

High-elevational occurrence of two tick species, *Ixodes ricinus* and *I. trianguliceps*, at their northern distributional limit

Nicolas De Pelsmaeker (✉ nicolas.de.pelsmaeker@usn.no)

University of South-Eastern Norway <https://orcid.org/0000-0002-5908-040X>

Lars Korslund

University of Agder: Universitetet i Agder

Øyvind Steifetten

University of South-Eastern Norway: Universitetet i Sorost-Norge

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Abstract

Background: During the last decades a northward and upward range shift has been observed among many organisms across different taxa. In the northern hemisphere, ticks have been observed to have increased their latitudinal and altitudinal range limit. However, the elevational expansion at its northern distribution limit remains largely unstudied. In this study we investigated the altitudinal distribution of the exophilic *Ixodes ricinus* and endophilic *I. trianguliceps* on two mountain slopes in Norway by assessing larval infestation rates on bank voles (*Myodes glareolus*).

Methods: During 2017 and 2018, 1325 bank voles were captured during spring, summer and autumn at 10 trapping stations ranging from 100 m to 1000 m.a.s.l. in two study areas in southern Norway. We used generalized logistic regression models to estimate the prevalence of infestation of both tick species along altitude, considering study area, collection year and season, temperature, humidity and altitude interactions as extrinsic variables; and host body mass and sex as intrinsic predictor variables.

Results: We found that both *I. ricinus* and *I. trianguliceps* infested bank voles at altitudes up to 1000 m.a.s.l., which is a substantial increase in altitude compared to previous findings for *I. ricinus* in this region. The infestation rates declined more rapidly for *I. ricinus* compared to *I. trianguliceps*, indicating that the endophilic ecology of *I. trianguliceps* may provide shelter from limiting factors tied to altitude. Seasonal effects limited the occurrence of *I. ricinus* during autumn, but *I. trianguliceps* was found to infest rodents at all altitudes during all seasons of both years.

Conclusions: This study provides new insights into the altitudinal distribution of two tick species at their northern distributional limit, one with the potential to transmit zoonotic pathogens to both humans and livestock. With warming temperatures predicted to increase, and especially so in the northern regions, the risk of tick-borne infections is likely to become a concern at increasingly higher altitudes in the future.

Background

During the last decades increasing temperatures have been shown to have an impact on the distribution of species across a wide range of taxonomic groups [1–6]. Depending on the species' adaptability to a warmer climate and the ability to disperse, species may either 1) increase their distribution range due to conditions becoming more favourable in areas that were previously inhospitable [7–10], 2) contract in range as their habitat becomes increasingly unsuitable [11–13], or 3) move away from areas that have become unsuitable towards habitats that have become more favourable [2, 14, 15]. To date most species appear to expand their natural distribution range, and for the majority of species both a northward [e.g. 16–18] [19, 20] and an upward [21–23] range expansion seems to be the most common movement pattern.

Along with other organisms, certain ectoparasites such as ticks have undergone similar range expansions [24–28]. Ticks are generally limited in their distribution by environmental factors such as temperature and humidity [29, 30], but as hematophagous parasites they also depend on the presence of adequate hosts [31]. With a changing climate, ticks have been observed to have increased their distribution range northwards in the northern hemisphere [24, 32, 33], and several studies have also demonstrated the occurrence of ticks to increasingly higher altitudes in central Europe [25, 26, 29, 34–39]. For example, in Switzerland, *Ixodes ricinus* has been recorded at altitudes up to 1070 m.a.s.l. [40, 41], and in the Czech republic it has shifted its altitudinal range limit up to 700 m.a.s.l. since the 1990s [25], and in one instance up to 1100 m.a.s.l. [39]. According to [37] it may survive up to 1200 m.a.s.l. or higher if the habitat is favourable. Another tick species, *I. trianguliceps*, has been recorded at altitudes as high as 2300 m.a.s.l. in Switzerland [42], but because it does not quest in open vegetation like *I. ricinus*, it is likely to be less exposed to limiting environmental conditions, especially temperature, and hence able to survive in more extreme environments [31]. With any upward shift in range limit, the risk of exposure to tick-borne infections is likely to increase for both humans and livestock [38, 39], and is predicted to further increase in the future [7, 43, 44].

Most studies investigating the altitudinal dynamics of *I. ricinus* have occurred at its geographical center in Europe [25, 26, 29, 35–37, 41, 45], and very little is known about its altitudinal distribution at the northern range limit. Because the effects of climate change are expected to be stronger at higher latitudes [46], the increase in altitude expansion is likely to be more pronounced in Scandinavia. In Norway, *I. ricinus* has undergone a northward range shift similar to other Scandinavian countries [27, 47–49], and it has been found as far north as 69°N [27] and is considered to be permanently established at 66°N [50]. It has also expanded upwards in altitude and has been observed up to 583 m.a.s.l. [27]. Even so, data are scarce, and the occurrence of ticks in relation to altitude and its range boundary remain largely unknown. To the best of our knowledge no recent field studies have investigated the altitudinal distribution of ticks at their northern distributional limit in Europe. This study aims to determine the altitudinal distribution patterns of the exophilic generalist tick *I. ricinus* and the endophilic specialist tick *I. trianguliceps* in Norway, by studying the infestation rates of both species on a commonly found rodent, the bank vole (*Myodes glareolus*). Because of the nest-dwelling behavior of *I. trianguliceps*, we expect it to be less limited by altitude compared to *I. ricinus*.

