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1 **Ecological correlates of a tick-borne disease, *Anaplasma phagocytophilum*,**
2 **in moose in southern Norway.**

3
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16

Abstract

17 As the distribution and abundance of ticks increase, so do the risks of tick-borne diseases.
18 *Anaplasma phagocytophilum*, transmitted by *Ixodes* spp. ticks, is a widespread tick-borne
19 infection causing tick-borne fever (TBF) in domestic ruminants and human granulocytic
20 anaplasmosis. However, the role of wildlife in its epidemiology is poorly understood.
21 Evidence of infection has been detected in wild cervids but the pathogenicity and ecological
22 consequences are unknown. We conducted a serological study of moose (*Alces alces*) in two
23 populations in southern Norway, one where TBF was endemic (Telemark) and the other
24 where sheep ticks (*Ixodes ricinus*) were essentially absent (Hedmark). Seroprevalence to *A.*
25 *phagocytophilum* antibodies was 79% and 0% respectively. In Telemark, seroprevalence was
26 significantly higher among females that calved successfully (85%) than among others (50%).
27 Body mass and winter mass change were unrelated to serostatus. Relative abundance of
28 questing ticks in Telemark was highest in deciduous forest and lowest in mature coniferous
29 forest, and higher at easterly aspects and altitudes below 350 m. Habitat factors associated
30 with high tick abundance were risk factors for seropositivity among moose. Our findings
31 were consistent with anaplasmosis causing a persistent sub-clinical infection in moose
32 without population-level effects. Further work is needed to establish the importance of moose
33 as a reservoir for the disease in sympatric domestic livestock.

34

Keywords

36 *Alces alces*; climate change; deer; ehrlichiosis; wildlife disease

37

38 Introduction

39 Ixodid ticks, the primary arthropod vectors of zoonotic diseases in Europe, are
40 increasing in abundance and distribution, due partly to climate change (Scharlemann et al.
41 2008; Jaenson and Lindgren 2011; Jore et al. 2011) and an increasing abundance of wild
42 hosts (Scharlemann et al. 2008; Gilbert 2010). Consequently the risks of tick-borne diseases
43 are also rising (Gray et al. 2009). The rickettsial parasite *Anaplasma phagocytophilum*
44 (formerly known as *Ehrlichia phagocytophila*) is one of the most widespread tick-borne
45 infections in Europe (Stuen 2007). It is transmitted by *Ixodes* spp. ticks with clinical
46 manifestations in domestic ruminants (tick-borne fever; TBF), companion animals and
47 cervids, while in humans it can cause human granulocytic anaplasmosis (HGA), an emerging
48 tick-borne disease (Robinson et al. 2009). Symptoms in cattle and sheep include high fever,
49 loss of appetite, abortion, reduced milk production and, particularly, immunosuppression
50 leading to secondary infections (Alberdi et al. 2000; Stuen 2007; Woldehiwet 2008). As a
51 result, *A. phagocytophilum* affects livestock productivity globally (Lempereur et al. 2011)
52 and it is the tick-borne disease agent causing the greatest economic losses in sheep farming in
53 Norway (Grøva et al. 2011). Anaplasmosis is therefore a disease of socio-economic
54 importance with implications for public health.

55 The role of wildlife species in the epidemiology of anaplasmosis is not well understood
56 (Robinson et al. 2009), although small mammals and cervids are likely to be important
57 natural reservoirs (Alberdi et al. 2000; Bown et al. 2003). Evidence of infection with *A.*
58 *phagocytophilum* has been found in many wild ungulates, including moose, across Europe
59 and North America (Magnarelli et al. 1999; Alberdi et al. 2000; Liz et al. 2002; Stuen et al.
60 2006; Stefanidesova et al. 2008; Robinson et al. 2009). However, little is known of the
61 pathogenesis of *A. phagocytophilum* in wild ungulates (Alberdi et al. 2000), with no clinical

62 signs being observed in wild fallow, red or roe deer in the UK despite antibodies being
63 detected (Stuen 1996). Nonetheless, anaplasmosis was implicated in the death of a moose calf
64 (Jenkins et al. 2001) and the paretic condition of an *A. phagocytophilum* infected roe deer calf
65 (Stuen et al. 2006) in southern Norway. Pathogenicity differs between ungulate species, with
66 a severe clinical reaction observed in experimentally infected reindeer (*Rangifer tarandus*;
67 Stuen 1996) but a persistent subclinical infection observed in red deer (Stuen et al. 2001b).
68 Furthermore, pathogenicity and clinical manifestation may vary with genetic variant of *A.*
69 *phagocytophilum* (Stuen et al. 2006; Robinson et al. 2009).

