In both years, an equivalent numbers of kittiwake eggs were produced per nest (Table 2). However, significantly more chicks were fledged (or still alive at the last observation time) in 1999 than in 1998, suggesting that the overall quality of the breeding season was better in 1999 (Table 2). For this reason, we performed analyses separately for each year. Due to the natural loss of chicks at different stages of the experiment, sample sizes vary according to the variable considered.

Tick feeding success

Feeding success, as determined by minimum engorgement time, revealed a significant treatment effect in 1999, with a higher proportion of successful ticks on sympatric birds than on allopatric birds (t -test of difference: $t_{11} = 2.83$, $P_{\text{dir}} = 0.023$; Fig. 1b). In 1998, feeding success was similar for the two birds in a nest (t -test of difference: $t_7 = -0.63$, $P_{\text{dir}} = 0.69$; Fig. 1a). We found comparable results when we considered tick success

Table 2. Number of eggs and chicks produced per nest during the 1998 and 1999 breeding seasons in experimental kittiwake breeding cliffs

	1998		1999		Test		
	<i>n</i>	mean $\pm$ S.E.	<i>n</i>	mean $\pm$ S.E.	χ^2	d.f.	<i>P</i>
No. of eggs	89	2.02 $\pm$ 0.06	128	2.09 $\pm$ 0.05	0.64	1	0.422
No. of chicks	90	0.56 $\pm$ 0.08	127	0.87 $\pm$ 0.08	5.98	1	0.015

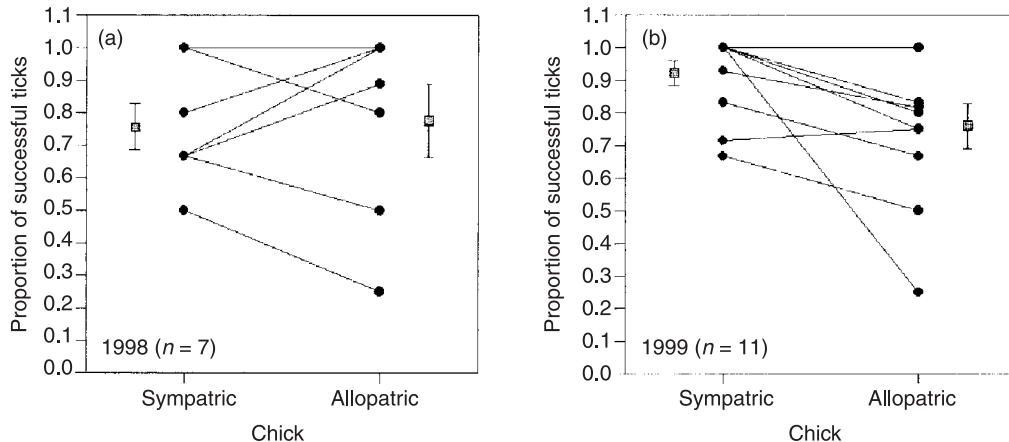


Fig. 1. Proportion of successful ticks on sympatric and allopatric chicks in a nest in (a) 1998 and (b) 1999. Tick success was determined indirectly by the minimum engorgement time. Only nests for which there were at least two observations on each bird were included. Lines match sympatric and allopatric birds in a nest. Squares represent overall success of ticks (mean $\pm$ standard error) for sympatric and allopatric chicks.

using direct observations of tick death and moulting/laying success; in 1999, there was a significant association between feeding success and whether ticks fed on sympatric or allopatric hosts, with a higher proportion of successful ticks feeding on sympatric birds (sympatric = 0.68, $n = 63$; allopatric = 0.47, $n = 38$; Fisher's exact test: $P_{\text{dir}} = 0.039$). This pattern was not found in 1998 (sympatric = 0.55, $n = 11$; allopatric = 0.68, $n = 25$; Fisher's exact test: $P_{\text{dir}} = 0.63$).