Methods

Study areas

This study took place along two mountain slopes in Norway during 2017 and 2018 (Fig. 1). The first study area was a southern facing mountain slope on the Lifjell massif (N59°26.495' E9°0.603'), north of Bø i Telemark. It is characterized by a continental climate, located within the boreonemoral to southern boreal zone. At lower altitude it is dominated by mixed deciduous and coniferous forest. The treeline is situated between 800 and 900 m.a.s.l., and the highest peak found on the plateau is 1288 m.a.s.l. The second study area was located in the Erdal valley (N61°05.817' E7°24.688') near Lærdalsøyri (hereafter referred to as Lærdal). It is a northern facing mountain slope close to the innermost part of the Sognefjorden fjord, approximately 150 km east of the western coastline. Due to its proximity to the fjord, the climate is more coastal than Lifjell, characterized by cooler summers and milder winters. The vegetation is predominantly deciduous forest, and the highest peak is at 1716 m.a.s.l. The treeline is situated between 900 and 1000 m.a.s.l.

Study species

I. ricinus is the most common and the most studied tick species in Europe [30]. It ranges latitudinally from North Africa to Scandinavia, and longitudinally from Ireland to Russia [51]. It is a three-host tick and each life stage feeds on a new host. Immature life stages (larvae and nymphs) feed predominantly on small mammals [52]. It is common to deciduous, and to some extent, coniferous forests, and is dependent on sufficient temperature and humidity to be able to quest (actively seeking a host). It is sensitive to desiccation and temperature extremes [53].

I. trianguliceps occurs throughout Europe, ranging latitudinally from Italy up to well above the arctic circle [54]. Contrary to *I. ricinus*, *I. trianguliceps* is a specialist parasite, feeding primarily on rodents and small mammals during all life stages [55, 56]. It is endophilic (nest-dwelling), spending its off-host time within the burrows of its host to molt and quest [57]. It occurs in widely different habitats, ranging from meadows, peat bogs to dark-coniferous forests, mixed and deciduous forests, as well as high altitude treeless zones [52, 55]. It is generally considered to be one of the most cold resistant ticks of the genus *Ixodes* in the Palearctic region [55]. Since it rarely infests humans or livestock due to its host seeking behaviour [58], cases of tick-borne infection are considered exceptional [27], but it does contribute to maintaining the infection cycle of several pathogens between *I. ricinus* and their hosts [59–61].

The bank vole is a commonly found rodent throughout Europe and occurs virtually everywhere in Fennoscandia [62], and it is the most common rodent species in both study areas. Other small mammal species present are the field vole (*Microtus agrestis*), tundra vole (*M. oeconomus*), grey red-backed vole (*Myodes rufocanus*), wood mouse (*Apodemus sylvaticus*), yellow-necked mouse (*A. flavicollis*) and house mouse (*Mus musculus*). The common shrew (*Sorex araneus*), pigmy shrew (*S. minutus*) and water shrew (*Neomys fodiens*) are also found in these areas. The bank vole is a reservoir host for several tick-borne pathogens such as *Borrelia burgdorferi* [63], *Babesia microti* [64], *Candidatus Neorickettsia mikurensis* [65], and granulocytic-Ehrlichia [66]. It is possibly the most important host for all life stages of *I. trianguliceps* [52], and is heavily infested by the immature stages of *I. ricinus* [67–69]. Because it was common at both study areas and at all altitudes, we chose to base our analysis on this species.

Host trapping

In both study areas, 10 trapping stations were set up along a vertical gradient ranging from 100 to 1000 m.a.s.l. at every 100 m altitude interval. At each trapping station, two plots of 20 traps each were deployed, one with live traps (Ugglan Special Nr. 2, Grahnb AB, Sweden, www.grahnb.se), the other with lethal traps (Rapp2 Mousetrap, www.rappfellene.no). The traps in both plots were arranged in a 4 by 5 grid, with 10 meters spacing between each trap. Live traps were baited with a slice of apple for hydration and whole oats for caloric value, and a lining of sawdust was provided on the trap floor as insulation. Lethal traps were baited with peanut butter for practical reasons as it is easily applied to the inside of the trap body. Trap type do not influence tick burden size on the captured animals (De Pelsmaeker et al., in press). At each altitude, the live and lethal plots were placed at approximately 100 m distance from each other, to prevent overlap of host home ranges. As humidity and temperature have a direct influence on tick activity, they are important drivers of phenological patterns and host-seeking behavior [70]. For this reason, a datalogger (TinyTag Plus 2 – TGP 4017, housed in a DataMate instrument cover ACS-5050) was placed in between the two plots at each trapping station, approximately 50 cm above ground level measuring air temperature and relative air humidity at a 1-hour interval for the duration of the trapping period. Trapping took place during the spring (May 20th – 30th), summer (July 20th–30th) and autumn (September 20th–30th) seasons of the years 2017 and 2018. As an exception, during the spring season of 2017, capturing took place from June 1st until June 7th, and only up to 700 m.a.s.l. in both areas, as there was too much snow to allow for the operation of traps earlier and above this altitude. During each trapping period, traps were checked every 24 hours, and the collection of trapped animals started at 8h30. When checking the trapping grids, triggered lethal traps were rebaited and reset. All animals captured in live traps were euthanized by cervical dislocation of the head, and each one was kept separately in a sealed and coded plastic bags. Activated live traps were emptied of the remaining contents, and new insulation and food was provided before resetting the traps. At the end of every collection day, all animals were placed in a freezer at -20 °C.

