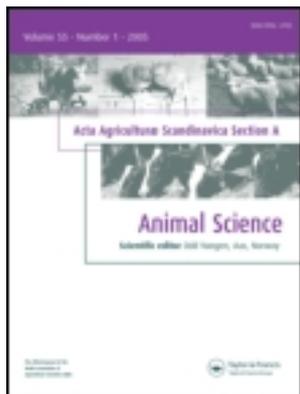


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ORIGINAL ARTICLE

The effect of sheep (*Ovis aries*) presence on the abundance of ticks (*Ixodes ricinus*)

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Abstract

The distribution of ticks is increasing in many parts of the world, including Norway. It has been suggested that this is linked to climate change while the role of different land use practices appears less clear. Here, we investigate the variation in abundance of questing ticks on the west coast of Norway and relate this to the presence of sheep, a tick host that also modifies the landscape through grazing. We found that questing tick abundance was higher in areas without sheep, suggesting that sheep alter vegetation in turn reducing tick survival. However, we cannot exclude that other mechanisms may also lead to reduced abundance of questing ticks; sheep may negatively affect the local density of red deer which is an important alternative host. In any case, sheep farming may contribute to limiting the local abundance of questing ticks and related diseases.

Keywords: Disease, grazing, parasites, shrub encroachment, ungulates.

Introduction

Vector-borne diseases are of global concern to human and animal health. The tick *Ixodes ricinus* is a multi-competent vector of several pathogens (Kjelland et al., 2010; Hasle et al., 2011; Medlock et al., 2013) and is found throughout the northern hemisphere with Norway being the northern distribution border. In Scandinavia, they are most common in coastal ecosystems from the southeast to latitudes of approximately 69°N but are currently spreading in north and inland and the reasons for this are debated (Mehl, 1983; Jore et al., 2011; Medlock et al., 2013).

In northern areas, increased temperatures and higher precipitation following climate change is likely to favor the ticks range and abundance through positive effects on the microclimate (Daniel et al., 2004). Higher temperatures provide longer development periods for ticks as well as a longer questing season, increasing the probability to find hosts (Mejlon & Jaenson, 1997). A number of studies

provide evidence that climate change plays a major role for increased abundance of ticks (Estrada-Pena, 2008; Gray, 2008; Jaenson & Lindgren, 2011; Jore et al., 2011) while the role of other potential drivers such as (1) shrub encroachment and (2) increased abundance of vertebrate hosts are less well studied in northern forest ecosystems in Scandinavia (but see Jaenson & Lindgren, 2011; Medlock et al., 2013).

(1) *Shrub encroachment*. The cessation of use of outfields for pasture, logging and fodder harvesting has resulted in a corresponding shift in plant communities, in particular facilitating growth of forest species (Austrheim et al., 2011). Shrub encroachment may be defined as the invasion by shrubs or tree seedlings into grassland or other open vegetation communities changing the open/grassland ecosystem to a shrub ecosystem. Tick population persistence depends on microclimate with high humidity at ground level (Milne, 1948a). Hence, the shrub encroachment of semi-natural grasslands and cultural landscape is likely to increase tick abundance since ticks survive better in lush and dense vegetation and

shaded microhabitats associated with high humidity (Lees, 1948). Grazing of sheep has been shown to reduce shrub encroachment (Jauregui et al., 2009) resulting in open vegetation types exposed to sunlight. A shift in land use practices, from livestock grazing to browsing of wild cervids, can consequently improve the habitat for ticks (Daniel et al., 1998; Gray et al., 2009). In Norway, the number of livestock grazing in rangeland has been reduced by 50% from 1949 to 1999, while the cervid populations increased with 276% biomass per square kilometer in the same period (Austrheim et al., 2011). The increased tick abundance and distribution in Norway may be partly caused by the regime shift from grazers to browsers.

