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

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Preface and acknowledgement

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Hege Hammerstad Steigedal

Abstract

The prevalence of ticks is increasing in many parts of the world, including Norway. There are uncertainties why this is happening, but the suggested main three drivers are climate, encroachment and increased abundance of vertebrate hosts. In this thesis I investigate the variation in abundance of ticks in four areas in Møre and Romsdal, Norway, and relate this specifically to the presence of sheep (*Ovis aries*). The cloth-lure method was used to collect ticks on transects with known previous presence of sheep and compared with control transects with no sheep. In this thesis I test the following two hypotheses; *The increased host hypothesis* (H_1) predicts that since tick reproduction is facilitated by the presence of larger mammals tick abundance will be higher in sheep areas than in control areas. The alternative hypothesis, *the reduced encroachment hypothesis* (H_2), predicts that sheep keep vegetation low and therefore reduce tick survival. Consistent with the reduced encroachment hypothesis H_2 I found that tick abundance was higher in control areas than in areas with sheep. There was a seasonal variation in tick density. The tick abundance peaked in summer in both sheep and control areas. The main management implication of my thesis is that sheep grazing effects are an efficient tool to reduce vegetation height and shrub encroachment which reduce tick abundance.

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1 INTRODUCTION

Vector-borne diseases are of global concern to human and animal health and are of importance both from a medical and economic perspective. The sheep tick *Ixodes ricinus* (Acari: Ixodidae) is a multi-competent vector of several pathogens including *Borrelia* spp., *Babesia* spp., *Anaplasma* (*Ehrlichia*) spp., *Rickettsia* spp., *Francisella tularensis*, and arboviruses such as Louping ill virus (LIV) and tick-borne encephalitis-virus (TBEV) (Neelakanta et al., 2010, Kjelland et al., 2010, Hasle et al., 2011). Ticks inhabit coastal ecosystems in Norway from Østfold in the southeast to latitudes of approximately 69°N in Nordland (Jore, 2011, Kjelland et al., 2010) and are currently spreading. The prevalence of ticks is increasing in North America and Europe and there are uncertainties why this is happening. The main three candidate drivers are (1) climate, (2) encroachment and (3) increased abundance of vertebrate hosts.

(1) Climate change

The tick has a four stage life cycle; from egg, larvae, nymph to adult. The lifespan is usually completed in three years, but can vary from 2-6 years depending on climatic conditions (Stanek et al., 2012). Ticks are sensitive to low temperatures, hence cold winters with low mean ground temperatures and frost for several days can eradicate a large proportion of the tick population. Thick snow cover will facilitate survival of ticks because the snow isolate the ground from severe cold temperatures (Neelakanta et al., 2010). Climate change towards increased temperatures and higher precipitation are likely to affect the distribution and abundance of ticks through positive effects on the micro-climate for these arthropods. Ticks are spread throughout the northern hemisphere with Norway being the northern border for its distribution (Randolph, 2009). Possible effects of climate change would be more evident close to the ticks' geographical distribution limits. Further do the increased temperatures provide longer period for ticks to develop, conducting questing behavior and more time to find hosts.

(2) Encroachment

Tick population persistence depend on microclimate with high humidity (>c. 85 RH%) at ground level (Stafford, 1994). In lush, dense vegetation humid conditions are stable and relatively high. When sheep graze and reduce vegetation height, they alter the vegetation composition and modify the landscape to become more open and less forested. Open areas are less preferred habitat for the ticks, due to the lower humidity and exposure of direct sunlight.

The shift in land use practices, from livestock grazers to browsing cervids, can consequently facilitate habitat increase for ticks (Stanek et al., 2012, Milan Daniel, 2004). This shift in tick distribution range is likely a consequence of habitat change through a regime shift in land-use practices. Livestock grazing in the outfields have been reduced with more than 50 % from 1949 to 1999 (Austrheim et al., 2008). The changes in utilization of outfields, regarding pasture, logging and hay harvesting have resulted in a corresponding shift in plant communities as well as ecological processes. Changes in land use practices has facilitated growth for forest species (Blom, 2011). The overgrowth of semi-natural grasslands and loss of cultural landscape are likely to influence the expansion of tick populations, since ticks prefer lush and dense vegetation which hold high relative humidity and have shaded microhabitats (Lees, 1948). Grazing of sheep has shown to control shrub encroachment (Jauregui et al., 2009) and a result of the grazing effects is that sheep can contribute to maintain semi-natural grasslands, hence reduce suitable habitat range for tick populations.

(3) Increased abundance of large herbivores

I. ricinus is a 3-host parasite, which means they need three host animals to feed blood on during their life span to develop from larvae to adults. Larvae and nymphs target small vertebrates such as rodents, insectivores, birds, reptiles and bats, while adult ticks target sheep, cattle, humans, dogs and other medium to large mammals (Mehl, 1983). During the growing season, some 2 million sheep are released to graze on outlying ranges in Norway, making it the most abundant large herbivore during this period of the year. Sheep are known to be a susceptible host for ticks at all life stages (MacLeod, 1932). The host requirements of adult ticks are a significant number of large animals such as sheep. Adult female ticks, with few exceptions, only engorge successfully on animals larger than a hare (*Lepus* spp) (> 1 kg)(Gray, 1998, Mehl, 1983). The sheep abundance in the outfields of Norway is therefore potentially an important component in assessing and controlling tick abundance. Sheep farmers in Norway use land fields in the spring and autumn and the outfields for shorter periods during the summer. In the summer months, ticks are exhibiting questing behavior (H. A. Mejlon, 1997), hence the sheep are candidate hosts for ticks. There is an increasing problem with tick disease for the sheep farming industry, and there is a lack of knowledge regarding how important sheep are for affecting the population levels of ticks. Sheep is not the only available large host. Deer species populations in Norway have expanded their range and increased in density the last decades (Mysterud et al., 2002).

In this thesis I investigate the variation in abundance of ticks in four areas in Møre and Romsdal, Norway, and relate this specifically to the influence of sheep density. To facilitate this I use the cloth lure method (Randolph et al., 2002, Vassallo et al., 2000) to compare abundance of ticks in four areas with sheep compared to four adjacent areas without sheep (controls). The aim for this study is to test two hypotheses of how sheep may affect tick abundance.

H_1. *The increased host hypothesis*. I predict that since tick reproduction is facilitated by the presence of larger mammals (Wilson et al., 1988), tick abundance will be higher in sheep areas than in control areas.

H_2.*The reduced encroachment hypothesis*. Alternatively, sheep may modify the landscape in a way that reduce tick survival by lowering vegetation height and reducing recruitment of shrubs.