Laboratory processing

At the end of every trapping season, captured bank voles were examined for ticks in the laboratory. The day before the examination, the voles were removed from the freezer and left to thaw overnight at 10 °C. The voles were examined one by one and taken out of the plastic bags individually. The empty bags were checked for ticks that might have dropped off. It was our observation that a number of ticks would drop off the host when the animals were placed in the freezer, possibly in an attempt to escape the extreme temperatures. Animals that were wet were dried with a hairdryer before examination. The hosts were checked for ticks starting with the head, ears and snout, followed by the neck and throat, back and abdomen, legs, feet and tail. Attached or detached ticks were removed from the host using tweezers. Collected ticks were removed and placed in a 1.5 mL plastic Eppendorf tube containing a 70% ethanol solution (1 vial per host). Finally, a lice comb was brushed through the fur of the animal from tail to head (against the hair orientation), and the vole was shaken by the tail above a white plastic tray to collect any ticks that might have been missed during the examination. The hosts were then weighed to the nearest 10th of a gram, and the sex was determined. The minimum amount of time needed to process one animal was 20 minutes. After the examination the animals were bagged in new plastic bags and refrozen at -20 °C.

Ticks were determined for life stage and species under a Zeiss Discovery V20 stereomicroscope, using established publication keys as reference [52, 71]. Because more than 94% and 75% of all *I. ricinus* and *I. trianguliceps* collected were larvae, only the larval stage was included in the analysis.

Data analysis

The statistical analyses were performed using the software package R version 3.5.3 [72]. The analysis of *I. ricinus* larvae and *I. trianguliceps* larvae was performed separately. As is usually the case with tick presence on small mammals [73] neither species was evenly distributed on the hosts, and 13.8 and 82.0% of the hosts had no *I. ricinus* and *I. trianguliceps* larvae present, respectively. We therefore chose to use the presence or absence of larvae as the response variable and applied generalized linear modeling with a binomial distribution, i.e. logistic regression. The probability of encountering a tick is defined as prevalence. As predictor variables we considered altitude (ranging from 100 m.a.s.l. to 1000 m.a.s.l. – as a continuous variable), study area (Lifjell and Lærdal), collection year (2017 and 2018), season (spring, summer and autumn) and humidity (%). Because altitude and temperature were negatively

correlated (Pearson correlation test, $t=-8.1578$, $df = 1323$, $p < 0.001$, $r=-0.219$), temperature per se was not used as a predictor variable to avoid introducing collinearity into the model. Two-way interactions between season and altitude, study area and altitude, year and altitude, study area and year, as well as year and season were included in the starting model. We also considered individual bank vole body mass (in grams) and sex (male or female) as intrinsic co-variables. Starting with a full starting model containing all variables and the two-way interactions listed above, we used a backward step model selection process to progressively remove non-significant predictors - by comparing the residual deviance and degrees of freedom of nested models using a Chi-square test - until an optimal model, containing only significant predictor variables ($\alpha = 0.05$), was found. To visually represent the infestation probabilities of both species across study areas, collection years and seasons, we created multiple regression line plots using the *ggplot2* package in R [74].

Ethics statement

This study was carried out in strict accordance with regulations issued by the Norwegian Environment Agency, and a permit was provided prior to the start of the sampling (Miljødirektoratet, reference number: 2017/4651) for the duration of the trapping period. The trapping protocol for animal capture was approved by the Animal Ethics Committee of the Department of Nature, Health and Environment (University of South-Eastern Norway). All efforts were made to minimize animal suffering.

Results

During 2017 and 2018, a total of 43920 trap nights were performed, capturing 1325 bank voles (976 and 349 captures in 2017 and 2018, respectively). Altogether 5372 tick larvae were collected from the trapped voles at all altitudes of the gradient. Larvae of *I. ricinus* were 7.4 times more numerous compared to *I. trianguliceps* (88.1% and 11.9% of ticks, respectively). Larval burdens ranged from 1-100 ticks for *I. ricinus*, and from 1-29 for *I. trianguliceps*, and more than half of the bank voles (57.4%) were infested with at least one larva of either tick species. For *I. ricinus* and *I. trianguliceps*, respectively, 46.8% and 18.0%, of voles carried at least one larva. Of all the voles, 7.3% were infested with at least one larvae of both tick species. For a total number of ticks collected from voles at every altitude see Fig. 2. Mean burdens can be found in Table 1.

I. ricinus

The best model shows that there was a clear negative overall effect of altitude on the prevalence of *I. ricinus* presence ($z=-3.954$, $p < 0.001$), and a significant interaction between altitude and season ($c^2 = 12.3$, $df = 2$, $p = 0.002$) illustrate that this effect was stronger in autumn than in spring and summer (Table 2, Fig. 3). In addition, a significant interaction between altitude and site ($c^2 = 11.1$, $df = 1$, $p < 0.001$) shows that the negative altitude effect was stronger in Lærdal than in Lifjell (Table 2). This is mainly caused by the fact that, while the prevalence is low at 1000 m at both sites, the prevalence at the lower altitudes was higher in Lærdal (close to 1) compared to Lifjell (around 0.75 or less) (Fig. 3). The model further shows that the overall prevalence of *I. ricinus* was highest among voles captured in spring, lower, but not significantly so, among voles captured in summer ($z=-1.14$, $p = 0.25$) and significantly lower among voles captured in autumn ($z=-2.65$, $p = 0.08$) (Table 2, Fig. 3). The prevalence of *I. ricinus* was overall lower in 2018 ($z=-2.06$, $p = 0.04$), but the season effect, with lower prevalence in autumn, was much stronger in 2017 than in 2018, as indicated by a significant interaction between year and season ($c^2 = 26.7$, $df = 2$, $p < 0.001$) (Table 2, Fig. 3). Finally, the significant interaction between site and season shows that the season effect was stronger in Lærdal than in Lifjell ($c^2 = 12.3$, $df = 2$, $p = 0.002$) with especially the autumn prevalence being lower in Lærdal ($z=-2.73$, $p = 0.006$) (Table 2, Fig. 3).