(2) *Increased abundance of large herbivores.* The tick *I. ricinus* is a three-host parasite. Larvae and nymphs feed on hosts of all sizes, from rodents to cervids and sheep, while adult ticks quest higher on the vegetation so they are confined to larger hosts (Mejlon & Jaenson, 1997; Randolph & Storey, 1999). In the summer season, two million sheep are released to graze on outlying rangeland in Norway, making sheep the most abundant large herbivore during this period of the year. Sheep are known to be a susceptible host for ticks (MacLeod, 1932). The abundance of sheep in rangeland in Norway is therefore potentially an important driver for tick abundance. One of the main challenges for the Norwegian sheep industry is tick-borne fever (TBF) caused by the bacterium *Anaplasma phagocytophilum*, which is a pathogen of sheep in tick-infested areas of Norway (Stuen et al., 2002). Yet, there is not enough knowledge regarding the importance of sheep for the abundance of ticks. Furthermore, cervid species have expanded their range and increased in density during the last few decades (Mysterud et al., 2002), contributing to an increased host abundance for ticks (Jaenson & Lindgren, 2011; Medlock et al., 2013).

In this study, we investigate sources of variation in abundance of questing ticks in four areas on the west coast of Norway and relate this specifically to the influence of sheep presence. We used the cloth lure method (Milne, 1943; Vassallo et al., 2000) to estimate abundance of questing ticks in areas with confirmed presence of global positioning system (GPS)-marked sheep in preceding years, compared to adjacent areas with long-term absence of sheep (controls). The aim of this study was to test two hypotheses of how sheep may affect tick abundance. H_1 . *The increased host abundance hypothesis* predicts that since tick reproduction is facilitated by the presence of larger mammals (Wilson et al., 1988; Gray et al., 1992; Medlock et al., 2008), tick abundance will be higher in sheep areas than in

control areas. H_2 . *The reduced shrub encroachment hypothesis* predicts that sheep grazing may alter vegetation structure and recruitment of shrubs resulting in a colder (in winter) and drier (in summer) microhabitat with lower tick survival.

Material and methods

Study area

The study areas are located in the county of Møre and Romsdal on the west coast of Norway. The collection of ticks was conducted in four areas in the municipalities Aure (63°10'3,1116"N 8°26'19,943"E), Tingvoll (62°54'49,212"N 8°12'17,017"E), Vestnes (locality: Fiksdalen; 62°37'03 "N 6°50'59"E) and Rauma (locality: Isfjorden; 62°34'36,844"N 7°42'5,0976"E; Figure 1A, B). Landscape morphology and topography in this region are characterized by large altitudinal variation with ancient, fluvial valleys and fjords. The vegetation is a mix of boreal, coastal woodlands and subalpine heather. A broad coastal belt of birch (*Betula pubescens*) and heather (*Calluna vulgaris*, in the field layer is found in areas exposed to strong wind. Forests are found in wind-protected valleys, with the dominating tree species being white birch (*B. pubescens*), common hazel (*Corylus avellana*), planted Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The understorey plant communities are dominated by common heather (*C. vulgaris*), northern bilberry (*Vaccinium uliginosum*) and in moist and nutrient areas deer fern (*Blechnum spicant*) and hairy wood rush (*Luzula pilosa*). Atlantic marshland heath landscape is common throughout the region. The meadows are dominated by timothy (*Phleum pratense*), sedges (*Carex* sp.), wood anemone (*Anemone nemorosa*), spreading wood fern (*Dryopteris expansa*) and other grass species. Furthermore, these outlying fields hold large populations of red deer *Cervus elaphus* (Mysterud et al., 2002). In 2010, 28% of the total number of deer harvested in Norway were shot in Møre and Romsdal, Aure being the municipality with the third highest outtake numbers (Statistics Norway, 2012). The boreal, oceanic climate has mild winters and cool summers with humid conditions and plant-growing season of 200 days (Abrahamsen et al., 1977). During 2010, summer (May to September) temperatures were 2.5°C above, and the preceding winter (November to March) was 2.5°C below the long-term mean. The summer precipitation was ca 65% below and winter precipitation was only 52% of the normal. The winter of 2009/2010 was the driest winter since 1899/1900 in this region (Meteorologisk Institutt, 2012).