2 METHODS

2.1 Study areas

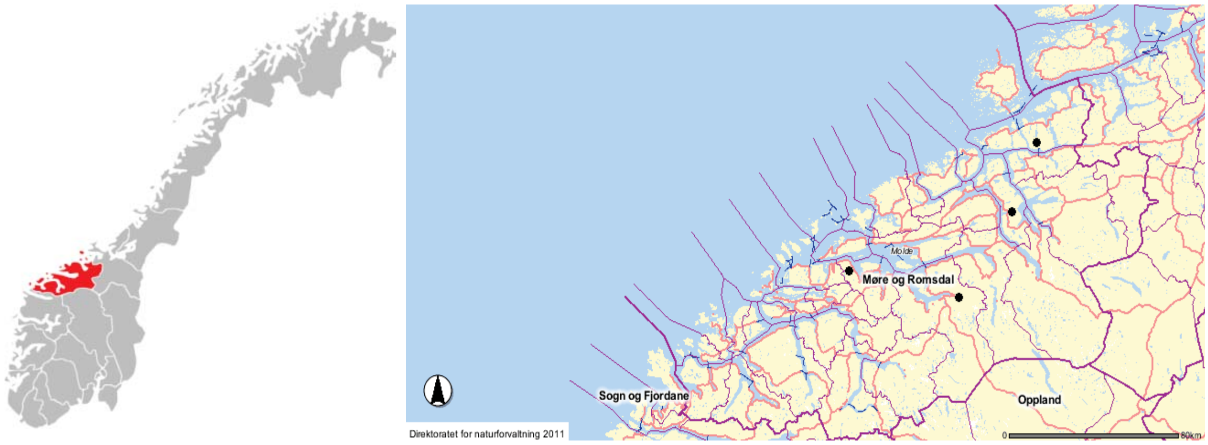

Figure 1. This is a map of the county Møre and Romsdal. The black spots illustrate the four study-sites where ticks were collected. From north, the areas are Aure, Tingvoll, Fiksdalen and Isfjorden.

The collection of ticks was conducted in the northwest of Norway, in the county Møre and Romsdal. The study areas were the municipalities Aure (63°10’3,1116”N 8°26’19,943”E), Tingvoll (62°54’49,212”N 8°12’17,017”E), Fiksdalen (62°37’03”N 6°50’59”E) and Isfjorden

(62°34’36,844”N 7°42’5,0976”E). At each destination, one area where sheep are grazing from May to October was selected; from now on called *sheep areas*, and one control area without grazing sheep; called *control areas* (Fig. 2).

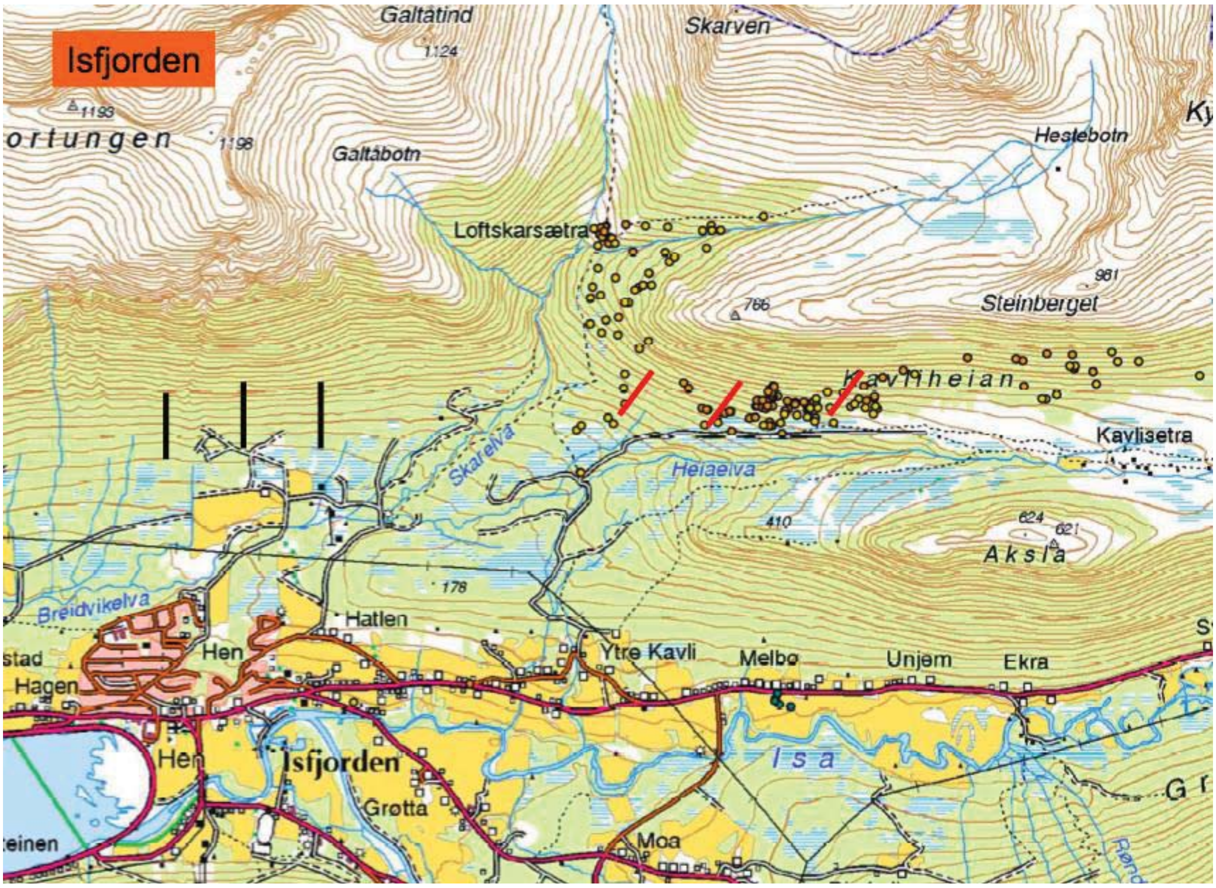

Figure 2. This map shows transects in one of the study areas, Isfjorden. The black lines are transects in control area where sheep are absent, and the red lines show transects in sheep area.

