Heidi Storvassli

Vertical distribution of ticks in southern Norway
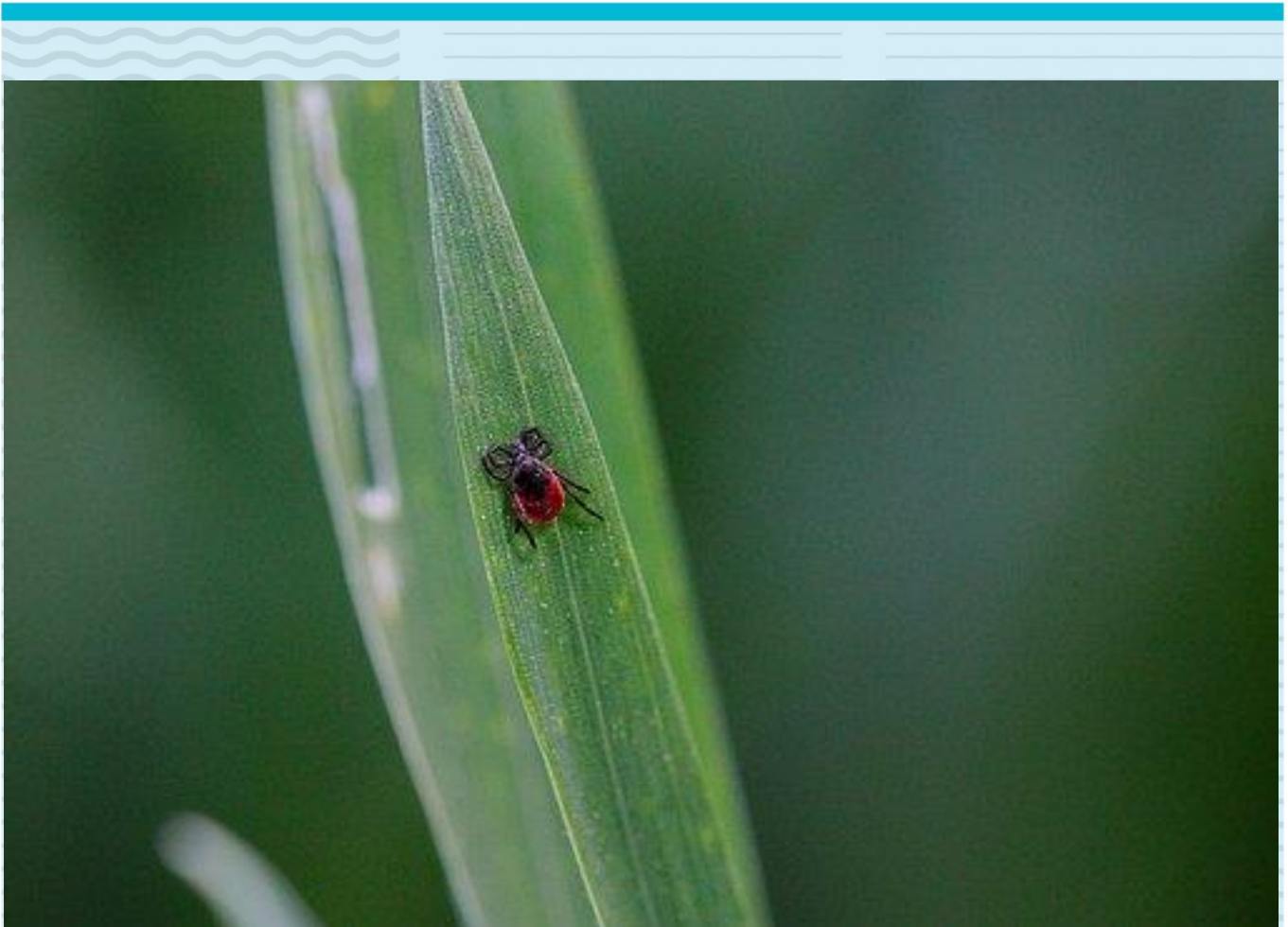
This thesis is worth 60 credits

Preface

This master's thesis is part of a two-year study project where I have cooperated with Nicolas De Pelsmaeker, which has been in charge of the project. The study method has not been done before, and within Norway we are the first to trap and collect rodents instead of flagging to give an estimation of tick density along altitude gradients. I have gotten much help along the way from both supervisor Øyvind Steifetten and Nicolas De Pelsmaeker. There were many good and interesting moments in the lab with fellow master and bachelor students working on different angles on the same topic. All of this could not have been done without all the assistance from people willing to help out with the field work. It is highly appreciated. Final, but not least, I would like to thank my roommate for help and support.

Bø i Telemark, 15.05.2018
Heidi Storvassli

Contents

Abstract

Due to climatic changes, plant and animal species have expanded their range vertically. One might therefore expect to find species at a higher elevation point than usual. By using both live and lethal traps, small mammals was collected in the field for three separate months along two transect lines to estimate tick burden and density. The method used is easier and less weather dependent than flagging. There was a strong effect among tick density and elevation, species, season and area. No correlation was detected for temperature or humidity. One can conclude that ticks may be found in the mountain region, preferably in a higher abundance in the coastal region in Lærdal, than the inland region in Bø, but that they do still have an altitude limit, and that it is season dependent.

1. Introduction

Animal and plant species seek higher terrain towards cooler conditions. (Roth *et al.,* 2014). Induced climate warming accelerate species richness in mountain areas (Steinbauer *et al.,* 2018). Species may disperse vertically, while others becomes extinct. Bird species have expanded higher upslope than usual, caused by climatic warming (Kirchman & Keuren, 2017). The mountain ant species *Aphaenogaster abies* have gradually been replaced by the lowland species *A. rudis*. In the end, warm-tolerant, lowland species may outcompete the local population community (Warren *et al.,* 2016). Not only do species expand their range shift, they also tend to disappear from mountain areas. The alpine marmot (*Marmota marmota*) is declining throughout the alpine landscape, due to less snow cover leading to fat depletion during hibernation, using more energy staying warm (Tafani *et al.,* 2013).

Climate warming and shorter winter seasons may cause geographic colonization between host-parasite invasions (Masters & Norgrove, 2010). Worldwide, approximately 7.7 million species acts as parasites (Nuwer, 2016). Within the Acari subclass, there are 720 known species of hard ticks (Ixodidae) (Barker & Murrell, 2008), with 249 species in the genus Ixodes. Due to high risk of disease transmission, the Ixodes genus is of great importance. Ticks inhabit all continents (Kjelland *et al.,* 2014), meaning they can disperse great distances. *Ixodes uriae* went from Australia to Fuglefjell (Northern Hemisphere) by bird transportation where it has a reproducing population and can occasionally feed on humans (Muñoz-Leal & González-Acuña, 2015). Some species might even withstand seawater for longer periods of time (Moon *et al.,* 2015). Population of hedgehog tick (*I.hexagonus*) have increased due to a rise in temperatures (Sherrad-Smith *et al.,* 2012). Norway has 13 known species of hard ticks (Flåttsenteret, 2018), where the sheep tick (*I. ricinus*) is regarded as the only one transmitting pathogens to humans (Kjelland *et al*., 2014). Hard ticks go through three life stages: larvae, nymph and adults. The adult ticks are more resilient regarding the weather, while larvae have less resilience (Barker & Murell, 2008; Gilbert *et al*., 2014), and around 10% survive and merge for the next stage. Usually population of ticks emerge from diapause during spring to queast, then gradually decline in summer due to warm, dry air with low humidity leading to desiccation, and again achieve a second peak during autumn (Schulz *et al*., 2014).