While host weight did not affect the prevalence of *I. ricinus* ($c^2 = 0.106$, $df = 1$, $p = 0.75$), it was significantly more often found on male than on female host, resulting in a significant sex effect in the best model ($c^2 = 15.0$, $df = 1$, $p < 0.001$).

I. trianguliceps

The best model, explaining the prevalence of *I. trianguliceps* on bank voles, ended up being much simpler than that for *I. ricinus* (Table 2). Also for this species there was a clear negative overall effect of altitude on the prevalence ($c^2 = 11.7$, $df = 1$, $p < 0.001$) (Table 2). However, the overall prevalence was much lower than what was found for *I. ricinus* (Fig. 3). The overall prevalence of *I. trianguliceps* was significantly lower in Lærdal than in Lifjell ($c^2 = 34.7$, $df = 1$, $p < 0.001$) and significantly higher in 2018, compared to 2017 ($c^2 = 27.0$, $df = 1$, $p < 0.001$) (Table 2, Fig. 3). The model further shows a clear effect of season ($c^2 = 35.7$, $df = 2$, $p < 0.001$) with the overall prevalence of *I. trianguliceps* being higher among voles captured in autumn, and with an equal prevalence in spring and summer (Table 2, Fig. 3)

Neither host weight ($c^2 = 2.66$, $df = 1$, $p = 0.10$) nor host sex ($c^2 = 1.11$, $df = 1$, $p = 0.29$) did affect the prevalence of *I. trianguliceps* presence on bank voles.

Table 1

Mean larval burden sizes \pm SD of *I. ricinus* and *I. trianguliceps* found on bank voles at every altitude during 2017 and 2018 in Lifjell and Lærdal. NA indicates no larvae were captured, or that not enough data was available to compute a standard deviation.

Lærdal	2018	Autumn	2.1 \pm 1.6	1.6 \pm 2.8	4.3 \pm 3.0	1.4 \pm 3.5	0.5 \pm 0.7	0.4 \pm 1.0	0.3 \pm 0.6	1.2 \pm 3.3	1.0 \pm 1.8	1.6 \pm 2.3	0.2 \pm 0.4	0.7 \pm 1.1	0.0 \pm 0.0	1.1 \pm 3.0	0.2 \pm 0.4	1.0 \pm 2.4	NA		
		Summer	6.3 \pm 4.6	0.2 \pm 0.4	19.4 \pm 19.1	0.1 \pm 0.3	2.8 \pm 4.0	0.2 \pm 0.4	1.0 \pm 1.4	0.6 \pm 1.2	2.6 \pm 3.2	1.4 \pm 4.3	0.4 \pm 0.9	0.5 \pm 0.9	0.4 \pm 0.9	0.4 \pm 0.9	0.2 \pm 0.4	0.4 \pm 0.9	0.0 \pm 0.0	0.0 \pm 0.0	
		Spring	43.3 \pm 32.6	0.0 \pm 0.0	31.6 \pm 25.0	0.5 \pm 0.9	10.6 \pm 6.9	0.2 \pm 0.4	9.5 \pm 15.3	0.3 \pm 0.5	12.7 \pm 10.5	0.1 \pm 0.3	2.1 \pm 2.6	0.3 \pm 0.8	0.3 \pm 0.6	0.0 \pm 0.0	0.2 \pm 0.4	0.0 \pm 0.0	0.0 \pm 0.0	NA	
	2017	Autumn	10.5 \pm 9.8	0.6 \pm 15	8.9 \pm 4.9	0.4 \pm 0.8	0.7 \pm 1.1	0.7 \pm 1.4	0.2 \pm 0.6	0.3 \pm 0.5	0.0 \pm 0.2	0.5 \pm 1.9	0.0 \pm 0.0	0.1 \pm 0.3	0.0 \pm 0.0	0.1 \pm 0.4	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 1.0	0.0 \pm 0.0	
		Summer	19.7 \pm 20.3	0.1 \pm 0.3	13.2 \pm 9.1	0.3 \pm 0.7	3.1 \pm 3.3	0.0 \pm 0.0	1.6 \pm 1.6	0.0 \pm 0.2	4.1 \pm 2.6	0.3 \pm 1.4	1.6 \pm 1.5	0.0 \pm 0.0	1.4 \pm 1.9	0.1 \pm 0.5	0.2 \pm 0.4	0.1 \pm 0.4	0.9 \pm 0.9	0.0 \pm 0.0	0.0 \pm 0.0
		Spring	84.0 \pm 25.2	0.3 \pm 0.6	23.8 \pm 9.8	0.0 \pm 0.0	19.5 \pm 13.7	0.0 \pm 0.0	8.1 \pm 7.3	0.0 \pm 0.0	14.5 \pm 8.0	0.1 \pm 0.3	13.8 \pm 12.9	0.1 \pm 0.4	2.0 \pm 3.3	0.3 \pm 0.8	NA	NA	NA	NA	NA
Lifjell	2018	Autumn	4.8 \pm 5.3	4.6 \pm 6.5	NA	NA	NA	NA	0.0 \pm NA	4.0 \pm NA	NA	NA	NA	NA	NA	NA	0.0 \pm 0.0	2.0 \pm 1.4	NA		
		Summer	0.0 \pm 0.0	1.0 \pm 1.4	NA	NA	NA	NA	0.0 \pm 0.0	0.0 \pm 0.0	NA	NA	0.0 \pm 0.0	0.5 \pm 0.7	0.0 \pm NA	0.0 \pm NA	NA	NA	NA	NA	
		Spring	19.0 \pm NA	0.0 \pm NA	NA	NA	NA	NA	0.5 \pm 1.0	0.5 \pm 0.6	0.5 \pm 1.2	1.2 \pm 1.3	0.0 \pm NA	0.0 \pm NA	NA	NA	0.0 \pm 0.0	0.0 \pm 0.0	NA	NA	
	2017	Autumn	0.2 \pm 0.5	1.6 \pm 3.4	2.9 \pm 1.6	0.9 \pm 1.1	0.6 \pm 1.4	1.6 \pm 2.8	0.0 \pm 0.0	2.3 \pm 4.9	0.0 \pm 0.2	1.5 \pm 3.9	0.1 \pm 0.3	0.5 \pm 1.1	0.0 \pm 0.0	0.2 \pm 0.5	0.0 \pm 0.0	0.0 \pm 0.0	0.2 \pm 0.7	0.0 \pm 0.0	
		Summer	0.8 \pm 1.0	0.2 \pm 0.7	8.1 \pm 7.4	0.0 \pm 0.0	1.5 \pm 2.4	0.0 \pm 0.2	0.9 \pm 1.9	0.6 \pm 1.1	0.1 \pm 0.4	0.5 \pm 0.9	1.1 \pm 1.2	0.1 \pm 0.9	0.1 \pm 0.9	0.0 \pm 0.0	1.3 \pm 5.9	NA	NA	0.1 \pm 0.4	
		Spring	0.3 \pm 0.7	1.3 \pm 2.2	15.0 \pm 10.9	0.4 \pm 1.0	1.1 \pm 0.7	0.0 \pm 0.0	0.9 \pm 1.3	0.3 \pm 0.6	0.5 \pm 0.8	0.3 \pm 0.6	0.2 \pm 0.4	0.4 \pm 0.7	2.8 \pm 7.9	0.0 \pm 0.0	NA	NA	NA	NA	
			<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>	<i>I. tri.</i>	<i>I. ric.</i>		