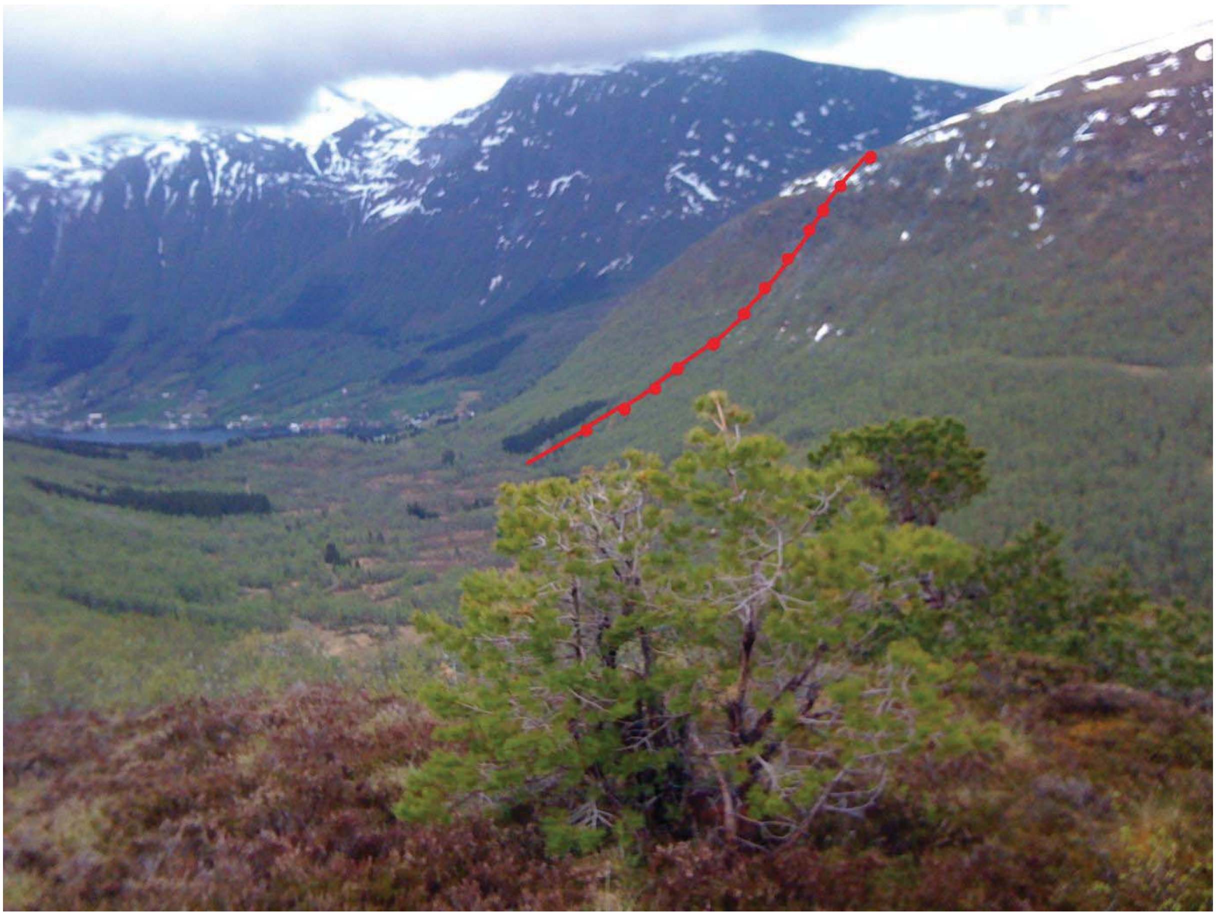

Figure 3. Transect in control area in Fiksdalen. Photo: Hege Hammerstad Steigedal

Landscape morphology and topography in this region are characterized by large altitudinal variation with ancient, fluvial valleys and fjords (Fig. 2 and 3). The boreal, oceanic climate has mild winters and cool summers with humid conditions and vegetative growing season of 200 days and cool summers (Abrahamsen, 1977). The meteorological conditions in Møre and Romsdal during the summer season were 2.5 – 3 °C above normal temperatures which is 11 - 12 °C. Precipitation in the summer for the county was 60-70 % below the normal average. The mean winter temperature was 2.5 °C below normal. The precipitation during the winter was only 52% of the normal and made the winter of 2009/2010 the driest winter since 1899/1900 (Meteorologisk institutt, 2012). The vegetation is a mix of boreal, coastal woodlands and subalpine heather. A broad coastal belt of birch (*Betula pubescens*) and heather (*Calluna vulgaris*), dominated by *Erica cinerea,* in the field layer is found in areas exposed to strong wind. Deciduous forests are found in wind-protected valleys, and Atlantic marshland heath landscape is common throughout the region. Vegetation is dominated by boreal deciduous- and pine (*Pinus sylvestris*) forest with spruce (*Picea abies*) plantation on hill slopes. The dominating tree species are white birch (*Betula pubescens*), common hazel (*Corylus avellana*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with under-storey plant communities dominated by common heather (*Calluna vulgaris*), northern bilberry (*Vaccinium uliginosum*) and in moist and nutrient areas deer fern (*Blechnum spicant*) and hairy wood rush (*Luzula pilosa*), vegetation-types in categories from A1 – A5 (Fremstad, 1997). The meadows are dominated by timothy (*Phleum pretense species*), sedges (*Carex specie*), wood anemone (*Anemone nemorosa*), spreading wood fern (*Dryopteris expansa*) and other grass species. Furthermore, the county has large areas of outlying fields and hold large populations of red deer *Cervus elaphus* (Mysterud et al., 2002). In 2010, 28% of the total amount of deer harvested in Norway were shot in Møre and Romsdal, and Aure was the municipality with the third highest outtake numbers (Statistics, 2012).

2.2 The study species *Ixodes ricinus*

Figure 4. Development stages of *Ixodes ricinus*. From left; larva, nymph, adult female and adult male. (Stanek et al., 2012).

Ticks spend their whole life in the vegetation, engorged, moulting and quiescent, with the exception of three brief periods when they feed on their hosts. During the three feeding periods it sucks blood from different hosts for approximately 3 – 12 days (MacLeod, 1932, Lees, 1948). The tick's development rates are temperature-dependent and in temperate latitudes as in Norway, the tick abundance shows seasonal patterns. Nymphs and adults are active between March and July, and larvae is active between April/May and August (Steele and Randolph, 1985). In March/April the gorged and fertilized females lay 2400-3200 eggs 15-22 days after she drop of the host. After 9-10 weeks the eggs hatch in vegetation debris. Eggs laid in September hatch in May the following year. The metamorphosis from larva to nymph takes approximately 4 weeks (10 – 18 weeks in wintertime with temperatures >10 °C)(MacLeod, 1932). Metamorphosis from nymph to adult last for 8 weeks in summer-season, and 28 weeks (up to 48 weeks) in the winter (MacLeod, 1932). *I. ricinus* possess an extraordinary longevity; fasting ticks kept alive in the laboratory for up to 31 months (MacLeod, 1932).