Mammals play an important role in transferring tick-borne pathogens among tick species. At the same time, bird species are main reservoir hosts of zoonotic diseases, giving the pathogen a wider distributional range. The vole tick (*I. trianguliceps*) act as indirect

vector, maintaining a high infection rate in their reservoir hosts, transmitting the disease to the sheep tick if feeding on the same host, transmitting the pathogen to humans (Gern L *et al*., 1998; Mysterud *et al*., 2015; Perez *et al*., 2016). Sheep ticks are non-nidicolous species, meaning they actively seek out their host and many of them are less successful in finding one compared to the vole tick, a nidicolous tick, which lives in or near shelters used by their vertebrate hosts meaning they would have access to a host most of the time (Barker & Murrell, 2008). On the other hand, there is a risk of the nest or burrows being abandoned while moulting to the next life stadium (Randolph, 2014). Small mammals are hosts for different tick species including specialists that are specialized in one species or generalists who can thrive on a larger range of species (Kjelland *et al*., 2014). The distributional range of the sheep tick stretches from Africa to Scandinavia. The Scandinavian winter and natural barriers can be an obstacle for its survival (Kjelland *et al*., 2014).

It has been assumed that the sheep tick population mainly was distributed along the coastal region of Norway (Jore *et al*., 2011). However, the species has been documented in the colder parts of Norway. In 2017, observations of this species were made for the first time at 69°N (Finnsnes, Tromsø). In addition, the species was found on small islands as far north as 61°N (Austbø, Nordland) (Artsobservasjoner, 2018). However, these findings may be more sporadic, transported by birds, cervids, or domestic animals (Hvidsten, 2014). Distribution of the vole tick is more unknown. Since it does not transmit diseases to people, it may therefore not be seen as a big threat. Different tick species may adapt to local climates, making them withstand a changing climate (Gilbert *et al*., 2014), but they might also disappear from an area if the conditions get too dry or too wet. The sheep tick would have to find habitats that are more suitable further up in elevation where conditions are less dry and would then slowly disappear from the lowlands (Cadenas *et al*., 2007). With a relative humidity (RH%) of 80% at 24°C, ticks prefer questing at night (Randolph, 2014). Requena-García *et al*. (2017) found that *Hyalomma lusitanicum* had a high questing activity during increased temperatures and low activity at periods of high humidity, meaning temperature and humidity (saturation deficit), a measure of atmospheric drying power are critical factors for tick survival. Ticks found above the upper altitude (and latitude) limit with saturation deficit have not yet established local populations (Daniel, 1993; Léger *et al*., 2013; Hvidsten, 2014). However, as the climate becomes milder, ticks spread faster along an altitude and latitude gradient giving a higher survival rate among larvae and nymphs (Lindgren *et al*., 2000; Lindgren & Gustafson, 2001).

The aim of this study was to estimate the tick density along an altitude gradient by looking at how the distribution range in the mountain would be affected by seasonality and latitude. The tick species were collected by trapping small mammals using live and lethal traps in order to see which was most efficient for collecting enough ticks, and it was important to consider the scenario of ticks leaving the dead host.

2. Materials and methods

2.1 Study sites

To examine tick species abundance along an altitudinal gradient, two transects for each altitude following an approximately straight line were selected in mountainous regions of a south-facing slope located in Bø (southeast Norway, 59°N, 9°E) and a north-facing slope situated in Lærdal (west Norway, 61.06°N, 7.35°E) ranging from 100 to 1000 m above sea level (m.a.s.l) (fig. 1).
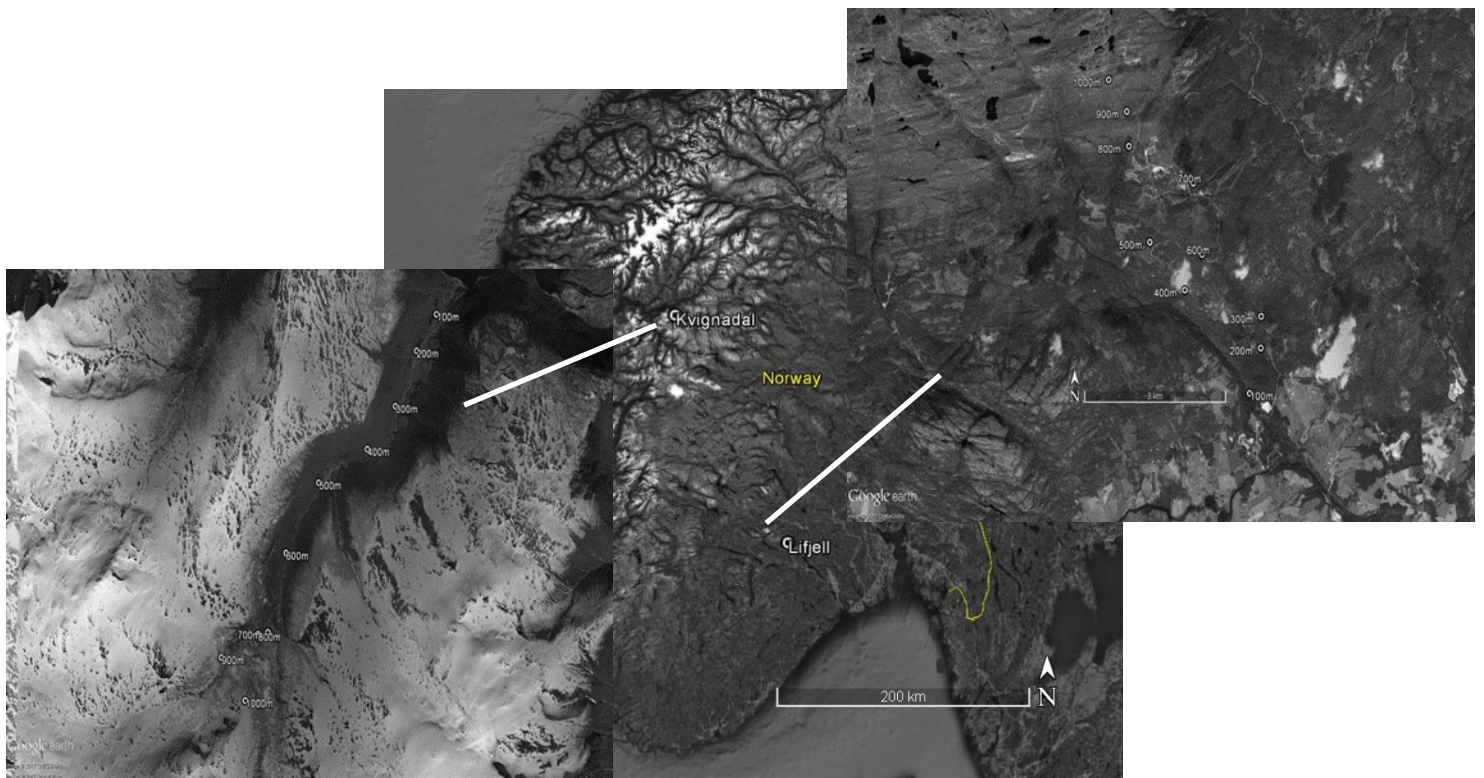
Figure 1. The study sites, consisting of a north-facing slope in Kvignadal (Lærdal) in the western region (left picture) and south-facing slope in Lifjell (Bø), east Norway (Upper right picture) (Source: google earth).