Engorgement times

Nymphs took significantly shorter blood meals than adult ticks (nymph = 4.82 ± 0.16 days, $n = 172$, range = 1.0–12.26; adult = 7.23 ± 0.23 days, $n = 59$, range = 1.0–10.93; $t_{229} = 8.11$, $P < 0.001$). Thus, each life stage was considered separately when examining the length of successful blood meals on sympatric and allopatric birds. For both years, there was a tendency for successful nymphs on sympatric birds to take shorter meals than successful nymphs on allopatric birds (t -test of difference, 1998: $t_8 = -1.50$, $P_{\text{dir}} = 0.11$; 1999: $t_8 = -1.63$, $P_{\text{dir}} = 0.092$); this trend was significant if we pooled the 2 years ($t_{16} = -2.22$, $P_{\text{dir}} = 0.026$; Fig. 2a). If we considered only data from nymphal ticks that were observed to moult successfully, we found the same trend; times were longer for ticks that fed on non-resident birds (Fig. 2b), although this difference was not significant (Wilcoxon two-sample test: $Z = 1.04$, $n_{\text{sympatric}} = 21$, $n_{\text{allopatric}} = 9$, $P_{\text{dir}} = 0.186$).

The analysis of adult engorgement times was not possible in 1998 due to low sample sizes. In 1999, there was no significant effect of treatment group on the engorgement times of successful adult ticks; the feeding times on allopatric birds were similar to those on sympatric birds (sympatric = 7.61 ± 0.19 days, allopatric = 7.70 ± 0.42 days) (t -test of difference: $t_6 = -0.18$, $P_{\text{dir}} = 0.54$). However, when we examined feeding times of collected adult

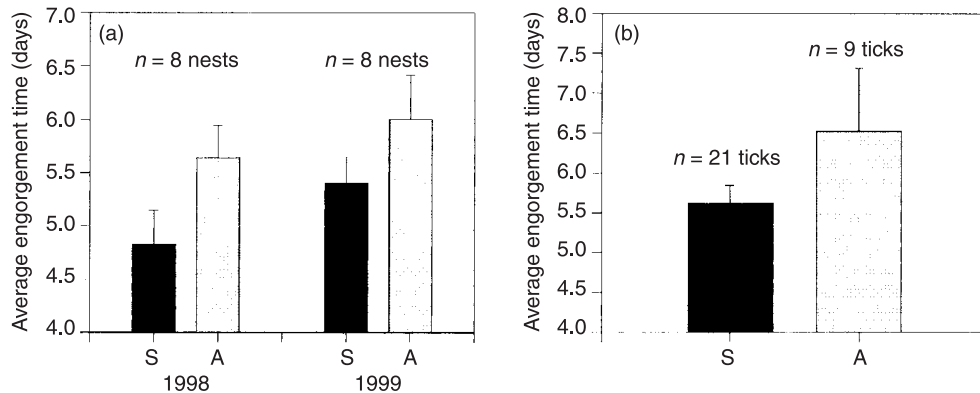


Fig. 2. Average engorgement time of successful nymphal ticks on sympatric (S) and allopatric (A) birds. (a) Successful ticks as determined by minimum engorgement times (i.e. ticks that fed for at least 4 days). Only nests for which there was at least one observation per bird were included. (b) Successful ticks as determined through direct observation of moulting/laying success.

ticks that were observed to lay eggs, we found longer engorgement times of adult ticks on allopatric birds than on sympatric birds (sympatric = 5.70 ± 0.20 days, $n = 4$; allopatric = 6.52 ± 0.18 days, $n = 6$) ($t = -2.99$, $P_{\text{dir}} = 0.011$).

Tick infestation levels

Overall, tick loads were similar in infested nests in the 2 years of study (1998: 21.08 ± 4.63 , $n = 12$; 1999: 24.70 ± 6.01 , $n = 30$) (Wilcoxon two-sample test: $Z = 0.67$, $P = 0.50$). There was no difference between the infestation levels of sympatric and allopatric hosts in a nest in either 1998 (t -test of difference: $t_6 = 0.24$, $P_{\text{dir}} = 0.74$) or 1999 ($t_{15} = -0.88$, $P_{\text{dir}} = 0.24$). Infestation levels of chicks in a nest were strongly correlated in both years (1998: $r = 0.94$, $n = 14$, $P < 0.001$; 1999: $r = 0.92$, $n = 19$, $P < 0.001$; Fig. 3).

Chick growth

In 1998, we found a marginally significant interaction between treatment group and parasite infestation level; sympatric birds had lower growth rates than allopatric birds when infested by ticks, but similar growth rates when ticks were absent (treatment $\times$ infestation interaction, $F_{1,35} = 4.32$, $P = 0.055$; Fig. 4a). There was also a significant effect of nest on growth rates ($F_{17,35} = 3.27$, $P = 0.013$), suggesting that food provisioning by parents might have varied between nests. This same pattern was not found in 1999; in this year, there were no significant effects of any of the factors considered (all $P > 0.20$; Fig. 4b). As 1999 was a relatively high-quality year for kittiwakes on Hornøya, it is possible that the availability of food overcame any influence of parasites or food provisioning rates on chick growth. In agreement with this hypothesis, overall growth rates tended to be higher in 1999 than in 1998, but not significantly so (1998: 14.16 ± 0.33 g $\cdot$ day $^{-1}$, $n = 36$; 1999: 14.92 ± 0.46 g $\cdot$ day $^{-1}$, $n = 48$) ($t_{79,4} = -1.33$, $P = 0.19$).