Tick abundance is positively associated with abundance of large mammals (Gilbert, 2010). The relationship between host availability and adult ticks is essential in the persistence of a given tick population. When the abundance of large mammalian hosts decline, ticks at their larval stage become less abundant in the spring which indicates that the adult ticks generally failed to feed and reproduce (Wilson et al., 1988). If the abundance of suitable hosts for adult ticks continues to be marginal, the effect of small cohorts can be continual and reduce the tick population during a few years. This indicates that the presence of large mammals is a prerequisite for dense tick populations (Wilson et al., 1988), and sheep are known to be a susceptible host for ticks at all life stages (MacLeod, 1932). When the larva is 22 days old it climbs up on the tip of the grass-blade/ground vegetation where it waits for a passing host. The ticks use the two pairs of hind legs to cling to the blade and the forelegs are waving about in the air. An experiment conducted by MacLeod (1932) revealed that immediately when the grass was disturbed by movement, the larva became excitedly alerted. It rose on its hind-legs and waved its fore-legs in the air, ready to transfer itself to the passing object. This reaching out was so evident that several actually fell down from the leaves. If the object appeared to be unsuitable for feeding, the tick drops off and quest for another opportunity. Questing activity increases as the temperature rise throughout the day. During night, when temperatures drop, activity rates decrease and it seems to be a threshold for active behavior at 5 ° C (Lees and Milne, 1951). The ticks are in average active for five periods during the growing season and each period lasts for approximately 4-5 days (Lees and Milne, 1951). The reason for the relative short time spent on active seeking a host has to do with risk of dehydration when the tick s are in the upper layer of the vegetation compared to the higher humidity close to the ground. This means that the ticks spend most of their life quiescent and are only active for approximately 20-25 days every year.

2.3 Sampling design

The ticks were collected in three seasons, spring, summer and autumn. In this study we concentrated on collecting ticks in the last two stages of their life cycle, nymphs and adults. At each study site, we collected ticks in four or six transects divided equally on sheep areas and control areas (Fig. 2). When we selected location for the transects, the aim was to keep all other factors than presence of sheep (such as vegetation, elevation, aspect, slope) as similar as possible between sheep areas and control areas. Each transect was approximately 500 meters. Transects were drawn on maps based on local knowledge of land use practices of pasture (Fig. 2). Each transect contains 12 segments randomly picked from a cheat with stochastic numbers. The segment's coordinates were saved as waypoints in a Garmin GPS to enable me to trace the same transect next season.

2.4 The cloth lure method

Each segment is 10 m^2 and the ticks are collected according to the *cloth-lure method* (Vassallo et al., 2000, Randolph et al., 2002). Terry-cloth towels (1x0.5m) were swept over the vegetation 4 times (2 m^2) before the towel were examined for ticks. Hence, in each segment (10 m^2), ticks were collected 5 times (every 2 m) and then I summarized the number of nymphs, adult females and adult males for the segment. The *cloth-lure method* allows us to estimate the vertical distribution in vegetation of ticks exhibiting *questing behavior*. Due to the short time of questing activity there are reasons to believe that this study does not represent the total tick population, but the density of questing ticks. However, the study was carried out in spring, summer and autumn when temperatures never fell below 5° C, the threshold for ticks to be active, hence the ticks in the study areas are capable to exhibit questing behavior.

Figure 5. Collection of ticks according to the cloth lure method. Photo: Kennet Mæhlumsveen

Another possible limitation in the data has to do with the tick species; there are possibilities of other tick species but *I. ricinus* to be present in our data material. A total of 14 tick species have been localized in Norway (Mehl, 1983, Jore et al., 2011). Nevertheless, there are most likely that a larger quantity of the ticks is *I. ricinus* in our sample, since this is definitive the most common and dispersed tick species in Norway (Kjelland et al., 2010, Hasle et al., 2009, Mehl, 1983).

The design of the field work was to collect questing ticks according to the cloth lure method. If I did not find any ticks after one hour's search, we had decided to quit sampling attempts in this particular transect.

2.5 Variables

The reason for this study was to find out whether sheep stocking density might influence tick abundance. Earlier studies show that tick abundance is heavily influenced by climatic factors and plant composition (MacLeod, 1932, Lees, 1948, Lees and Milne, 1951). Therefore, I recorded the weather and the habitat at the beginning of each segment. Recorded weather variables consist of wind, temperature and precipitation. Wind-speed was calculated with an anemometer and was in general low (0 to 3 m/s), except from one day in Tingvoll when we collected ticks in a sheep area, the wind was 10 m/s. Precipitation is an limiting factor for questing behavior and ticks are quiescent when it rains (H. A. Mejlon, 1997), hence I did not conduct fieldwork when it was heavy rain. Precipitation was categorized as either *no rain* or *light rain* and only 43 out of 480 (8.96 %) segments were conducted in light rain. The habitat variables encompass substrate and density of canopy cover. Substrate was registered at the start of each segment in the categories *marsh* (38.9%), *heather* (11.9%), *grass* (42.8%) and *other* (6.4%). Spruce forest was the dominating substrate type in the category *other.* A densiometer was used to measure the density of canopy cover. This tool enable us to estimate the percentage of cover from the tree canopy which reflect the degree of shade in the microclimate.

2.6 Statistical analysis

The data were analyzed in the software program R, version 2.11.1 (R Developing Core Team, 2012). The response variable of the analyses is the sum of nymph and adult ticks per 10 meter segment along a transect line. I ran several preliminary analyses to check the data. First, the default for analyzing count data would be to use a generalized linear model with Poisson distributed errors. However, a Poisson distribution was rejected based on over-dispersion diagnostics (Agresti, 1990). The reason for this is that is that many segments contained zero ticks. Such zero inflation is often the case when estimating parasite abundance, since the parasites often are clustered in their distribution and that very many segments contain no ticks. Secondly I ran preliminary generalized additive models (GAM;(Wood, 2006) to check for linearity of the only continuous predictor variable, canopy cover. The analysis was run in the package *mgcv* in R and revealed a close to linear relationship between percentage of canopy cover (shading) and tick abundance. Finally, all candidate variables were checked for co-linearity to ensure that they could be included as sufficiently independent variables.