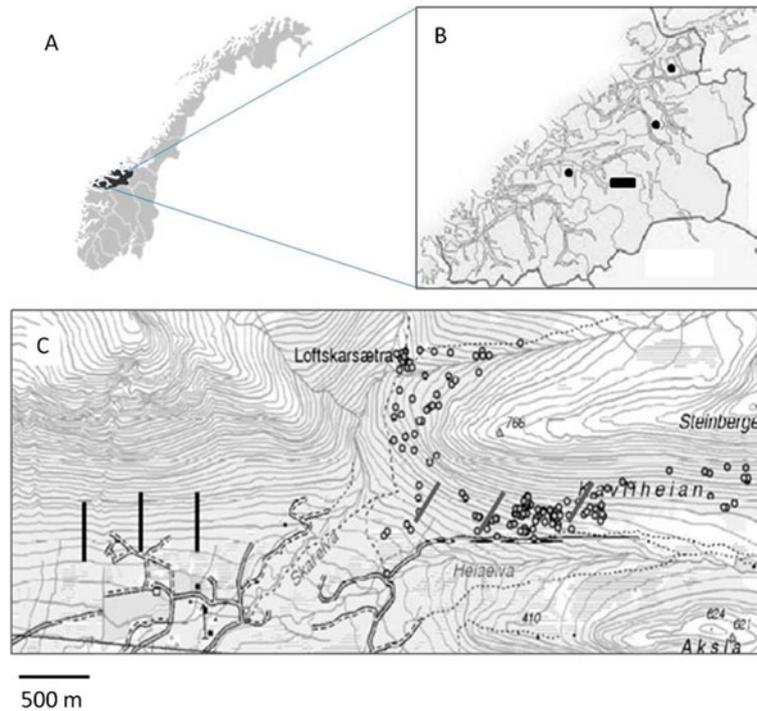


Figure 1. The location of the study areas in Møre and Romsdal at the west coast of Norway (A) The black spots (B) locate the four study-sites where ticks were collected, from north the sites are Aure, Tingvoll, Fiksdalen and Isfjorden. The black square is the study site Isfjorden detailed in (C), where black lines represent control transects and gray lines are the sheep transects. Dots are locations used by GPS-marked sheep the previous summer that were used to guide the placement of transects.

The tick species I. ricinus

Ixodes ricinus passes all developmental phases (engorged, molting and quiescent) in the litter layer of the vegetation, with active questing ticks found on the upper vegetation. During the feeding periods, it sucks blood from a host for approximately 3–12 days (MacLeod, 1932; Lees, 1948). The tick's development rates are temperature-dependent which may be a limiting factor at northern temperate latitudes such as in Norway (Medlock et al., 2013). Tick abundance shows seasonal patterns with nymphs and adults being active between March and July, and larvae being active between April/May and August (Steele & Randolph, 1985). A weekly average maximum daily air temperature of 7–8°C is estimated to be the minimum necessary for the onset of questing of *I. ricinus* nymphs following winter diapause (Perret et al., 2000; Tagliapietra et al., 2011). Adult females can be visually separated from males by their larger size, the characteristic red color on their alloscutum (the “back part”), and that the alloscutum covers only the anterior part of the dorsum (and not the whole as in males). Nymphs cannot be visually separated according to sex.

Sampling design

In each of the four study areas, one subarea where sheep were grazing from June (released on outfield

pasture 10–15 June) to October (from now on called *sheep areas*) and one control area without grazing sheep (*control areas*) were selected (Figure 1C). The mean distance between the sheep and the control area pairs was 4.3 km (Isfjorden: 2.7; Tingvoll 3.3; Fiksdalen: 5.5 and Aure: 5.8 km). Information on sheep presence and absence was based on two sources, GPS-data and interviews. GPS-data provided confirmation of presence of sheep in sheep areas in the year prior to our study. The GPS-data consist of 7700 locations from 51 individual sheep fitted with collars from spring to autumn in 2009 (Aure: 12; Fiksdalen: 17; Isfjorden: 9; and Tingvoll: 13 GPS-marked sheep). Presence of sheep in the actual year of study was in most cases confirmed during fieldwork. Control areas were never used by the GPS-marked sheep. Because control areas could have been used by sheep that were not GPS-marked interviews with local sheep farmers were used to confirm the absence of sheep. The time since each of the areas had been used for sheep grazing ranged from ca 3 to 10 years. Typically, use was terminated because the previous owner no longer held sheep and that the grazing land was not taken into use by other shepherds. Although sheep are free-ranging, each herd tends to use the same traditional areas, thus there can be closely spaced areas with and without sheep, despite neither sheep areas nor control areas being fenced. Sheep in our study were treated with