The climate in Bø is cold and temperate, with significant amount of precipitation. The yearly annual mean temperature is 6°C and yearly annual mean precipitation is 754 mm. In Lærdal, the climate is slightly different with a mild, warm and temperate climate, and there is more precipitation during winter than summer. The yearly annual mean temperature is 5.8°C and yearly annual mean precipitation is 961 mm (Climate-data.org).

The vegetation in Lifjell consisted of conifers and mixed forest, and became more shrub dominated at the higher altitudes. The treeline was somewhere between 800-900 m.a.s.l. The vegetation in Kvignadal had a higher density of deciduous forest dominating by birch (*Betula spp.*) with a richer bottom vegetation than in Lifjell., and the treeline was between 900-1000 m.a.s.l. Grazing sheep could be found up to 500 meters in Kvignadal, and from 800 m in Lifjell.

2.2 Collection of small mammals

A total of 800 traps (400 live & 400 lethal) was used for sampling of small mammals (rodents and shrews). It was of interest to use two trap types due to uncertainty of which works best for estimation of tick burden. One plot of 20 live traps (Ugglan special nr. 2) and one plot with 20 lethal traps (Rapp 2) with a minimum distance of 100 meters between the inner edges of the plots was deployed at 100 meter intervals from 100 to 1000 m.a.s.l (fig. 2). A data logger was placed in between the two plots, 50 meters above the ground. Traps were placed ten meters from each other, creating a square-shaped plot (Myllymäki *et al.,* 1971). Above every deployed trap, a coloured ribbon was hung above or beside the trap, and traps were numbered 1-20 for a better overview, which proved to be useful in the dense vegetation.

All traps were checked every 12 hours (morning and evening) for the duration of the field session. To make a more accurate estimation of tick burden a Vaseline ring was smeared on the icebox lid for the lethal traps in case any would escape from the host after it died.
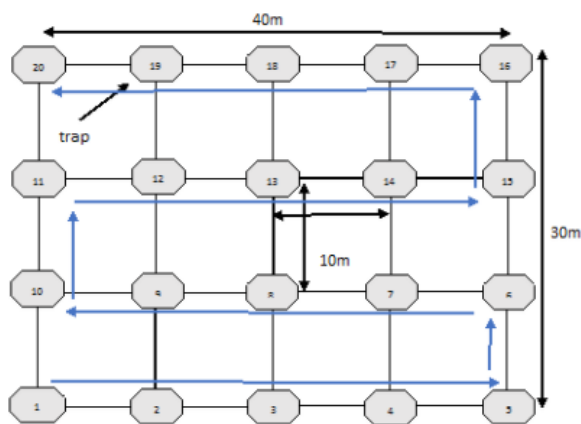

Figure 2. Schematic representation of a plot. Traps were placed at 10 m intervals from each other in 4 rows of 5 traps.

Sawdust and a piece of apple were put inside the live traps to avoid dehydration and hypothermia, and whole wheat grains to lure them in. The upper cervical was dislocated by using a metal ruler. Captured animals were put in separate bags marked with location-altitude-trap type-date-time-trap#. Animals trapped together were bagged separately. The trap was re-baited after each capture. Lethal traps were baited with peanut butter placed on the inside wall of the trap and a few kernels of whole oat in front of the trap to lure them in. Bait for both live and lethal traps were refreshed every 48 hours or after each captures. After each session, the samples were frozen down to below -20°C for later examination. Air temperature and relative humidity was recorded hourly at every altitudes.

Traps were checked morning and evening for ten days, occurring every other month from June to September, 2017 (2-8 June, 20-30-July, 20-30-September). Due to longer snow cover duration at 800-1000 m.a.s.l, only 100-700 m.a.s.l were accessible during spring. To avoid overharvesting, the limit was set to 50 captures per altitude, at which point the traps would be deactivated. Any excess animals in the live traps were released. In some occasions, traps were accidentally deactivated due to sheep grazing in the plotted areas, which mostly occurred with the lethal traps. Occasionally, by-catches occurred, finding weasels in the live traps, which were released back in the wild.

2.3 Tick collection and identification

Before examining the rodents for parasites in the lab, they were thawed for at least 12 hours (usually overnight). The bag containing the animals was checked for parasites, and if some was present, it was placed in an Eppendorf tube containing 70% ethanol to prevent desiccation (1 tube per rodent/shrew). It was preferable for the fur to be dry when examining the mammals, so a hair-dryer was used for wet animals. By following identification features illustrated by Fauna, (1999), Quéré and Louarn, (2011) and Muir and Morris (2013), species and sex were confirmed by fur color, length of the tail and by looking at their teeth. Thereafter, the small mammals were examined for ticks and other parasites (fleas, lice, and mites) by searching the ears, snout, cheeks, underside of the chin, legs, tail, along the abdomen and torso from the genital area up to the chin, and along the back from the tail up to the head in between the ears using tweezers and a finished touch with a lice comb. Lastly, in case any parasites were overlooked, the animals were shaken by the tail and the parasites would fall down in the tray. The tubes containing the ticks were later placed in a petridish and identified down to species and life stages by using identification keys written by Arthur

(1963) and Hillyard (1996). Identification features consisted of the dorsal plate to see either a rounded shape (vole tick) or a slight inward bend (sheep tick), spurs on the first coxae, mouthparts including the palpi, and the anal groove (adults).