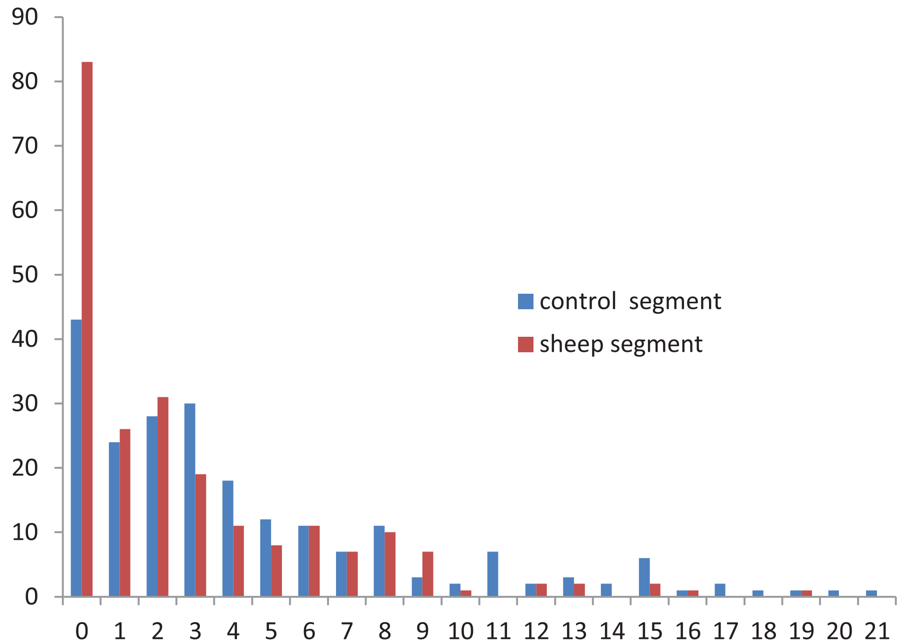

Figure 6. The distribution of the data material. Note the large proportion of the segments where there was found zero ticks (column 1).

Based on the preliminary analyses I chose to use a negative binomial model using the glm.nb function in the library MASS. This model fitted the data much better based on dispersion diagnostics. As in the preliminary tests, the total number of ticks (adults and nymphs) per segment was used as the response variable. Sheep presence (treatment 1 versus control 0) was

the predictor variable of primary interest. In addition season, substrate, precipitation, canopy cover from the densiometer and the interaction between sheep presence and season were included as predictor variables. I decided to use hypotheses testing instead of model selection in my thesis because I am predominantly interested in the effect size and p-values of all the variables I test. The negative binomial model was used to graphically present the most important results from the model. However, counts are dependent within transects. Therefore, the most robust model is to extent the negative binomial model into a negative binomial mixed model using each transect identity as a random intercept. For this we used the function glmm.adbm in the R library glmmADBM. However, this is a very complex and new model type that does not allow for graphical presentation. The output from the final analyses is therefore presented only in table from but I have inspected that the results corresponds very well with the graphical output from the simpler model.
I determined which variables influenced tick abundance and proceed with a mixed binomial model represented in the table in the results.

3 RESULTS

In 2010 a total of 1551 ticks were captured in four study sites. The number of ticks collected in spring, summer and autumn, were 157, 769 and 625 ticks respectively. The abundance of nymphs and adults were distributed on 1297 nymphs (83.62%), 145 adult males (9.35%) and 109 adult females (7.03%).

3.1 Tick abundance in relation to presence of sheep and seasonality

As predicted from the encroachment hypothesis H_2, there was less ticks of all age and sex classes on sheep transects compared to control transects (Fig. 7). The difference in tick abundance between areas with and without sheep was dependent on season (Fig. 8; significant interaction between season and sheep in Tab. 1). The difference in tick abundance between sheep and control transects was higher in all seasons but the difference was larger in autumn than in summer (Fig. 8). Due to small sample size tick abundance estimates in spring are uncertain (large standard errors; fig. 8).

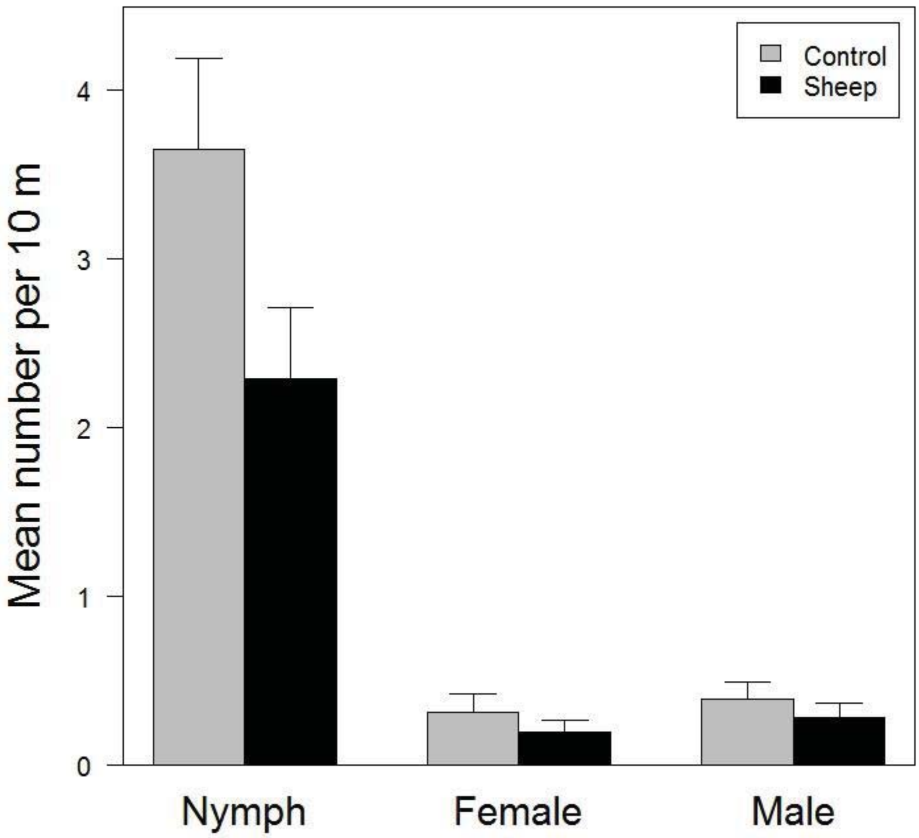

Figure 7. The histogram shows estimates for the number of nymphs, adult females and adult males in control areas as compared to sheep areas.