acaricides (i.e. pour-on pyrethroids like Bayticol[®], Bayer A/S or Coopersect[®], Intevet) when turned out on range pasture for summer grazing. However, short efficacy of 3–5 weeks of such acaricides does not protect the sheep from ticks for the complete grazing period (Stuen et al., 2012).

When we selected sheep-control pairs, the aim was to keep all factors other than presence of sheep (such as vegetation, elevation, aspect, slope) as similar as possible between sheep and control areas. Ideally, we should have monitored the density of alternative hosts, in particular small rodents and red deer, which are important hosts for ticks in this area (Handeland et al., 2013). The only density index available for red deer is at the level of municipality, much too coarse for this study. Individual red deer range over very long distances compared to the distance between sheep and control areas, and typically with strong seasonal and diurnal patterns (Godvik et al., 2009; Bischof et al., 2012). We therefore argue that the most feasible indices of small-scale deer density, visual observations and fecal sampling (although used in Scotland; Gilbert et al., 2012) would have been poor proxies of differences in real deer density on our scale. However, lack of information of alternative hosts is a limitation of our study, and we cannot exclude the possibility that the presence of sheep affect the density of deer, either directly (interference competition with deer) or indirectly (modify habitat for rodents and scramble competition with deer).

The cloth lure method

At each study site, we spaced out four or six transects divided equally between sheep areas and nearby control areas (Figure 1C). The distance between transect lines was ca 500 m, and the length of each transect was ca 500 meters. Tick abundance was estimated along the same transects in three seasons; spring (21–27 May; before sheep were released on outfield pasture), summer (12–31 July) and autumn (7–17 September) in 2010.

Along each transect line, questing ticks were sampled in 12 segments with the *cloth lure method* (Milne, 1943; Vassallo et al., 2000). First, terry cloth towels (1 × 0.5 m) were swept over the vegetation four times (2 m²) before the towel was examined for ticks (nymphs and adults). This was repeated five times (every 2 m) and the total number of nymphs, adult females and adult males was recorded. Sampling in each segment thus covers an area of 10 m². The *cloth lure method* provides a density index of ticks exhibiting questing behavior, when accounting for between-transect differences in vegetation and other factors. We assume here that there is a correlation

between questing ticks and the total tick population, but similar to most studies, this correlation is not known explicitly. However, the study was carried out in spring, summer and autumn when temperatures never fell below 7–8°C (the lower limit for questing behavior; see above), hence the ticks were always capable of exhibiting questing behavior. Questing behavior is affected by moisture stress. The number of questing ticks is negatively correlated with the saturation deficit and activity is low above 5 mmHg (Randolph & Storey, 1999). We did not measure saturation deficit in our study. It is important to emphasize that the effect of sheep presence is robust to variation in temperature and moisture as these variables affect sheep transects and control transects similarly.

Variables

Earlier studies show that tick abundance is heavily influenced by climatic factors, plant composition and the depth of leaf litter (MacLeod, 1932; Lees, 1948; Lees & Milne, 1951; Medlock et al., 2012). Weather and habitat variables were recorded at the beginning of each 10 m segment. Wind speed was calculated with an anemometer and was in general low (0–3 m/s), except from 1 day in Tingvoll (10 m/s). Although ticks can be active in light rain, precipitation is a limiting factor for questing behavior of ticks (Mejlon & Jaenson, 1997), hence we did not conduct fieldwork when there was heavy rain. Precipitation was categorized as either *no rain* or *light rain* and 43 of the 480 (9%) segments were conducted in light rain. The habitat variables encompass substrate and percentage canopy cover. Substrate was registered at the start of each segment as one of the categories *marsh* (38.9%), *heather* (11.9%), *grass* (42.8%) and *other* (6.4%). “Dry spruce needles” (debris) was the dominant substrate type in the category *other*. A concave densiometer (Construction Safety Products, LA, USA) was used to measure the percentage tree canopy cover (following the approach in Mysterud & Østbye, 1999) which influences the degree of shade in the microhabitat.