2.4 Statistical analysis

Because many different variables had to be taken into consideration, a normal distribution could not be assumed. A variation inflation factor (VIF) (Pearson correlation coefficient) were analysed for elevation – temperature, elevation – humidity and temperature – humidity. If correlated (corr >0.6), one variable would be excluded from the final analysis. Temperature and humidity were both highly correlated (corr >0.6), so temperature which had the highest value would therefore be excluded from further analysis. Thereafter the variables were run in two separate models using a general linear model (GLM) in the statistical program R (version 3.4.3). The proportion of ticks were run in the first model using a binominal distribution to check if altitude, season, temperature, relative humidity, species, and location had a significant impact on their presence. By using a stepwise approach, variables were excluded if the p-value was above the significant level. Only two out of six variables in the first model were eligible and significant. Density of ticks was run in a second model using the Gaussian distribution. Only one variable was excluded from the last model due to no significant values.

3. Results

A total of 10 173 ticks were collected from 11 species of small mammals adding up to 2484 individuals (Table 1). Out of the tick species, 8638 (85%) were sheep ticks, and 1533 (15%) vole ticks (table 2 and 3). Approximately 90 ticks were unidentifiable and thereby excluded from analysis. The maximum density of ticks was collected from one shrew containing 185 ticks at 200 m in Lærdal. The bank vole and common shrew was the dominant species captured at both locations. There was a clear difference in the proportion and density of ticks between the two locations, resulting in 52% sheep ticks and 46% vole ticks alongside a south-facing slope in Lifjell, compared to 92% sheep ticks and 7% vole ticks along a north-facing slope in Kvignadal. Majority of sheep ticks consisted of larvae and a few nymphs, but no adults at either locations.

Humidity and temperature differed between the two study sites as shown in appendix 1 and 2, and both decreased with altitude.

Table 1. Percentage of animals captured at the two study sites (NA: not available).

Species	Latin name	Lifjell %	Lærdal %
Long-tailed field mouse	*Apodemus. sylvaticus*	0.2	0.5
Yellow-necked field mouse	*A. flavicollis*	0	0.08
Field vole	*Microtus agrestis*	4.3	2.3
Tundra vole	*M. oeconomus*	0.2	1.9
Bank vole	*Myodes glareolus*	43.4	57.3
Grey red-backed vole	*M. rufocanus*	0.08	2.5
House mouse	*Mus musculus*	0	0.08
Shrew	*Sorex*	2.3	0.5
Common shrew	*S. araneus*	48.6	34.4
Eurasian pygmu shrew	*S. minutus*	0.4	0.2
Taiga shrew	*S. isodon*	0.08	0
Eurasian water shrew	*Neomys fodiens*	0	0.08
NA		0.3	0.08

Table 2. Total number of sheep ticks and vole ticks collected from spring to fall at ten altitudes in southwest Norway including larvae, nymph and adults stage, respectively in parentheses (NA: Not active).

Site	No. *I.ricinus*			No. *I.trianguliceps*		
Lifjell	June	July	September	June	July	September
100m	8 (5, 3, 0)	42 (41,1,0)	9 (5, 4, 0)	43 (26, 16, 1)	28 (14, 12, 2)	81 (78, 1, 2,)
200m	236 (227, 9, 0)	414 (393, 21, 0)	74 (73, 1, 0)	33 (22, 10, 1)	13 (6, 7, 0)	139 (137, 2, 0)
300m	34 (34, 0, 0)	73 (69, 4, 0)	17 (17, 0, 0)	4 (2, 2, 0)	8 (4, 3, 1)	32 (29, 2, 1)
400m	30 (23, 7, 0)	31 (27, 4, 0)	2 (1, 1, 0)	145 (123, 22, 0)	39 (26, 8, 5)	60 (58, 2, 0)
500m	17 (17, 0, 0)	9 (7, 2, 0)	2 (2, 0, 0)	72 (44, 28, 0)	29 (21, 7, 1)	50 (49, 1, 0)
600m	5 (4, 1, 0)	35 (35, 0, 0)	2 (2, 0, 0)	41 (14, 24, 3)	14 (9, 5, 0)	31 (30, 1, 0)
700m	34 (34, 0, 0)	0	0	6 (0, 6, 0)	43 (37, 5, 1)	17 (17, 0, 0)
800m	NA	0	0	NA	14 (6, 8, 0)	5 (0, 4, 1)
900m	NA	7 (7, 0, 0)	0	NA	7 (4, 3, 0)	12 (12, 0, 0)
1000m	NA	1 (1, 0, 0)	0	NA	0	0

Table 3. Total number of sheep tick and vole tick collected from spring to fall at ten altitudes in the west Norway including larvae, nymph and adults in, respectively in parentheses (NA; Not active).

Site	No. *I.ricinus*			No. *I.trianguliceps*		
Lærdal	June	July	September	June	July	September
100m	722 (705,17,0)	686 (667,19,0)	337 (326,11,0)	13 (6,7,0)	11 (5,4,2)	30 (27,3,0)
200m	1043 (1037,6,0)	1009 (997,12,0)	558 (548,10,0)	27 (12,15,0)	21 (8,8,5)	23 (21,2,0)
300m	1069 (1062,7,0)	142 (13,12,0)	43 (39,4,0)	24 (8,16,0)	4 (1,1,2)	88 (87,1,0)
400m	348 (344,4,0)	113 (112,1,0)	25 (24,1,0)	38 (3,32,3)	11 (1,10,0)	19 (12,7,0)
500m	488 (486,2,0)	159 (158,1,0)	5 (5,0,0)	66 (15,51,0)	41 (12,23,6)	43 (37,6,0)
600m	497 (496,1,0)	62 (62,0,0)	2 (2,0,0)	26 (10,10,6)	5 (1,4,0)	12 (9,3,0)
700m	90 (90,0,0)	54 (54,0,0)	15 (14,1,0)	20 (10,9,1)	6 (5,1,0)	2 (1,1,0)
800m	NA	15 (15,0,0)	0	NA	7 (2,3,2)	4 (4,0,0)
900m	NA	72 (71,1,0)	0	NA	24 (9,15,0)	1 (1,0,0)
1000m	NA	1 (1,0,0)	0	NA	0	0

With seasonal variations, the density of sheep ticks in Lærdal declined from 25% to below 15% past 300 m in spring and from 44% to below 10% past 200 m in summer and even more rapidly in autumn with 57% to below 5% past 200 m. In Bø, there was a more rapid decline past 200 m every field month, ranging from approximately 60% at 200 m to below 20% above this altitude (fig. 3).

      Meanwhile, fluctuations in the vertical distribution of the vole tick occurred more frequently, which is the opposite of the sheep tick, which more or less had a steady decline. Overall, the density of the sheep tick seemed to be highest at 200 m, having a higher abundance in Kvignadal.