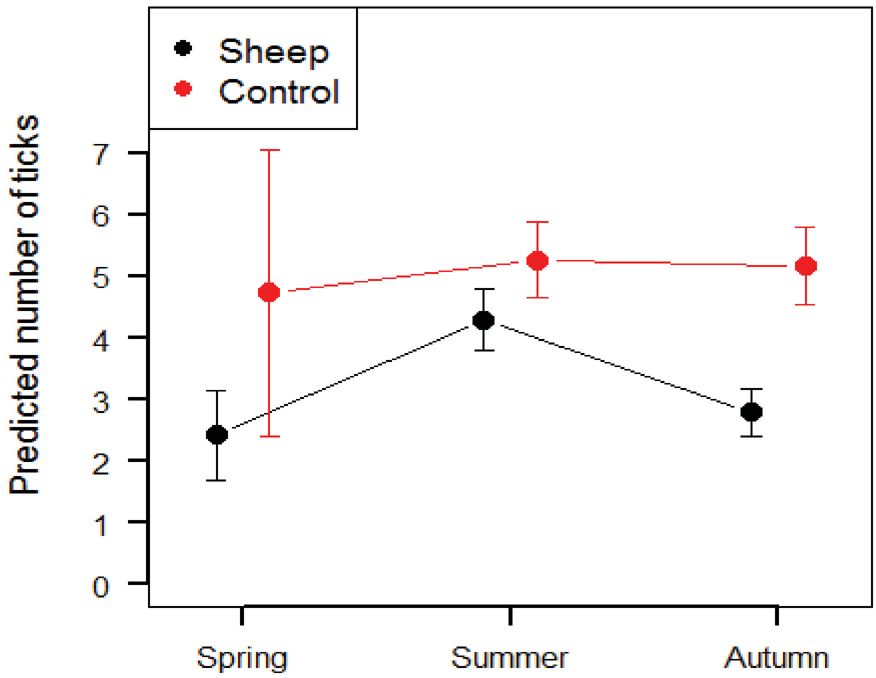

Figure 8. The relationship between the predicted number of ticks in the three seasons. The abundance of ticks was higher in the control areas compared to the areas with sheep for all three seasons.

3.2 Canopy cover

Tick abundance increased with canopy cover (Fig. 9). In segments where the canopy cover was scattered and open, approximately three ticks were found per 10 m. As the canopy coverage increased, the number of ticks collected increased to approximately eight ticks with full canopy coverage (Fig. 9).

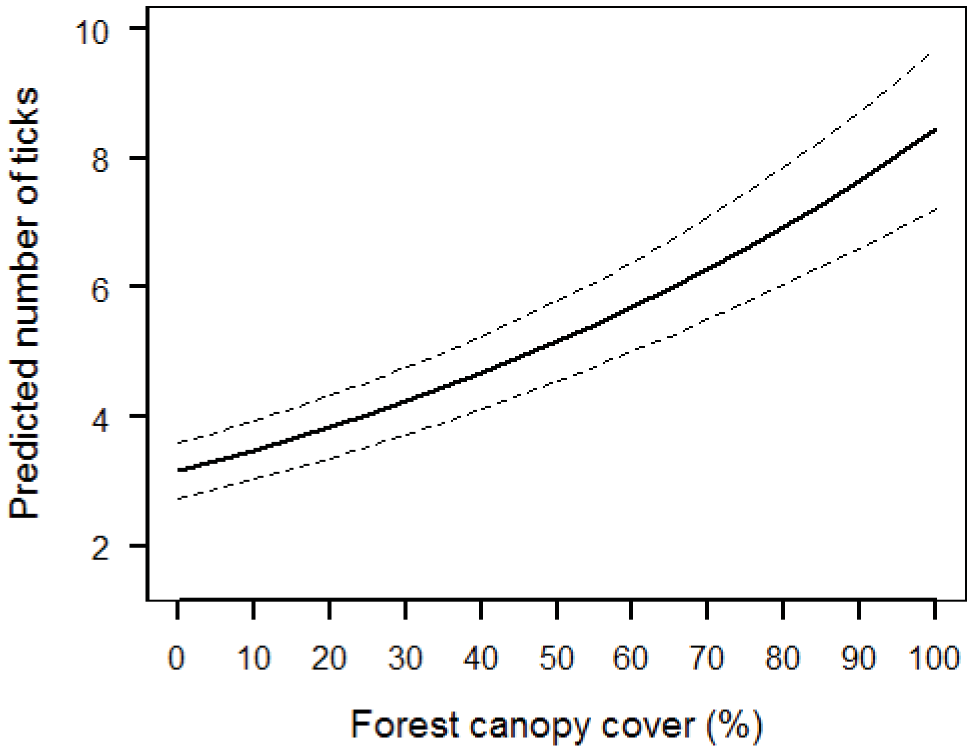

Figure 9. The relationship between an increasing canopy cover and tick abundance.

3.3 Substrate

There were less ticks in vegetation types *other* (ca 4 less ticks per 10 m) (p= 0.004) and in *marsh* (ca 2 less ticks per 10 m) (p= 0.013) compared to *grass* (Fig. 10; Tab. 1). The number of ticks in *heather* was slightly higher than the number of ticks in *grass* (Fig. 10; Tab. 1).

The category other (mainly spruce needles) hold a significant lower tick abundance that the three other categories of fresh vegetation, heather, marsh and grass (Fig. 10)

In the substrate category other, there was ca 1 tick. In marsh vegetation, there were ca 4 ticks per 10 m. On grass substrate, there were ca 5 ticks and on heather vegetation, there were ca 6 ticks per 10 m (Fig. 10).

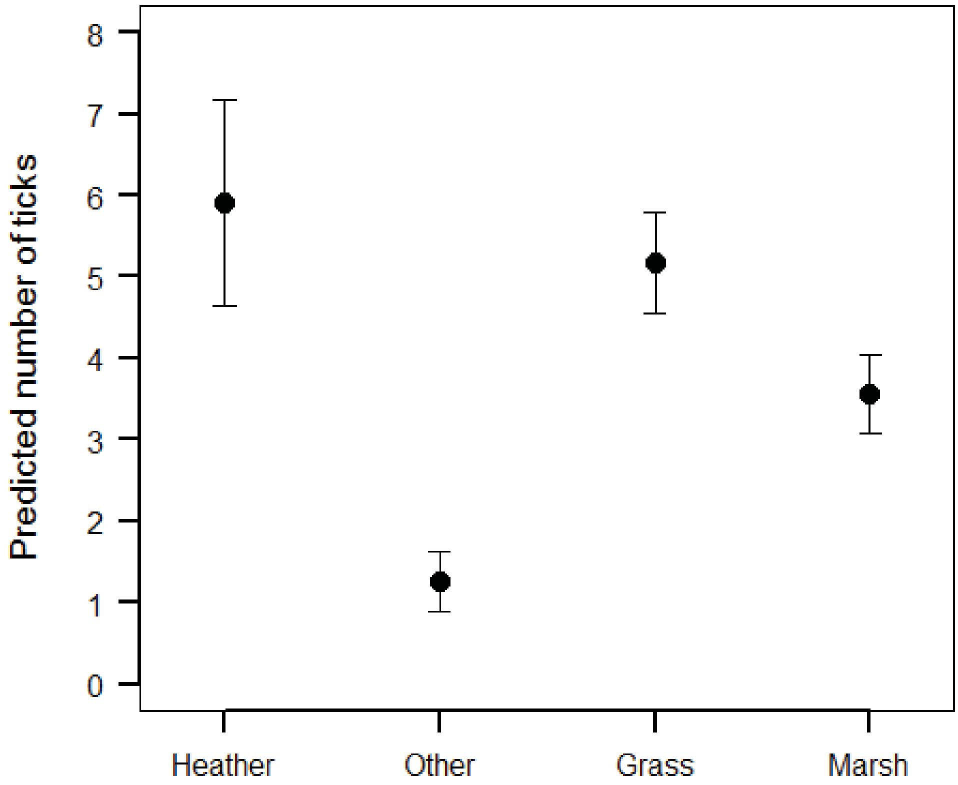

Figure 10. The numbers of ticks found on different substrate; heather, other (spruce needles), grass and marsh.