100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m	1000 m
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Table 2
 Parameter estimates for the infestation prevalence on bank voles indicating the probability to be infested with at least one tick, using a binomial distribution model. Baseline for study area is Lifjell, year 2017, spring season and male voles.

	Estimate	Std. Error	z - value	p - value
<i>I. ricinus</i> larvae				
Intercept	1.7429	0.5243	3.32	0.001
Study area Lærdal	4.2441	0.5824	7.29	< 0.001
Altitude	-0.0044	0.0011	-3.95	< 0.001
Sex Female	-0.6724	0.1719	-3.91	< 0.001
Year 2018	-0.7789	0.3780	-2.06	0.039
Season Summer	-0.6515	0.5701	-1.14	0.253
Season Autumn	-1.6039	0.6048	-2.65	0.008
Altitude : Season Summer	0.0012	0.0012	1.03	0.305
Altitude : Season Autumn	-0.0023	0.0014	-1.59	0.112
SiteLærdal : Altitude	-0.0029	0.0009	-3.39	0.001
Study area Lærdal : Season Summer	-0.7681	0.4656	-1.65	0.099
Study area Lærdal : Season Autumn	-1.5402	0.5646	-2.73	0.006
Year 2018 : Season Summer	-0.6665	0.4740	-1.41	0.160
Year 2018 : Season Autumn	1.4512	0.4858	2.99	0.003
<i>I. trianguliceps</i> larvae				
Intercept	-1.1554	0.2461	-4.70	< 0.001
Study area Lærdal	-0.9831	0.1690	-5.82	< 0.001
Altitude	-0.0011	0.0003	-3.37	0.001
Year 2018	0.9297	0.1785	5.21	< 0.001
Season Summer	0.0412	0.2257	0.18	0.855
Season Autumn	0.9133	0.2114	4.32	< 0.001

Discussion

Climate change is one of the most important drivers of the expansion of ticks in Europe [75], and poses a health risk to both humans and animals [39]. In fact, tick-borne diseases were identified by several European Ministries of Health to be the biggest health risk resulting from climate change [76]. Ticks have increased their distribution range northwards in Scandinavia [24, 77], and whereas *I. ricinus* was historically assumed to be limited to coastal areas in Norway, it is now increasingly occurring further inland, and its latitudinal distribution limit has shifted approximately 400 km northward since the early 1980s [27]. The highest recorded observation for *I. ricinus* has up until now been 583 m.a.s.l. [27], but here we show that both *I. ricinus* and *I. trianguliceps* were present at an altitude of at least 1000 m.a.s.l. in two locations located in the eastern and western part of Southern Norway. We can therefore assume that in this region, both species are established at altitudes up to 1000 m.a.s.l.

The effect of altitude on prevalence

Although both tick species decreased in abundance as altitude increased, both were found at all altitudes of the gradient. We expected altitude to have a stronger effect on *I. ricinus* compared to *I. trianguliceps*, and our results support this. Although in both study areas, at low altitudes, the prevalence with *I. ricinus* larvae was generally higher than that of *I. trianguliceps*, infestation of the former showed a stronger decline with increasing altitude during all three seasons. The prevalence of *I. trianguliceps* larvae also declined with altitude, but less so. The stronger decline for *I. ricinus* is mostly a result of a much higher prevalence of this species at lower altitudes. The strongest decline in *I. ricinus* occurred during the autumn season, where the prevalence at the top of the gradient (above 900 m.a.s.l.) was zero, while still a substantial part of hosts were infested at lower altitudes. The generally higher prevalence found for *I. ricinus* at lower altitudes compared to *I. trianguliceps* might be a direct consequence that *I. ricinus* is able to make use of more types of hosts, such as cervids. Indeed, field experiments have shown that excluding roe deer (*Capreolus capreolus*) as tick hosts, reduced the larval burden of *I. ricinus* on small rodents, but not that of *I. trianguliceps* [78]. At higher altitudes it is possible that both tick species are limited by the lower overall temperatures and/or the shorter snow free season, but that *I. trianguliceps* are less affected by such environmental conditions due to its endophilic nature. It is reasonable to expect that *I. ricinus*, which requires a minimum temperature to initiate questing [79], cannot be active for as many days at 1000 m compared to lower altitudes. This would reduce the

probability of finding a host, leading to a lower population density. *I. trianguliceps* however, seeking a small mammal host within its burrows, is not as limited by low ambient temperatures [80] and should thus be more capable of completing its life cycle at higher altitudes. This distinction might explain the difference in slope between the two tick species in our study.