      The vole tick reached up to 900 m but none was found at 1000 m. In September, no adults were present on the host, except from two at 100 m, one at 300 m and one at 800 m in Lifjell, also the nymph stadium declined, leaving a higher proportion of larvae.

a)
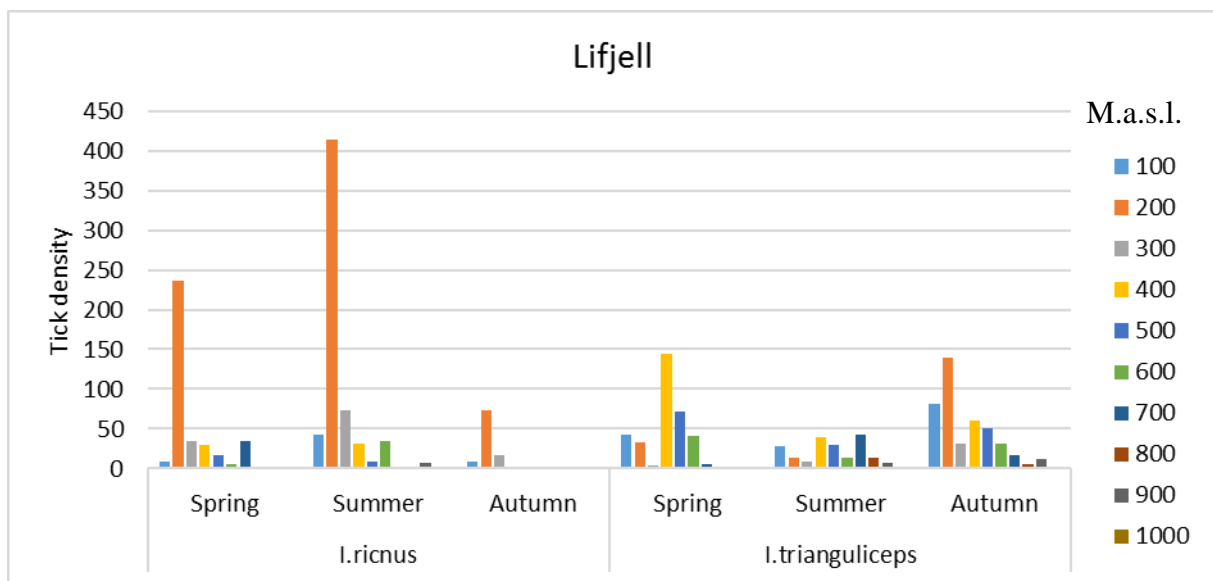
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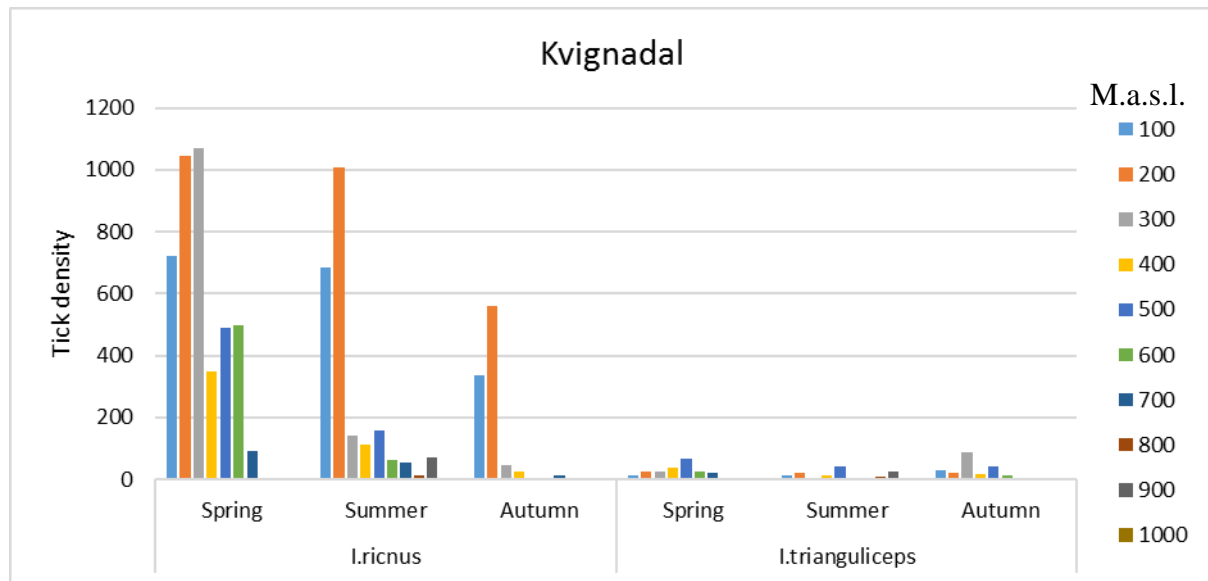
Figure 3. Seasonal change in tick density of the sheep tick and the vole tick along the transect line ranging from 100-1000 m.a.s.l. in a) Lifjell and b) Kvignadal.

Air temperature and humidity had no impact on the proportion of ticks (P = 0.9). However, there was a strong association with elevation (P = <0.001), indicating that ticks decrease with altitude and also with seasons (P = 0.01), meaning temperature and humidity alone cannot explain the changes in the abundance.

More factors influenced the tick density (table 7) rather than the proportion, where again, altitude had the strongest effects (P = <0.001). In addition, the rodents/shrews had a significant higher density of the sheep tick rather than the vole tick (p = <0.01).

Table 6. Proportion of ticks affected by season and elevation, by looking at the estimate, standard error, z – value and p – value.

Coefficients	Estimate	Std. Error	z value	P-value
Intercept	2.31	0.74	3.10	<0.01
Elevation	-0.0032	0.00095	-3.34	<0.001
Season	-0.74	0.29	-2.55	<0.05

Table 7. Tick density affected by elevation, species, season and area, giving an estimate, standard error, z – value and p – value.

Coefficients	Estimate	Std. Error	z value	P-value
Intercept	354.093	89.31	3.96	<0.001
Elevation	-0.23	0.062	-3.81	<0.001
Species	-131.62	33.73	-3.90	<0.001
Season	-51.80	21.91	-2.36	<0.05
Area	112.51	33.73	3.33	<0.01

4. Discussion

Since the mid-20th century, ocean and land surface temperatures increased by nearly 1°C (0.8°C) globally. The Northern Hemisphere have gotten more precipitation since the beginning of 1900. In addition, snow cover has reduced by 1.6% since the last century. With reduced snow cover, permafrost is getting more frequent, giving unsuitable conditions for foraging animals and plant communities (IPCC, 2014). After 1988 up to today, the annual mean temperature in Norway has increased with a tendency for continued warming. In addition, the trend in precipitation during the last 100 years show an 21% increased precipitation rate (dybdahl, 2016, Meteorologisk institutt, 2017).

4.1   Altitude

The proportion of ticks decreased along the transect line, implying they are not yet as well-adapted to the Nordic mountain environment. Similar conclusions were made by Materna *et al*. (2005), Daniel *et al*. (2009) and Ragagli *et al*. (2016), where ticks reached up to the timberline, but was also declining, indication that the timberline may be a limiting factor of their distributional range. It is difficult to compare spring with the other two months, since the three upper altitudes was not accessible until July, but one can assume no ticks were present. It was only during July that sheep ticks occurred at every altitudes.
The vole tick was never present above 900 m.a.s.l.