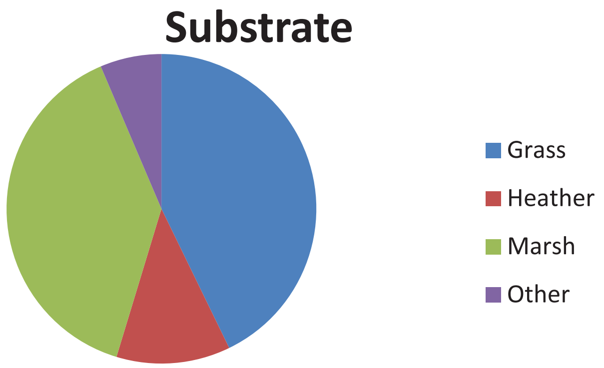

Figure 11. The distribution of substrate types in the four categories of substrate were grass (42.8%), heather (11.9%), marsh (38.9%) and other (6.4%).

Table1. The estimated effects from a mixed negative binomial model predicting tick abundance in areas with and without sheep in Møre and Romsdal, Norway. The reference to the estimates is control-area with grass in autumn**.**

	Estimate	**Std. Error**	**Z**	**P**	
(Intercept)	1.097	0.19075	5.75	8.90E-09	***
Sheep area	-0.71654	0.25705	-2.79	0.0053	**
Season - spring	-0.29531	0.64304	-0.46	0.6461	
Season - summer	-0.0357	0.2286	-0.16	0.8759	
Substrate – heather	0.10255	0.30129	0.34	0.7336	
Substrate – marsh	-0.33382	0.13442	-2.48	0.013	*
Substrate - other	-1.0595	0.36234	-2.92	0.0035	**
Precipitation (yes-no)	-1.0457	0.35909	-2.91	0.0036	**
Canopy cover	0.00947	0.00159	5.94	2.90E-09	***
Sheep area: season spring	0.2251	0.83024	0.27	0.7863	
Sheep area: season summer	0.57256	0.34087	1.68	0.093	

4 DISCUSSION

In this thesis I document for the first time that tick abundance is lower in areas with sheep compared to areas without sheep. My findings support the encroachment hypothesis; that sheep foraging maintains open habitats that are associated with lower tick abundance. Reduced encroachment apparently had stronger effect than adding sheep as an additional large mammal host in the system. The density of alternative hosts is an unknown variable in my study. As an alternative explanation to the observed pattern red deer may be an abundant tick host that may be negatively associated to the sheep in space (Clutton-Brock and Albon, 1989). The management implication of my study is irrespective of mechanisms that presence of sheep is expected to reduce the local abundance of ticks which has important consequences for animal and human health and welfare.

Increased densities of ticks in Norway are likely caused by the effects of several factors. Climate change and vegetation shift in latitudinal and altitudinal range is expanding areas of suitable habitat for ticks. Increased abundance of cervids all over the country is ameliorate host availability, hence facilitate successful reproduction of ticks (Mehl, 1983). Other vertebrate species, including birds and rodents, are also susceptible hosts for ticks at larva and nymph stage. More stable rodent population facilitate host availability for ticks at its early life stages and there is reason to believe that this factor promote higher tick abundance due to more constant host availability. In all four study areas in all three seasons, there were a significant higher number of nymphs compared to adults. The high number of nymphs compared to adults has also been evident in other studies on *I. ricinus* (Gilbert, 2010, Randolph et al., 2002) and may be caused by; 1) only a small number of nymphs survive to the adult stage, 2) the survival rate of adults is lower than for nymphs, 3) the adult ticks are attached to a host when the study is conducted, or 4) the adult ticks do not attach to the cotton towel as easily as nymphs. A previous study conducted on adult *I. scapularis* ticks revealed that unfed adults had a lower survival rate during the winter compared to unfed nymphs (Lindsay et al., 1995). Winter temperatures are also crucial for tick populations to persist. Temperatures below zero without snow cover are likely to impact tick populations negatively, although studies on *I. scapularis* indicate that engorged ticks and ticks infected by *Anaplasma phagocytophilum* may have a better chance of surviving in the cold (Lindsay et al., 1995, Neelakanta et al., 2010). Snow cover however, insulates habitat close to the ground and temperatures rarely falls below 0°C and thereby facilitate tick survival (Lindsay et al., 1995).

The winter in Møre and Romsdal in 2009/2010 was very dry (precipitation was 48 % below normal)(Meteorologisk institutt, 2012). This was the year before this study was conducted. The low precipitation may have lead to reduced snow cover, hence it is possible that survival rate of adult ticks was lower than the survival rate of nymphs.

4.1 Historical distribution of ticks in Norway

Tambs-Lyche conducted an estimate of tick distribution in Norway from 1935 to 1942 (Tambs-Lyche, 1943). 40 years later, Reidar Mehl (Mehl, 1983) described the geographical distribution and the hosts suitable to the ticks. Mehl's data concluded that the distribution of ticks was limited to a narrow coastal zone from the Oslofjord to Jæren in altitudes from 50-150 m above sea level, and along the western coast of Norway where the distribution extended into the fjords, reaching up to 400 m above sea level. Mehl consolidated Tambs-Lyches' distribution range and found no definite changes in geographical distribution from 1943 to 1983 (Mehl, 1983). This indicates no change of tick distribution range up to 1983. In 2011, Jore and her co-workers carried out a meta-analysis of latitudinal and altitudinal range shift in tick distribution in Norway (Jore et al., 2011). They found that the northern distribution limit has expanded by approximately 400 km from 1983 to 2011, and that the ticks now are inhabiting coastal municipalities in north to approximately 69°N, as compared with 66°N in 1943 and 1983 (Jore et al., 2011). This indicates that the ticks have reached new areas of both altitude and latitude, and that the distribution of suitable tick habitat has increased the last decades. The causation for the expansion of tick distribution may be the three drivers which are described in the introduction; climate change, encroachment and host availability.