M Daniel [29] found that suitable tick hosts generally are present at altitudes above the distribution limit of ticks, hence other factors, such as microclimatic conditions (e.g. temperature or humidity), is probably limiting the occurrence of ticks above a certain altitude. Materna et al. [39] found that this range limit is not necessarily restricted by survival per se. In fact, ticks (especially engorged females, imported by the movement of large hosts) can survive above their natural distribution limit for quite a long time [29]. The molting success of immature stages or oviposition by females also doesn't seem to be limited by altitude. According to Materna et al. [39], it appears that a reduced hatching success of the egg batch is what is hindering the developmental cycle of ticks, thus preventing them from establishing permanent populations. The presence of feeding larvae on rodents at high altitudes in this study indicates that the two species are capable of completing their life cycle. Because we only investigated infestation rates up to 1000 m.a.s.l. the actual altitudinal range limit of *I. ricinus* and *I. trianguliceps* in these areas of Norway is still unknown, but we have demonstrated *I. ricinus* to be present at altitudes well exceeding that of 583 m.a.s.l. found by Jore et al. [27]. A follow-up study at altitudes above 1000 m.a.s.l. may reveal the actual distribution limit of ticks in these areas.

The effect of season on prevalence

The prevalence of *I. ricinus* larvae was generally highest in spring, compared to the other seasons and all altitudes, with the exception of Lifjell in 2017, where summer and spring prevalence was more or less equally high. Other studies in Switzerland [35], Italy [81] and Great Britain [54] showed that *I. ricinus* larvae have a bimodal activity pattern, peaking in spring and autumn, or only peaking in early summer [82]. In our study, spring and summer of 2017 had almost equally high prevalences, but seemed to drop before the summer of 2018. In 2018 both spring and summer were somewhat drier, and although humidity was not a reliable predictor of infestation for the two species, this could explain the lower levels of *I. ricinus* in summer of 2018. Overall it seems that *I. ricinus* larvae are not considerably inhibited by summer drought in this region, and the relatively cool and humid conditions enable it to continue questing for hosts throughout the summer until low temperatures in autumn inhibit their activity. *I. ricinus* depend on a relatively humid environment for questing and survival [83]. Surprisingly, higher infestation rates were found in Lærdal despite having a lower relative humidity than Lifjell. As humidity was not correlated with altitude in neither study areas, it is unlikely to have had a limiting effect on the presence of *I. ricinus* throughout the seasons at any altitude.

Larvae of *I. trianguliceps* were overall less frequent in both locations compared to *I. ricinus*, but were infesting voles during all active seasons of the year and at all altitudes of the gradient. In contrast to *I. ricinus*, *I. trianguliceps* was most frequently found on bank voles in autumn. *I. trianguliceps* is dependent on a very humid environment [84]. We had no data on the relative humidity inside the burrows for *I. trianguliceps*, but it could potentially be higher than above the surface [85, 86], and it is possible that generally more rain and lower temperatures in autumn leads to more favorable conditions for *I. trianguliceps* at this part of the year.

The effect of host on prevalence

Vole sex was a determining factor in prevalence of *I. ricinus* larvae, with males having higher infestations than females. Male voles have larger home ranges [87] and have higher mobility than females [88]. As *I. ricinus* quest for a host in open vegetation [70, 89], they are dependent on a passing host in order to attach [30], especially in the case of larvae as this life stage disperses the least, and their distribution is highly clumped. As males roam around more than females, the probability of encountering ticks is higher, and this could explain the sex difference in the infestation rates of *I. ricinus*. No significant difference was found in infestation with *I. trianguliceps* larvae between male and female voles. As *I. trianguliceps* is a nidicolous tick [53], and as both male and female voles visit these burrows, both sexes are potentially equally exposed to infestations of *I. trianguliceps* larvae. This is in concurrence with the findings of Cotton and Watts [54] in Britain where *I. trianguliceps* infested male and female voles equally.

Conclusions

Historically, *I. ricinus* was believed to be limited to coastal regions in Norway [90], but has since been found to expand further inland [27]. With ticks expanding to higher altitudes as well, there is an increasing risk for tick bites in such areas, and therefore an increased risk of human infection with tick-borne diseases. *I. ricinus* is a well known vector of several European zoonotic pathogens in humans [91–93], and between 400 and 500 cases of tick-borne Lyme borreliosis are diagnosed annually in Norway (Norwegian Surveillance System for Communicable Diseases - <http://www.msis.no>). Also, Norwegian sheep farmers tend to let the sheep graze freely outside of the winter season, and mortality due to tick-borne anaplasmosis has been found to be damaging to the sheep husbandry [94]. Thus, the occurrence of tick-borne infections has both social and economical consequences, but so far these problems have been restricted to low altitude areas. Even though *I. ricinus* occurrence decreases with altitude, the prevalence of tick-borne pathogens that are potentially dangerous to humans and livestock, does not necessarily decrease with tick abundance. Danielova et al. [37] found that although fewer ticks are present at higher altitudes, the prevalence of *B. burgdorferi* s.l. (the causal agent of Lyme disease) in those ticks did not decrease, and they retained the same infection rates at high altitudes.