Abiotic factors may be important for explaining questing tick activity. At the same time, the climate may not be a sole factor for tick species to reach to higher altitudes. If there is low amount of host available, they are less capable of survival and reproducing. It took longer time to reach the capture limit of rodents/shrews at the higher altitudes. If less animals pass the area, the ticks may not be as active and would be at risk of reduced fat reserves (Gern *et al.,* 2008). At the two lowest altitudes in Kvignadal during spring, 100% of the captured animals had ticks on them. Grazing sheep can be a source of transporting ticks to new locations. Like with flagging, this method can be seen as a way of estimating the density of active ticks, providing knowledge in their distributional range with altitude. Another parameter is the vegetation within the transect. Even the soil could have had an effect.

4.2   Seasonality

There was a high difference in seasonal activity among the two species. It was not until july that the minimum temperature passed 10°C, which could be a factor for the summer peak in Lifjell, and they were not as active during the beginning of june. In Lærdal the density declined over the seasons. The tick species may have had earlier access to a host, and by the end of the summer most were finished their questing season and crawled back to the vegetation for diapause. Ticks might be questing in the low vegetation regardless of saturation deficit, meaning neither air temperature or humidity play a direct significant part (p=0.6). Although, there is still a possibility it might have an indirect effect, at least regarding the microclimate.

No adult sheep ticks were present on any of the hosts. One explanation for this is that they climb higher up in the vegetation the older they become, being passed by the rodents (Randolph, 2014). Sheep ticks thrive best in a deciduous forest containing high bottom vegetation, providing a lower risk of desiccation (Gjerde, 2001). Since the vegetation may be richer in the west coast, having a more suitable microclimate, one can expect to find a higher density of this species (Qviller *et al*., 2014).

4.3   Region

Lærdal is situated by the coastal region where the climate is more temperate and milder. In addition, spring begins earlier than in Bø. Overall, the tick population has more tolerable climatic conditions in the western region. Still, we can see that even if the climate is dryer and colder in Bø, there is a relatively high density of both species. At least in the lower altitudes. In spring, it was 1.5°C warmer at 700 m in Lærdal. Since it is warmer by the coast, then perhaps more eggs and larvae survived the previous winter and may have gotten better time to quest after a host.

It is not as dry along a north-facing slope as compared with the south-facing slope due to position of the sun and the amount of latent heat (Oke, 1987). More tree species thrive on a north-facing slope giving a higher tree density consisting of more deciduous forest, while conifers are more dominant in south-facing slopes (Måren *et al.,* 2015, Williams, 2018), which is consistent with our study sites.

By autumn, the data logger at 800 m.a.s.l in Bø, became slightly defect during certain days and did not record humidity for approximately halfway through September.

As long as ticks have protection from their surroundings, like wind and overheating, they have a better survival rate. This also applies having access to a host. If no animals are passing by, even in a perfect tick habitat, they will starve and lose fat reserves leading to exhaustion. It is still unclear how long ticks stay on their host after the host dies. The portray of an estimated density might therefore be slightly skewed, since there is a possibility some ticks left their host when the animal died. In addition, the Vaseline smeared on the lid around the lethal trap had no effect on the ticks. This is something worth further investigation. By using a simulation model, Ogden *et al*. (2014) estimated an increased northern distributional pattern of the blacklegged deer tick (*I. scapularis*) in Canada, having a higher chance of surviving, due to a rise in temperatures.

5. Conclusion

Temperature and humidity had no effect on the tick burden in mountain regions of Bø and Lærdal, but there was still a strong effect among the other variables, implying that it may be possible to find ticks in higher altitudes, but that it may be season dependent. There might be less chance of finding ticks at higher elevation during autumn than rest of the year. How well they are thriving are more difficult to conclude upon, with only one year of study in these two areas. It would then be of interest to obtain more knowledge using long-term studies to see how the vertical distribution changes over the years.

References

Arthur D.R., 1996, *British ticks,* Lincoln, UK, Butterworth.

Artsobservasjoner, 2018, Skogflått (*ixodes ricinus*), read 09.04.18 at
https://artsobservasjoner.no/Occurrence/TaxonOccurrence/4/126576.

Barker S.C., Murrell A., 2008, Systematics and evolution of ticks with a list of valid species
names, In Bowman A.S., Nutall, P.A. (ed.), *Ticks: biology, disease and control*,
United Kingdom, Cambridge university press, pp. 8, 30.

Barry R.G., 2008, *Mountain weather and climate*, 3.ed., United Kingdom, Cambridge
University press.

Cadenas F.M., Rais O., Jouda F., Douet V., Humair P.F., Moret J., Gern L., 2007, *phenology
of Ixodes ricinus and infection with Borrelia burgdorferi sensu lato along a north-
facing altitudinal gradient on Chaumont Mountain, Switzerland,* Journal of medical
entomology, 44, 683-693.

Climate-data, read 30.04.18 at https://no.climate-data.org/location/717686/ and
https://no.climate-data.org/location/278098/.

Companion vector-borne diseases, *Tick species,* Bayer, read 26.02.18 at
http://www.cvbd.org/en/tick-borne-diseases/about-ticks/tick-species/.

Daniel M., 1993, *Influence of the microclimate on the vertical distribution of the tick ixodes
ricinus (L.) in Central Europe,* Acarologia, 2, 105-112.

Daniel M., Materna J., Hönig V., Metelka L., Danielová V., Harčarik J., Kliegrová S.,
Grubhoffer L., 2009, *Vertical distribution of the tick Ixodes ricinus and tick-borne
pathogens in the Northern Moravian mountain correlated with climate warming
(Jeseníky mts., Czech Republic),* Central European journal of public health, 17, 139-
145.

Dybdahl A., 2016, *Klima, uår og kriser i Norge gjennom de siste 1000 år,* Cappelen damm,
Norway, pp. 183.

Fauna, 1999, Norsk forenings tidsskrift, 52.

Flåttsenteret, 2018, *flått,* read 09.04.18 at https://xn--flttsenteret-ucb.no/flatt/.

Gern L., Estrada-Pena A., Frandsen F., Gray J.S., Jaenson T.G.T., Jongejan F., Kahl O.,
Korenberg E., Mehl R., Nuttall P.A., 1998, *European reservoir hosts of borrelia
burgdorferi sensu lato,* Zentralblatt für Bakteriologie, 287, 196-204.

Gern L., Cadenas F.M., Burri C, 2008, *Influence of some climatic factors on Ixodes ricinus ticks studied along altitudinal gradients in two geographic regions in Switzerland,* International journal of medical microbiology, 248, 55-59.