Statistical analysis

The data were analyzed in the software program R, version 2.15.2 (R Development Core Team, 2012). We used chi-square tests to test for differences in canopy cover and substrate between sheep and control transect segments. To model variation in questing tick abundance, we used a mixed negative binomial model with zero inflation using the R package glmmADMB version 0.7.2.12 (Skaug et al.,

2012). The response variable of the analyses is the sum of nymph and adult ticks per 10 m segment along a transect line. Zero inflation is often the case when estimating parasite abundance (Rødven et al., 2009) since the parasites often are clustered in their distribution and that very many segments contain no ticks (see also Gilbert et al., 2012). To account for sampling dependency within each transect, transect line was included in the model as a random intercept. To investigate any residual effect of sheep after accounting for the canopy and substrate differences found in the first analysis, we used the following approach. First, a null model with only substrate, canopy cover and precipitation as fixed effects was fitted. Thereafter, the effect of sheep, season and the interaction between sheep presence and season were added in sequence and significance of each new term was tested with likelihood ratio tests (Pinheiro & Bates, 2000). All candidate variables were checked for co-linearity to ensure that they could be included as sufficiently independent variables (Zuur et al., 2010).

Results

A total of 1551 ticks were captured in the four study sites. The number of ticks collected in spring (late May), summer (late July) and autumn (early September) was 157, 769 and 625, respectively. The age and sex distribution consisted of 1297 nymphs (83.6%), 145 adult males (9.4%) and 109 adult females (7.0%).

As predicted from the shrub encroachment hypothesis H_2 , there were fewer ticks of all age and sex classes on sheep transects compared to control transects (Figure 2). Conversely, the increased host abundance hypothesis H_1 was not supported. Although selection of sheep and control areas based on maps and interviews aimed at finding areas of similar habitat, field measures revealed significant differences. A higher proportion of the control transect segments had canopy cover ($\chi^2 = 6.04$, degree of freedom [df] = 1, $p = 0.0140$; Figure 3) and vegetation composition in control and sheep transects differed ($\chi^2 = 7.25$, df = 1, $p = 0.007$) due to more heather and less grass in control areas (Figure 3). The predicted number of questing ticks was higher in grass than in other substrate types (Figure 4B), increased with canopy cover (Figure 4C) and decreased on rainy days (Figure 4C; Table I). Still, there was an effect of sheep presence after accounting for these effects (decrease in deviance = 5.25; df = 1; $p = 0.022$). The predicted effect from sheep presence alone was a 33% decrease from 4.9 ticks to 3.3 to per 10 m (Figure 4A; Table I). Adding season (deviance = 2.81, df = 2, $p = 0.245$) and the interaction between season and

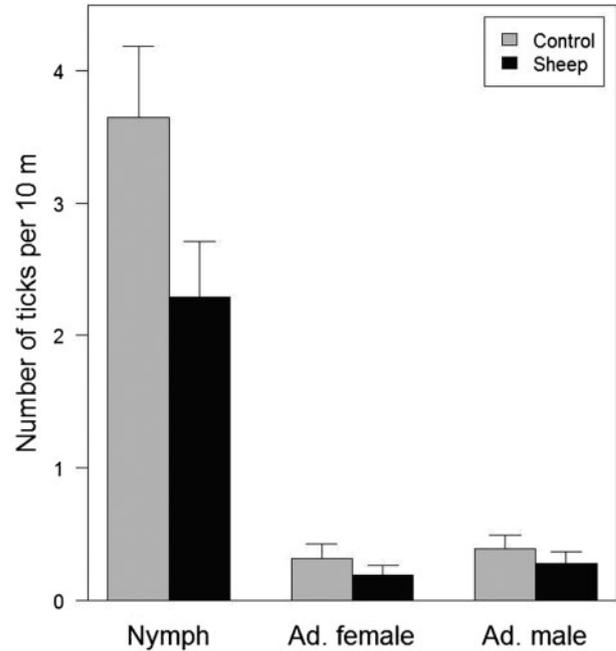


Figure 2. The mean number of nymphs, adult female and adult male ticks per 10 m over the full year of sampling in control and sheep transects in Møre and Romsdal county on the west coast of Norway. Error bars represent 1 SE.

sheep presence (deviance = 5.57, df = 4, $p = 0.234$) was not supported.