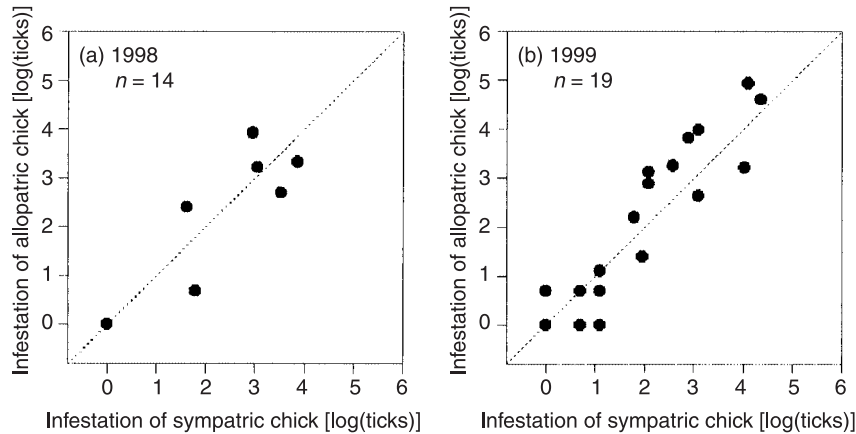


Fig. 3. Correlations of tick infestation levels of sympatric and allopatric chicks at age 20 days in (a) 1998 and (b) 1999. Each dot corresponds to a nest. Several observations are represented at the infestation level of zero–zero.

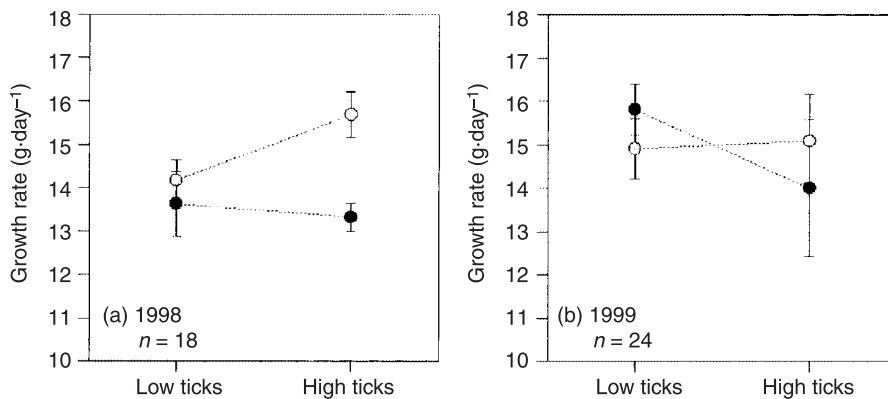


Fig. 4. Average growth rates of sympatric (●) and allopatric (○) chicks with low and high tick infestation levels in (a) 1998 and (b) 1999.

Immune response

Contrary to predictions, there was no significant difference in the strength of the T-cell immune response of sympatric and allopatric chicks in parasitized nests in either of the 2 years of study (treatment $\times$ infestation interaction, 1998: $F_{1,30} = 0.77$, $P = 0.39$; 1999: $F_{1,40} = 0.06$, $P = 0.81$). However, in 1998, there was a tendency towards an increased immune response in the presence of ticks ($F_{1,30} = 3.48$, $P = 0.073$; Fig. 5). This was not the case in 1999 ($F_{1,30} = 0.00$, $P = 0.96$; Fig. 5). These results may suggest that, in poor-quality years, ticks have a greater influence on kittiwake nestlings (i.e. higher virulence) than in high-quality years.