Gilbert L., Aungier J., Tomkins J.L., 2014, *Climate of origin affects tick (ixodes ricinus) host-seeking behavior in response to temperature: implications for resilience to climate change,* Ecology and evolution, 4, 1186-1198.

Gjerde B., 2001, *Skogflåtten Ixodes ricinus,* Norsk vetrinærtidskrift, 113, 279-283.

Hillyard P.D., 1996, *Ticks of North-West Europe*, Shrewsbury, UK, Field studies council.

Hvidsten D., Stuen S., Jenkins A., Dienus O., olsen R.S., Kristianse B.E., Mehl R., Matussek A., 2014, *Ixodes ricinus and Borrelia prevalence at the arctic circle in Norway,* Ticks and tick-borne diseases, 5, 107-112.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (Eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jore S., Viljugrein H., Hofshagen M., Brun-Hansen H., Kristoffersen A.B., Nygård K., Brun E., Ottesen P., Sævik B.K., Ytrehus B., 2011, *Multi-source analysis reveals latitudinal and altitudinal shifts in range of Ixodes ricinus at its northern distribution limit,* parasites and vectors, 84.

Kirchman J.J., Keuren A.E.V., 2017, *Altitudinal range shift of birds at the southern periphery of the boreal forest: 40 years of change in the Adirondack mountains,* the Wilson journal of ornithology, 129, 742-753.

Kjelland V., Korslund L., Slettan A., 2014, *Fakta om flått,* Oslo, Kagge forlag.

Léger L., Vourc H G., Vial L., Chevillon C., McCoy K.D., 2013, *Changing distributions of ticks: causes and consequences,* experimental and applied acarology, 59, 219-244.

Lindgren E., Gustafson R., 2001, *Tick-borne encephalitis in Sweden and climate change,* The Lancet, 358, 16-18.

Lindgren E., Tälleklint L., Polfeldt T., 2000, *Impacts of climatic change on the Northern Latitude limit and population density of the disease-transmitting European tick Ixodes ricinus,* Environmental health perspectives, 108, 119-123.

Masters G., Norgrove L., 2010, *Climate change and invasive alien species,* CABI working paper, 1, 1-30.

Materna J., Danielk M., Danielová V., 2005, *Altitudinal distribution limit of the tick Ixodes ricinus shifted considerably towards higher altitudes in central Europe: results of*

three years monitoring in the Krkonoše mts. (Czech Republic), Central European journal of public health, 13, 24-28.

Meteorologisk institutt, 2017, *klima de siste 150 år*, read 30.04.18 at https://www.met.no/vaer-og-klima/klima-siste-150-ar/regionale-kurver.

Moon K.L., Banks S.C., Fraser C.I., 2015, *Phylogeographic structure in penguin ticks across an ocean basin indicates allopatric divergence and rare trans-oceanic dispersal,* Plos one, 10.

Muir G., Morris P., 2013, *How to identify mammals*, Finland, the mammal society.

Muñoz-Leal S., González-Acuña D., 2015, *The tick Ixodes uriae (Acari: Ixodidae): hosts, geographical distribution, and vector roles,* Ticks and tick-borne diseases, 6, 843-868.

Myllymäki A., Paasikallio A., Pankakoski E., Kanervo V., 1971, *Removal experiments on small quadrats as a means of rapid assessment of the abundance of small mammals,* Annales Zoologici Fennici, 8, 177-185.

Mysterud A., Byrkjeland R., Qviller L., Viljugrein H., 2015, *The generalist tick Ixodes ricinus and the specialist tick Ixodes trianguliceps on shrews and rodents in a northern forest ecosystem – a role of body size even among small hosts,* Parasites and vectors, 639.

Måren I.E., Karki S., Prajapati C., Yadav R.K., Shrestha B.B., 2015, *Facing north or south: does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley?,* Journal of arid environments, 121, 112-123.

Nuwer R., 2016, *How parasites became so popular*, Smithsonian, read 10.04.18 at https://www.smithsonianmag.com/science-nature/untangling-origins-parasites-180959842/.

Ogden N.H., Radojević M., Wu X., Duvvuri V.R., Leighton P.A., 2014, *Estimated effects of projected climate change on the basic reproductive number of the lyme disease vector Ixodes scapularis,* Environmental health perspective, 122, 631-638.

Oke, T.R., 1987, *Boundary layer climates,* 2nd ed. New york, Methuen and co.

Perez G., Bastian S., Agoulon A., Bouju A., Durand A., Faille F., Lebert I., Rantier Y., Plantard O., Butet A., 2016, *Effect of landscape features on the relationship between Ixodes ricinus ticks and their small mammal hosts,* Parasites and vectors, 20.

Quéré J.P., Louarn H.L., 2011, *Les rongeurs de France,* Guide pratique, France.

Qviller L., Grøva L., Viljugrein H., Klingen I., Mysterud A., 2014, *Temporal pattern of questing tick Ixodes ricinus density at differing elevations in the coastal region of western Norway,* Parasites and vectors, 179, 1-12.

Ragagli C., Mannelli A., Ambrogi C., Bisanzio D., Ceballos L.A., Grego E., Martello E., Selmi M., Tomassone L., 2016, *Precence of host-seeking Ixodes ricinus and their infection with Borrelia burgdorferi sensu lato in the Northern Apennines, Italy,* experimental and applied acarology, 69, 167-178.

Randolph S.E., 2014, Ecology of non-nidicolous ticks, In Sonenshine D.E., Roe R.M. (ed.), *Biology of ticks, vol 2, 2nd. edition*, 3-38, New york, Oxford university press.

Requena-García F., Cabrero-Sañudo F., Olmeda-García S., González J., Varcárcel F., 2017, *Influence of environmental temperature and humidity on questing ticks in Central Spain,* experimental and applied acarology, 71, 277-290.

Roth T., Plattner M., Amrhein V., 2014, *Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude,* Plos one, 9.

Schulz M., Mahling M., Pfister K., 2014, *Abundance and sasonal activity of questing Ixodes ricinus ticks in their natural habitats in southern Germany in 2011,* Journal of vector ecology, 39, 56-65.

Steinbauer M.J., Grytnes J-A., Jurasinski G., Kulonen A., Lenoir J., Pauli H., Rixen C., Winkler M., Bardy-Durchhalter M., Barni E., Bjorkman A.D., Breiner F.T., Burg S., Czortek P., Dawes M.A., Delimat A., Dullinger S., Erschbamer B., Felde V.A., Fernández-Arberas O., Fossheim K.F., Gómez-García D., Georges D., Grindrud E.T., Haider S., Haugum S.V., Henriksen H., Herreros M.J., Jaroszewicz B., Jaroszynska F., Kanka R., Kapfer J., Klanderud K., Kühn I., Lamprecht A., Matteodo M., di Cella U.M., Normand S., Odland A., Olsen S.L., Palacio S., Petey M., Piscová V., Sedlakova B., Steinbauer K., Stöckli V., Svenning J-C., Teppa G., Theurillat J-P., Vittoz P., Woodin S.J., Zimmermann N.E., Wipf S., 2018, *Accelerated increase in plant species richness on mountain summits is linked to warming,* Nature, 556, 231-234.