Discussion

Here, we document for the first time that abundance of questing ticks is lower in areas with domestic

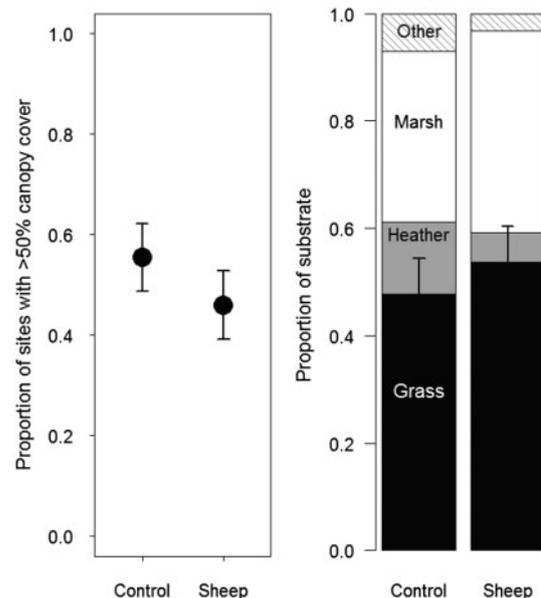


Figure 3. The proportion of segments with canopy cover (defined as more than 1% cover; left panel) and proportion of substrate categories (right panel) in sheep transects and control transects (no recent use of sheep).

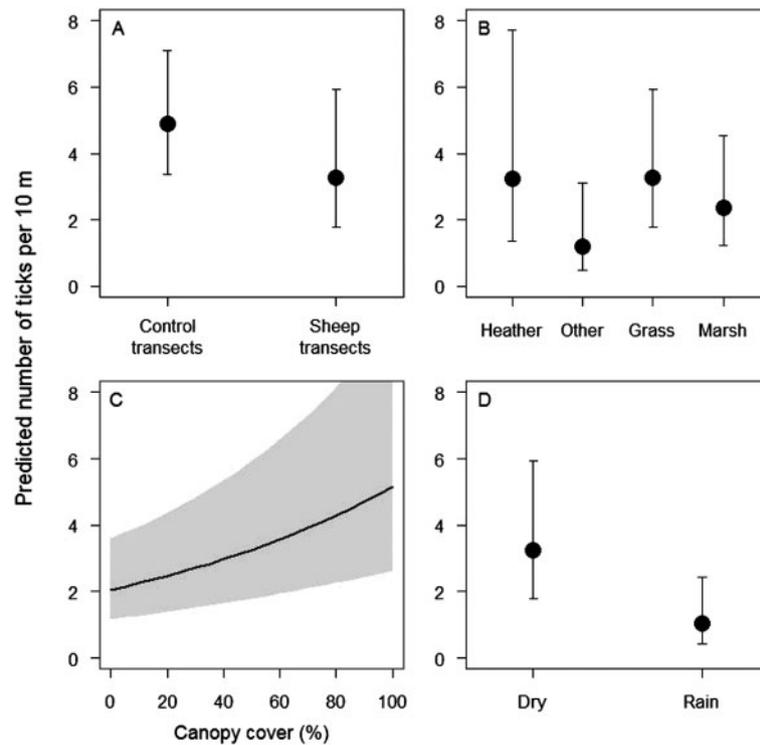


Figure 4. Predicted number of ticks per 10 m transect line segment as a function of (A) sheep presence, (B) substrate, (C) canopy cover and (D) precipitation. Effect sizes and 95% confidence interval are back-transformed from a zero-inflated mixed effects negative binomial model using each transect line as a random intercept.