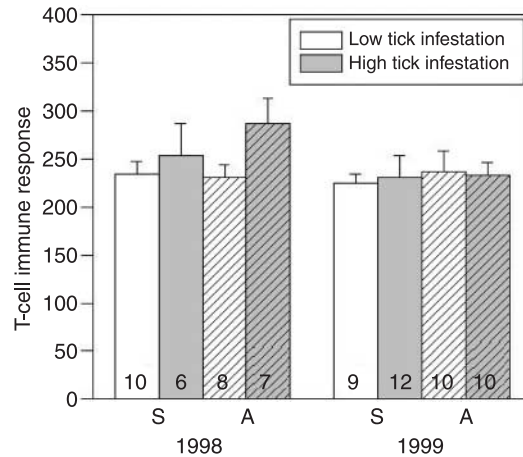


Fig. 5. T-cell immune response of sympatric (S – blank) and allopatric (A – barred) birds that experienced low (white) or high (grey) levels of tick infestation for 1998 and 1999. Sample sizes for each group are noted at the bottom of bars. Note that tick intensity in the high tick infestation group did not differ between years (1998: 27.85 ± 5.98 ; 1999: 31.23 ± 7.43) ($t_{33} = -0.31$, $P = 0.75$).

DISCUSSION

In this study, we tested for local adaptation in the *Ixodes uriae*–Black-legged kittiwake system using a cross-fostering experiment and measuring variables we considered important for host and parasite fitness. We found evidence suggesting that these ectoparasites are indeed locally adapted to their kittiwake hosts. Tick success was higher on local birds than on birds from other breeding cliffs in 1999, and ticks that successfully engorged on sympatric birds spent less time on the bird than ticks on allopatric birds, therefore exposing themselves to a lower risk associated with feeding on the host (i.e. defence responses or bird's departure for winter at sea).

Tick success differed between the 2 years of study. In 1999, the higher-quality year based on fledging success (Table 2), there was a clear difference in tick success on sympatric and allopatric hosts, which was not the case in 1998 (Fig. 1). This result may be linked to the availability of resources in 1998. Model predictions suggest that the intensity of antagonistic interactions should be higher when resource availability is high (Hochberg and van Baalen, 1998). In line with this, chicks should be able to invest more in defence in good years and thus we should see a stronger effect on tick success in those years. The difference between years may also be due to lower sample sizes in 1998 than in 1999. However, as the calculation of tick success in 1998 involved following an average of 4.23 ± 0.48 ticks per chick, the measure of the success per chick should still have been reliable for these nests.

Kittiwakes appeared to be maladapted to their local parasites. Sympatric chicks tended to have lower growth rates than allopatric chicks in tick-infested nests (Fig. 4). However, this result was only found in 1998, the year of lower quality. In this year, there was also a significant nest effect, suggesting that variables other than infestation, such as food provisioning by parents, varied spatially. In 1999, a higher abundance of food may have allowed chicks to compensate for such potentially negative factors. Thus, virulence of parasites (pathogenic effect per parasite) may change depending on the host resource base, suggesting

that magnitude of selection on chicks to adapt to local parasites may vary between years. As we only consider patterns over 2 years in the present study, this hypothesis merits further testing.

Although parasite adaptation and host maladaptation are typically treated as coupled effects in theoretical work (e.g. Gandon *et al.*, 1996; Lively, 1999), our results suggest that host and parasite fitness may be independent. In poor years, host maladaptation is expressed and the parasite shows no adaptation. In good years, the parasite may experience stronger selective pressures from the host and show local adaptation, but the host will show no maladaptation due to an ability to compensate for the pathogenic effects of parasites. This decoupled effect is logical if we consider that the parasite depends completely on the host for resources, while the parasite constitutes only a small part of the host's environment and may be negligible in certain years depending on the strength of other local factors.

For ectoparasites, and many endoparasites, pathogenic effects on the host will change with infection intensity such that there is a threshold above which parasitism affects host fitness. In this sense, parasite virulence is a trait of the interaction and not a property of the parasite itself. In our system, hosts may decide to disperse to a new parasite-free site if parasite infestation becomes too high to be tolerated. High tick densities may lead to increased breeding failures, which reduce breeding philopatry and cause birds to abandon long-used nest sites (Boulinier *et al.*, 2001). As tick populations tend to build up with the age of colonies (Danchin, 1992), this could set up a dynamic where local parasite adaptation occurs until parasites become too abundant. Hosts then become locally 'extinct' and, subsequently, cause parasite extinction (May and Southwood, 1990). Once hosts settle in a new location, the process could then start over again.