70 Parasite infections in wildlife often have subclinical effects (Gunn and Irvine 2003) but
71 can nevertheless impact host population dynamics if reproductive success is affected (Albon
72 et al. 2002). However, no ecological studies of wild ungulates in relation to *A.*
73 *phagocytophilum* have been carried out. Our objective was therefore to investigate the
74 relationships between anaplasmosis serostatus and ecological factors, including reproductive
75 success, in 2 populations of moose in southern Norway. One was in the coastal zone
76 (Telemark County), where TBF is endemic in domestic ruminants (Stuen et al. 2006) and
77 moose calving rates have been declining over recent decades (Grøtan et al. 2009). We
78 expected moose here to be exposed to anaplasmosis. The other study area, in Hedmark
79 County, has low sheep tick (*Ixodes ricinus*) abundance (Jore et al. 2011) and we expected
80 moose not to be exposed to anaplasmosis. As symptoms of TBF include loss of appetite and
81 abortion, we were particularly interested in the relationships with body mass and reproductive
82 success, two key factors in ungulate population dynamics (Gaillard et al. 2000). In addition,
83 we described the relative distribution of questing ticks in relation to habitat characteristics
84 and topography. Lastly we related the probability of a moose being seropositive to its use of
85 tick habitat.

86

87 **Methods**

88 Study areas

89 Our study areas were located in Siljan and Skien municipalities, Telemark County,
90 southern Norway, (59°21' N, 9°38' E) and in Stor-Elvdal municipality, Hedmark County,
91 south-eastern Norway (61°24' N, 11°7' E; Fig. 1a). Altitude ranged from 20 to 800 m in the
92 Telemark study area and from 250 to 1100 m in the Hedmark study area. In both areas
93 commercially managed coniferous forest, dominated by Norway spruce (*Picea abies*) and
94 Scots pine (*Pinus sylvestris*), was the main vegetation type, interspersed with deciduous
95 stands of birch (*Betula pubescens* Ehrh. and *B. pendula* Roth.), rowan (*Sorbus aucuparia* L.),
96 willow (*Salix* spp.) and aspen (*Populus tremula* L.). Deciduous stands were most abundant in
97 Telemark, but sub-alpine birch woodland occurred above the commercial forest line in both
98 areas. The climate was colder in the more continental Hedmark area. Average monthly
99 January and July temperatures were -2.9 °C and 17.1 °C respectively in Telemark and -8.2 °C
100 and 15.7 °C in Hedmark. Snow cover lasted from December to April in Hedmark and a
101 somewhat shorter period in Telemark.

102 Both moose populations were partially migratory with current wintering densities of
103 approximately 1.3 individuals km⁻² (Milner et al. 2012). Red and roe deer occurred in both
104 areas at low densities. At the county level, more than twice as many sheep grazed free-range
105 in summer in Hedmark as in Telemark (Norwegian Agricultural Authority 2012).

106

107 Tick sampling

108 We measured the abundance of questing exophilic ticks in mid-August 2008 in the
109 Telemark study area but not in the Hedmark area where sheep ticks were not encountered
110 during fieldwork or reported by hunters. Based on previous flagging studies in southern

111 Norway (Jore et al. 2011 suppl. mat.), all questing ticks were assumed to be sheep ticks.
112 Using standard methods (Hillyard 1996), a 1 m² piece of white blanket was dragged slowly
113 over the vegetation along 2 parallel 100 m transects spaced 50 m apart. Ticks were counted
114 and removed from the blanket every 10 m. As only nymphs and adults can transmit
115 anaplasmosis (Walker et al. 2001), we excluded larvae from the data presented here. Tick
116 sampling gave an index of active questing ticks, sufficient for relative abundances of ticks
117 between habitats (c.f. Gilbert 2010). Ticks were surveyed in 129 forest stands of differing
118 dominant tree species (pine, spruce or deciduous), age, altitude and aspect, with sampling
119 randomised with respect to time of day.