Table I. A zero-inflated mixed effects negative binomial model predicting tick abundance in Møre and Romsdal, Norway as a function of sheep presence, substrate, canopy cover and precipitation. Each transect line is treated as a random intercept. The reference levels of the factor variables are control areas (without sheep), grass substrate and no precipitation. Random effect variance = 0.161; negative binomial dispersion parameter: 1.68 (standard error [SE] = 0.323); zero inflation = 0.0491 (SE = 0.0397).

	Estimate	SE	z value	p value
Intercept	1.13	0.162	6.96	<0.001
Treatment (sheep vs. control)	-0.404	0.170	-2.37	0.018
Substrate (heather vs. grass)	-0.0101	0.278	-0.040	0.971
Substrate (marsh vs. grass)	-0.318	0.133	-2.39	0.017
Substrate (other vs. grass)	0.989	0.367	-2.69	0.007
Precipitation (rain vs. dry)	-1.15	0.303	-3.79	<0.001
Canopy cover	0.00917	0.00161	5.71	<0.001

sheep compared to nearby areas without sheep in a northern coastal forest ecosystem of Scandinavia. Our findings support the shrub encroachment hypothesis; that sheep foraging maintains open habitats that are associated with lower tick abundance. We suggest that two mechanisms are causing this pattern. First, we found that the habitat field measures differed between sheep and control transects, which may be caused by shrub encroachment and a change from grass to heather in the absence of sheep (Palmer et al., 2003). Second, there was increased tick abundance in control sites even when controlling for canopy cover and substrate. This suggests that sheep grazing result in small-scale changes such as reduced height of vegetation that disfavor ticks. At the current sheep densities, reduced shrub encroachment

apparently had stronger effect than adding sheep as an additional large mammalian host in the system. We cannot exclude sheep presence affect the density of alternative hosts. The most likely effect would be that sheep keep away deer (Osborne, 1984) that are even more important hosts. However, irrespective of the mechanism, presence of sheep at moderate densities resulted in fewer questing ticks which has important consequences for animal and human health and welfare.

The host availability hypothesis

Increased distribution of ticks in Europe is likely caused by several factors. Climate change and vegetation shift in latitudinal and altitudinal range

margins are expanding areas of suitable habitat for ticks (Jore et al., 2011; Medlock et al., 2013). Ticks use a large diversity of potential hosts and the west coast of Norway hold large populations of wild ungulates (in particular red deer but also roe deer and moose) and domestic animals (sheep and cows). These large mammal hosts have high-tick amplification potential and are essential for maintenance of tick populations due to their capacity of feeding sufficient numbers of adult ticks (Gray et al., 1992; Medlock et al., 2008), implying that presence of grazing sheep can in theory facilitate population growth in tick species. Deer in particular is regarded crucial for adult female ticks (Wilson et al., 1988; Gray et al., 1992; Rand et al., 2004; Gilbert et al., 2012). Abundance of deer has increased in large parts of North America (McShea et al., 1997) and in Europe (Milner et al., 2006). The local density of alternative hosts such as red deer is an unknown variable in our study. In the county of our study (Møre & Romsdal), the number of harvested red deer has increased from 863 in 1965 to 10,151 in 2011 (Statistics Norway, 2012).

We have addressed the question of whether the addition of another large host, the domestic sheep, would increase or decrease abundance of questing ticks. We did not find support for the host availability hypothesis, despite that the availability of large hosts has been found to influence tick abundance in other studies (Wilson et al., 1988; Gray et al., 1992; Medlock et al., 2008). This can be interpreted in several ways. First, our main interpretation is that sheep grazing also means more open habitat and altered vegetation (in particular reduced height and density), in turn reducing tick abundance. Second, red deer may be an abundant all-year available tick host that may be negatively associated to the sheep in space (Osborne, 1984; Clutton-Brock & Albon, 1989). Therefore, we cannot provide firm evidence that large host availability has increased in sheep areas compared to control areas. We found evidence of presence of red deer, including deer droppings, bed sites and paths in most of the transects. In our area at coarse scales, red deer densities are typically in the range of 5–15 red deer per square kilometer, roughly determined based on number of harvested animals being 1.7 red deer per square kilometer in Tingvoll and 2.4 red deer per square kilometer in Aure municipality. Sheep densities were generally higher with 9 sheep per square kilometer in Aure, 19 sheep per square kilometer in Tingvoll, 13 sheep per square kilometer in Fiksdalen and 36 sheep per square kilometer in Isfjorden (Norwegian Forest and Landscape Institute, 2012). Finally, we only have data on questing ticks, and we cannot fully exclude the possibility that more hosts mean less-questing