No theoretical studies have specifically addressed how temporal variation in virulence or number of infections could alter co-evolutionary dynamics. Theory predicts that local adaptation should increase with virulence under certain conditions (Lively, 1999). For ticks, this may mean that a run of several poor-quality years for the host (where the pathogenic effect per parasite is higher) will increase selection for host adaptation, which should, in turn, increase reciprocal selection on the parasites. Due to the relatively high fluctuations of local resource availability for pelagic seabirds (Erikstad *et al.*, 1998), this temporal variation may be particularly relevant for the kittiwake–tick system. If host and parasite populations are connected by limited gene flow, such patterns may set up a mosaic of co-evolution where outcomes in local populations may be quite variable (Thompson, 1999). Modelling the combined effects of fluctuating virulence in varying environments on the outcome of co-evolutionary interactions could thus prove interesting.

We found that tick infestation was strongly correlated between chicks in a nest. This suggests that the local environment may be the main factor determining infestation levels of chicks. In a previous study of another kittiwake population, evidence of a genetic basis for susceptibility to ticks has been reported (Boulinier *et al.*, 1997). Although chicks were equally infested by ticks, there was strong variation in levels of tick success (Figs 1, 2), indicating that ticks are not able to distinguish between 'good' and 'bad' host individuals before they engage in the blood meal. This implies that local selection pressures on ticks could be strong and thus may drive rapid local adaptation to the host.

We also compared a measure of chick immunocompetence, the capacity to mount a cell-mediated immune response to a novel immunogen, between sympatric and allopatric chicks. Previous work has shown that this response is correlated with host body condition

(Saino *et al.*, 1997). Contrary to predictions, we found no effect of treatment group on this measure (Fig. 5). This suggests that the influence of locally adapted ticks on host body condition might not have been strong enough to alter patterns of physiological investment. However, in 1998, it appears that ticks were able to generally influence this response; infested individuals tended to have higher responses than non-infested individuals (Fig. 5). Given year quality and the predicted investment in immune function, we cannot explain why immune responses were not higher on average in 1999 than in 1998. This pattern may be a reflection of an interaction between year quality and parasite virulence. Clearly, further work will be required to understand the interaction between chick condition, tick infestation and immunocompetence.

Here, we considered that ticks were locally adapted to the host breeding site, but it is also possible that the adaptation occurred at a different spatial scale. That 'cliff' could not explain more variation in response variables than nest, suggests that the cliff scale was too large. As kittiwakes return to the same nest to breed year after year and ticks are highly aggregated at this scale (Boulinier *et al.*, 1996; McCoy *et al.*, 1999), the breeding pair may exert strong selection pressure on local ticks. This suggests that nest site may be an appropriate scale for local adaptation in this system. We could have tested this assumption more fully by also switching chicks between local nests. However, because of the difficulty in matching hatching dates between nests, we decided not to attempt to combine this second manipulation in the present experiment. More information on the structure of tick populations at the scale of the breeding cliff, along with similar information on the host, could help verify at what spatial scale adaptation may occur.

As far as we know, there has only been one other study examining local adaptation of an ectoparasite. Duvfa (1996) found no evidence for local adaptation of Hen fleas (*Ceratophyllus gallinae*) exchanged between populations of its Great tit (*Parus major*) host. These results could have been related to the spatial scale considered. In this system, host dispersal and local turnover may be high enough that local adaptation occurs at the level of the metapopulation rather than population. Patterns of local adaptation may occur in other tick–host systems but, unlike for *Ixodes uriae*, most tick hosts are far-ranging and different tick life stages feed on different species (Sonenshine, 1993). This should select for a more general response in most tick species (Lawrie *et al.*, 1999) and thus might lower the probability of local adaptation, particularly at small spatial scales. Further examination of other ectoparasite systems, where ectoparasites have different host species associations during the life cycle, will be necessary to determine how general this pattern is.

The patterns of local adaptation we found have important implications for the dynamics of the tick–seabird interaction. For example, the ability of ticks to adapt locally to their host may speed up the process of speciation. Indeed, we have found evidence of host races in this species (McCoy *et al.*, 2001). If hosts have specific responses to feeding ticks, specificity for the host may be directly linked to the selection pressures associated with engorgement. As *Ixodes uriae* parasitizes many different host species over a wide geographic area, co-evolution can involve several types of local interactions (among groups of same-host and different-host species). This sets up the potential to find different patterns of co-evolution. Similar studies examining patterns of local adaptation in other *Ixodes uriae*–host populations, combined with specific models designed to make predictions in such systems, may help us to better understand co-evolutionary processes of such interactions.

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