Although human cases of tick-borne infections via *I. trianguliceps* are rare [27], this species help maintain the prevalence of pathogens in small mammal host populations by transferring tick-borne pathogens between hosts [59–61]. Although several recent studies have investigated the occurrence of tick-borne pathogens in *I. ricinus* ticks in Norway [95–101], no investigation has yet focused on disease dynamics in relation to altitude. In combination with the results of this study, an in-depth survey along altitudinal gradients investigating the prevalence of pathogens in ticks could provide valuable insights into the actual disease risk to humans and livestock in Norwegian mountains. As projections indicate a continuing trend in warming temperatures, particularly in the northern regions [102], the northward and upward progression of ticks under the influence of climate change is expected to continue in the future [75]. This will further expose humans and livestock to tick-borne infections in areas where no infection risk was present before.

Declarations

Ethics statement - Permission for capturing small mammals was issued by the Norwegian Environment Agency (Miljødirektoratet, reference number: 2017/4651).

Consent – All contributing authors are in agreement on the contents of the manuscript and to its submission.

Data Availability - Data set is deposited at usn.figshare.com. doi:10.23642/usn.12917960.

Competing interests – All contributing authors declare that there are no conflicts of interest involved in this study.

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Author's contributions – Nicolas De Pelsmaeker: data collection, formal analysis, manuscript writing; Lars Korslund: formal analysis, manuscript writing, supervision; Øyvind Steifetten: manuscript writing, supervision.

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Figures

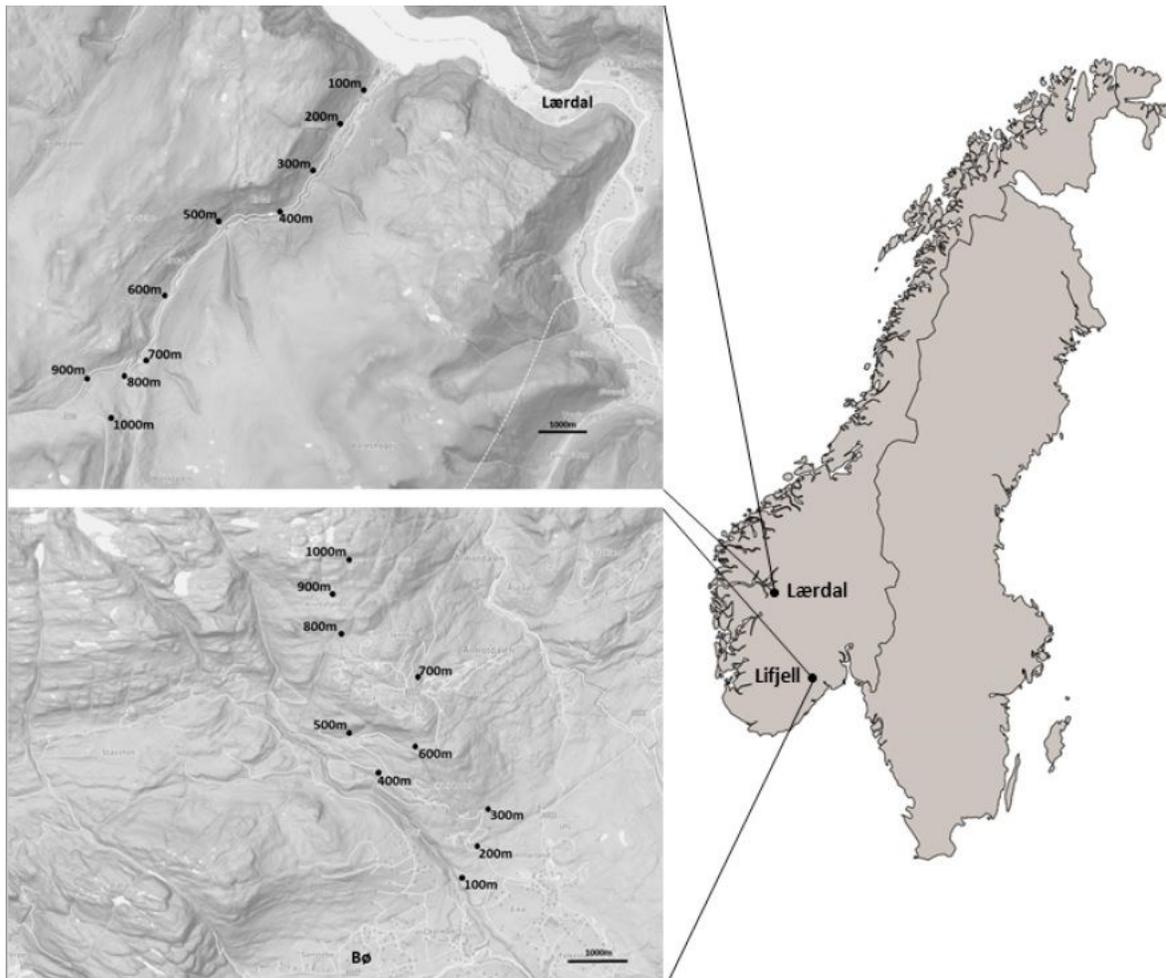


Figure 1

Location of the two study areas in Norway. Inset maps show the exact location of each trapping station along the altitudinal gradient in Lifjell and Lærdal. Each trapping station was placed at 100m altitude intervals ranging from 100 m to 1000 m above sea level.