ticks in the short term as they readily find a host (Perkins et al., 2006; Dobson & Randolph, 2011). This “mopping” mechanism has been found to be important in Scotland on grassland with high densities of sheep (Milne, 1948b; Dobson & Randolph, 2011). In our study system with lower densities of sheep and alternative hosts, we suggest that this is a less important mechanism, in particular because we found no support for an interaction between season and sheep presence (the first observation period is before sheep is released on outfield pasture). Sheep were treated with acaricide at the onset of grazing season, but we suggest that this too has a low effect on the observed difference due to the short efficacy of 3–5 weeks (Stuen et al., 2012) and the missing interaction between sheep presence and season.

Another important aspect of variables influencing local tick abundance is local populations of hosts for larvae and nymphs. Ticks at the first two life stages have a larger variety of hosts since they quest in lower vegetation (Mejlon & Jaenson, 1997; Randolph & Storey, 1999). In this study, we did not include abundance of rodents, birds, shrews, reptiles nor medium-sized mammals such as cats, badgers, hare and red fox. Therefore, the local tick abundance might have been influenced by population of other hosts which are not included in this study. Although our study contains data from only 1 year, the interannual variation in tick abundance in this area has been shown to be low (Qviller et al., [accepted](#)).

The reduced shrub encroachment hypothesis

Sheep grazing prevents tree and shrub encroachment (Adams, 1975; Speed et al., 2010). Over the last decades, the land use practices in Norway have gone through a regime shift and changed from being dominated by domestic grazers to now being dominated by wild deer being browsers (moose, roe deer) or mixed-feeders (red deer). Throughout the country, there is an ongoing process of shrub encroachment of semi-natural grasslands and cultural landscapes due to the new grazing regimes and forms of resource utilization (logging and hay harvesting) that have now ceased (Austrheim et al., 2011). The ticks survive better in lush and dense vegetation which hold high relative humidity and have shaded microhabitats, and the loss of grasslands and shrub encroachment of open landscapes may have facilitated an increase in the tick populations in Norway.

This study supports the hypothesis that ticks survive better in dense vegetation (MacLeod, 1932). The tick abundance increased as the canopy cover increased. The canopy cover provides shade, which prevent ticks to be exposed to direct sunlight

and further enhance humid microhabitat conditions. Ticks depend on microclimate with high humidity (Milne, 1948a) at ground level to avoid desiccation during summer. Where the tree canopy is enclosed, the shrub layer of vegetation is generally more dense compared to open landscapes. The exception is planted spruce forests, where the trees are so dense that the ground level has limited sunlight and the vegetation is marginal. However, the substrate holds low levels of humidity and very limited vegetation and therefore increases the possibility for ticks to dehydrate and also limits the opportunities for the ticks to climb the vegetation. This study found that questing tick abundances were clearly lower in substrate dominated by spruce needles than in the more lush vegetation as heather, marsh and grass.

Conclusions

TBF is one of the main challenges in Norwegian sheep farming during the grazing season in tick endemic areas causing both direct and indirect losses (Brodie et al., 1986; Stuen & Kjolleberg, 2000; Stuen et al., 2002; Grova et al., 2011). The increased abundance of ticks in Norway and the extension of the margins of the tick population (Jore et al., 2011) have given rise to concerns that challenges with TBF will increase in Norway in the coming years. Our results indicate that sheep may contribute to reduce tick abundance due to retaining open landscapes and short vegetation, and that this effect is stronger than the addition of sheep as another large host species. Sheep thus have a more important role as a landscape opener than as a tick host. As a secondary effect not quantified in our study, red deer which is the preferred host for adult ticks may avoid sheep. Irrespective of the mechanism, sheep farming may thus contribute to limit the local abundance of questing ticks and related diseases.

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