Tafani M., Cohas A., Bonenfant C., Gaillard J-M., Allainé D., 2013, *Decreasing litter size of marmots over time: a life history response to climate change?* Ecology, 94, 580-586.

Warren R.J., Chick L.D., DeMarco B., McMillan A., De Stefano V., Gibson R., Pinzone P., 2016, *Climate-driven range shift promps species replacement,* Insects sociaux, 63, 593-601.

Williams D.K., 2018, *Differences between north- and south-facing slopes, Sciencing read 30.04.18 at https://sciencing.com/differences-between-north-southfacing-slopes-8568075.html.*

Appendix

Appendix 1. Monthly change of minimum, maximum, and average temperature and of relative humidity in Lærdal.

Seasons	m.a.s.l.	Min T°C	Max T°C	Mean T°C	Median T°C	Min RH %	Max RH %	Mean RH %	Median RH%
June	100	12,2	16,6	11,6	11,4	61,1	84,4	80,2	79,4
June	200	11,4	18,1	11,7	11,6	58,1	85,7	81,8	85,6
June	300	11,1	17,0	11,0	10,9	59,1	85,3	81,4	82,7
June	400	10,1	20,7	11,7	10,9	49,5	85,4	77,5	83,1
June	500	9,3	16,1	8,9	8,8	59,4	85,6	83,9	86,7
June	600	10,0	16,9	10,0	9,5	56,4	85,6	80,8	85,3
June	700	7,8	17,6	8,7	8,2	49,5	85,1	77,0	79,9
June	800	NA	NA	NA	NA	NA	NA	NA	NA
June	900	NA	NA	NA	NA	NA	NA	NA	NA
June	1000	NA	NA	NA	NA	NA	NA	NA	NA
July	100	13,0	18,1	14,9	15,0	66,8	91,0	81,6	84,2
July	200	11,4	20,6	14,4	14,1	66,5	99,1	88,9	94,8
July	300	11,4	19,3	14,3	14,0	64,9	97,0	86,2	90,8
July	400	10,3	24,1	14,9	13,9	52,1	96,8	82,0	88,3
July	500	9,5	17,1	12,5	12,2	68,1	96,8	86,7	90,5
July	600	10,3	17,2	13,1	12,9	66,0	95,4	84,1	85,7
July	700	8,4	21,1	13,2	12,1	48,9	96,2	76,4	82,5
July	800	7,3	23,2	14,0	13,0	43,9	98,3	74,6	78,5
July	900	7,3	22,1	13,7	12,6	46,3	98,1	74,5	78,2
July	1000	8,3	17,8	12,3	11,3	57,8	92,7	76,6	79,7
Sept.	100	NA	NA	NA	NA	76,0	NA	NA	NA
Sept.	200	8,1	14,4	9,4	9,6	79,8	99,9	99,2	100,0
Sept.	300	7,8	13,6	9,1	9,2	76,5	99,1	97,5	99,0
Sept.	400	6,6	16,4	8,6	8,5	68,4	99,7	97,8	100,0
Sept.	500	5,9	11,9	7,2	7,3	82,6	99,2	98,6	100,0
Sept.	600	6,6	11,6	7,8	7,9	79,7	99,2	98,2	99,9
Sept.	700	4,6	14,1	6,7	6,7	65,7	99,1	95,0	98,0
Sept.	800	3,2	16,0	6,5	6,2	60,2	99,8	94,6	99,0
Sept.	900	3,6	13,5	6,1	5,9	64,3	99,0	92,5	94,2
Sept.	1000	4,0	9,9	5,2	5,4	76,9	98,1	95,2	96,0

Appendix 2. Monthly minimum, maximum, mean and median temperature and of relative humidity in Bø.

Month	m.a.s.l.	Min T°C	Max T °C	Mean T °C	Median T °C	Min RH %	Max RH %	Mean RH %	Median RH %
jun	100	8,3	19,3	11,4	10,9	56,6	98,7	89,8	99,9
jun	200	7,3	22,5	12,1	9,4	48,6	98,7	86,0	87,5
jun	300	9,4	18,1	11,0	10,6	55,6	91,4	86,9	97,9
jun	400	7,4	17,8	9,9	9,7	59,9	97,4	90,9	100,0
jun	500	8,5	15,4	9,2	9,0	63,9	93,6	90,1	100,0
jun	600	7,3	16,1	8,7	8,5	59,3	93,3	90,1	100,0
jun	700	6,3	14,8	8,1	8,2	65,0	96,3	91,2	100,0
jun	800	NA	NA	NA	NA	NA	NA	NA	NA
jun	900	NA	NA	NA	NA	NA	NA	NA	NA
jun	1000	NA	NA	NA	NA	NA	NA	NA	NA
jul	100	11,6	19,5	15,1	14,5	63,5	99,9	86,6	93,1
jul	200	11,0	22,5	16,3	15,4	54,8	99,6	79,9	87,6
jul	300	12,1	22,8	15,2	14,9	64,1	94,9	80,4	83,2
jul	400	10,8	18,3	13,9	13,4	74,2	98,8	88,1	93,7
jul	500	11,4	15,7	13,4	12,8	73,0	95,4	85,1	89,5
jul	600	10,4	16,0	12,9	12,3	70,6	96,5	85,0	90,7
jul	700	9,1	14,7	12,1	11,9	75,7	99,1	88,5	94,7
jul	800	7,9	24,9	14,6	11,9	46,4	99,1	77,2	87,4
jul	900	7,0	22,7	13,6	11,1	46,3	99,9	77,5	87,9
jul	1000	7,4	20,4	13,2	10,8	51,7	98,4	77,8	84,9
sept.	100	8,5	13,6	10,6	10,4	87,6	100,0	98,9	100,0
sept.	200	8,1	15,0	10,8	11,1	77,5	99,5	94,0	94,6
sept.	300	9,0	12,8	10,6	10,8	81,5	98,3	91,1	90,8
sept.	400	7,7	12,0	9,5	9,7	86,9	99,9	96,3	97,6
sept.	500	8,0	10,6	8,8	9,2	91,4	99,9	98,3	100,0
sept.	600	7,0	10,6	8,0	8,3	90,8	99,7	98,8	100,0
sept.	700	6,0	9,4	7,4	7,6	95,0	100,0	99,5	100,0
sept.	800	5,0	14,0	7,1	7,1	22,0	86,7	39,1	NA
sept.	900	4,8	15,1	8,6	6,5	67,9	98,4	90,5	100,0
sept.	1000	4,6	12,2	8,7	6,2	88,8	98,7	90,4	100,0