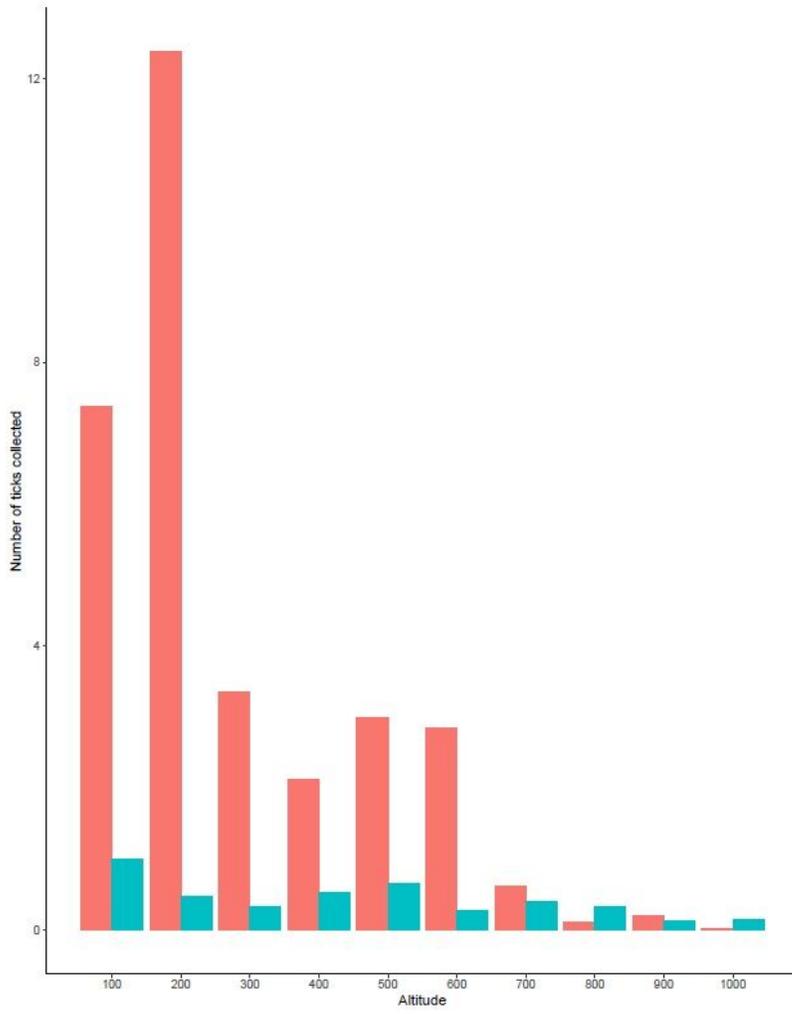


Figure 2
Total number of tick larvae collected from bank voles per altitude, for both study areas, years and seasons combined (red bars, *I. ricinus*; blue bars, *I. trianguliceps*).

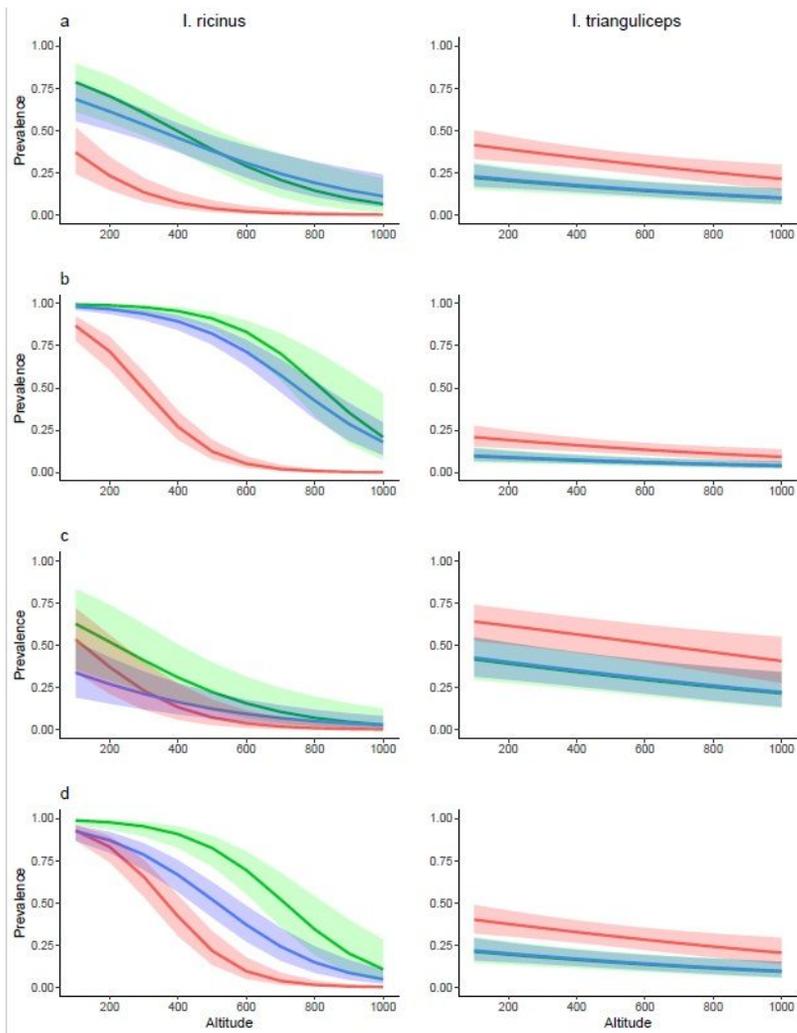


Figure 3
 Tick prevalence on bank voles along altitude in a) Lifjell 2017, b) Lærdal 2017, c) Lifjell 2018, d) Lærdal 2018. A prevalence of 1.0 represents a certainty of encountering at least one tick. Lines: spring (green), summer (blue), autumn (red). Ribbons represent standard error 95 % confidence intervals. For *I. trianguliceps*, spring and summer curves are closely overlapping.