4.2 The host availability hypothesis

I 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. Host availability is regarded crucial for ticks at all life stages (Mehl, 1983). 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 (Stanek et al., 2012). Host availability by grazing sheep can in theory facilitate population growth in tick species. However, in most of the transects where sheep were absent (control areas) we located evidences of presence of red deer, including deer droppings, sleeping spots and paths. Furthermore, the red deer is a mixed feeder tending towards being a grazer during the growing season, while, the other forest deer species are foraging mainly on wooded plant species and herbs and are therefore classified as browsers. Red deer prefer grass species like wavy hairgrass (*Avenella flexuosa-)*, moor grass (*Molinia caeruela*), bent grass (*Agrostis* spp.) and fescue (*Festuca* spp) (Hjeljord, 2008). These grass species are also preferable foraging species for sheep (Mysterud, 2000). This can result in foraging competition between deer and sheep and further that palatable vegetation can be a density dependent regulator if abundant deer and sheep graze in the same area. Since sheep and red deer graze the same grass species during the summer in the outfields, it is possible that abundant sheep stocking in a given area result in a less abundant deer population. The county Møre and Romsdal holds a large population of red deer, which function as an important host for nymphs and adult ticks. As Stanek et al. (2012) emphasize, high density of large mammals is essential for tick population to survive and maintain due to the supply of sufficient hosts for adult ticks to feed on. Red deer are an abundant available host in the control areas of this study and therefore the absence of sheep may not be as important regarding host availability.

And the explosion in deer populations in Norway is a possible driver for the increased tick abundance. In the1930s, the deer populations in Norway were at the lowest in modern time and only 100 animals were killed annually. In 2010, 106 269 deer were killed (Statistics Norway, 2012) . The biomass of deer species in the outfields, increased with 276% per km² from 1949 to 1999 (15.8 kg per km² to 59.4 kg per km²). This increase was significant in all geographical regions throughout the country (Austrheim et al., 1999). Studies show that the relationship between tick abundance and the presence of deer play an important role in the maintaining a dense tick populations. A study by Wilson and colleagues (1988) in USA revealed that when deer were removed from a tick-habitat, the prevalence of tick declined. Ticks at their larval stage became less abundant in the spring indicating that the adult ticks generally failed to feed and reproduce. The abundance of ticks at the nymphal stage declined more gradually. They concluded that the presence of deer is a precondition for dense tick populations (Wilson et al., 1988).

Another important aspect of variables influencing local tick abundance is local populations of susceptible hosts for larvae and nymphs. Ticks at the first two life stages have a larger variety of hosts since they need smaller amounts of blood. In this study, we did not include abundance of rodents, reptiles nor small mammals. The collection of ticks in this study encompassed a significant larger proportion of nymphs compared to larvae and adults. Therefore, the local tick abundance might have been influenced by population of other hosts which are not included in this study.

4.3 The reduced encroachment hypothesis

Pasture livestock and large game species have an important influence on ecological processes and the environment. The last decades, the land-use practices has gone through a regime shift and livestock grazing in the outfields have been reduced by more than 50 % since 1949 (Austrheim et al., 2008). Simultaneously as the domestic grazing animals have been considerably reduced, population of several deer species have grown rapidly (Austrheim et al., 2008). The regime shift in use of outlying fields, from dominated by grazers to now dominated by browsers, have consequences for the vegetation dynamics and plant compositions as well as ecological processes. Throughout the country, there is an ongoing process of encroachment of semi-natural grasslands and cultural landscapes due to the new grazing regimes and other forms of ceased resource utilization (logging and hay harvesting) (Blom, 2011). The loss of grasslands and encroachment of open landscapes may have an important influence on the explosion in tick populations in Norway. The ticks prefer lush and dense vegetation which hold high relative humidity and have shaded microhabitats.

This study supports the hypothesis that ticks prefer dense vegetation (MacLeod, 1932). The tick abundance increased as the canopy cover increased, from an average of three ticks in open landscapes, to more abundant tick populations in dense forests with an average of eight ticks. The degree of canopy cover implies several indirect variables on the ground level tick habitat, hence the local tick abundance. The canopy cover provides shade, which prevent ticks to be exposed to direct sunlight and further enhance humid microhabitat-conditions. 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. The temperatures at ground-level are lower and humidity higher when closed canopy occur. The microclimate conditions are essential for tick survival. Ticks depend on microclimate with high humidity (>c. 85 RH%) (Stafford, 1994) at ground level to avoid desiccation. This study indicates that ticks have preferences of substrate types. The relationship between vegetation types and variables such as humidity and temperature is an important variable on where we can expect to find abundant tick populations. I operated with four vegetation types; grass, heather, marsh and other. In the category "other", which is mainly spruce needles, the tick abundance is clearly lower than in the more lush vegetation as heather, marsh and grass. In spruce forests canopy cover is usual dense and the ground level often shaded, which is preferable for ticks. 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 ticks to climb up in vegetation and quest for a possible host. Ticks prefer heather, grass and also inhabit marsh, while spruce needles hold a less abundant population of ticks.

5 MANAGEMENT IMPLICATIONS

The increased abundance of sheep ticks in Norway is of great concern for farmers living of sheep stocking. Every year farmers experience severe losses of lamb caused by tick borne diseases such as the pathogens *Borrelia burgdorferi* and *Anaplasma phagocytophilum* along the south west coast of Norway. This problem is of such extent that the county administrator in Møre and Romsdal has initiated a project to estimate the tick abundance and further investigate the different pathogens the ticks are vector of. As a part of this project, called "Beiteprosjektet" (Grazing project), we contributed to assess tick abundance in 2010. Lyme disease, caused by the bacteria *Borrelia burgdorferi* is the most common tick-borne disease, and the main vector for this bacteria is the tick *I. ricinus* (Kjelland et al., 2010, Stuen, 2003).

Ticks also transmits the virus of louping-ill, a widespread disease of sheep, which is of considerable importance due to the debilitating effect upon infested animals and furthermore, its presence may predispose the sheep to the development of serious secondary affections (MacLeod, 1932).

My thesis contributes to the understanding of the spatial variation in tick abundance. The results indicate that sheep contribute to reduce tick abundance. This indicates that other susceptible tick hosts, such as deer, are likely to be of greater importance for tick populations to persist.

I suggest that sheep has a more important role as a landscape opener than as a tick host. Sheep farming may thus contribute to limit the local abundance of ticks and related diseases.

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