120

121 Moose sampling

122 Adult female moose accompanied by a calf were immobilised from a helicopter and
123 weighed in a net below the helicopter (Milner et al. 2013). Serum samples were collected
124 from the adults during initial capture and Global Positioning System (GPS) collaring in
125 Telemark in early January 2007 ($n=18$) and 2008 ($n=15$) and in Hedmark in January ($n=19$)
126 and March 2010 ($n=2$). Pregnancy status was determined from serum progesterone levels
127 (Milner et al. 2013). Thirty seven moose were recaptured, reweighed and pregnancy status
128 reassessed in late March of the same year. Spring calving success was monitored by
129 approaching marked females on foot in early June to determine the presence of any new-born
130 calves. Many of the marked moose were harvested between September and December as part
131 of the annual hunting quota, allowing ageing by counting annuli in the cementum of incisor
132 root tips (Rolandsen et al. 2008). Mean age at marking in Telemark was 7.5 years, (range 2.5
133 - 14.5 years; $n=25$) and 8.5 years in Hedmark (range 3.5 – 15.5 years; $n=11$).

134 Serum samples were analysed for antibodies to *A. phagocytophilum* by an indirect
135 immunofluorescence antibody assay (IFA) to a horse strain of *A. phagocytophilum* (Stuen et

136 al. 2002) at the Swedish Veterinary Institute, Uppsala. Sera were screened for antibodies at a
137 dilution of 1:40. A titre of 1.6 (\log_{10} reciprocal of 1:40) was regarded as positive (Stuen et al.
138 2002). If positive, the serum was further diluted and retested sequentially to a titre of 1:640.
139 Our expectation was that samples from Hedmark would act as uninfected ‘controls’.

140

141 Spatial analysis

142 Focusing on Telemark, where ticks occurred, collar failure reduced the sample size for
143 spatial analyses to 29 individuals. GPS data were screened for bias (see van Beest et al. 2011
144 for details, including collar fix success and location accuracy) and individuals were classified
145 as migratory ($n=16$) or resident ($n=13$), based on the net displacement distance between the
146 first and subsequent locations (van Beest et al. 2011). Using digital forest stand maps with a
147 resolution of 50 m x 50 m, we determined the forest type at each GPS location used, in terms
148 of dominant tree species and stand age, and recorded the altitude and aspect. We restricted
149 our analyses of habitat use to the period from April to October inclusive, when average
150 monthly mean temperature in Telemark was >5 °C (Norwegian Meteorological Institute data)
151 and ticks were expected to be active (Jaenson and Lindgren 2011). We defined habitat use in
152 terms of the proportion of time each moose spent in each forest type from April to October.
153 We also determined the proportion of time spent at each aspect and in relation to altitude. As
154 serum samples were collected at initial collaring, GPS data were only available for the period
155 after sampling. Therefore, in our interpretation of serostatus in relation to habitat use we
156 made the assumption that an individual’s habitat use patterns were consistent across years.

157

158 Statistical analysis

159 We modelled factors affecting the abundance of questing ticks using a Poisson GLM.
160 As there were many zeros and over-dispersion occurred, we corrected the standard errors
161 using a quasi-GLM model in which the variance was the product of the mean and dispersion
162 parameter (Zuur et al. 2009). Significance was assessed with the *F*-test statistic (Zuur et al.
163 2009). Potential explanatory terms were altitude, aspect and forest type. Aspect was defined
164 by the four cardinal directions but subsequently some classes were grouped. We initially
165 defined forest type in terms of dominant tree species and stand age but a simplification to
166 four types, namely young deciduous forest (< approximately 60 years), mature deciduous
167 forest (>60 years), young coniferous forest (<40 years) and mature coniferous forest (>40
168 years), provided the most parsimonious grouping.

169 To examine the relationship between serostatus and the individual covariates age,
170 body mass at sampling, relative over-winter mass change [$\log(\text{March mass}/ \text{January mass})$]
171 and reproductive status in the Telemark population, we grouped individuals into two
172 (seronegative vs. seropositive) and three (seronegative [antibody titre <1:40], seropositive-
173 low [titre 1:40 - 1:160] or seropositive-high [titre \geq 1:640]) serological classes. Serostatus was
174 fitted as the explanatory variable in univariate regression models.

175 We used multiple logistic regression to establish which factors influenced the
176 binomially distributed serostatus (0 seronegative; 1 seropositive) in the Telemark population.
177 Explanatory variables were the significant individual covariates identified above and
178 migration strategy, together with an individual's use of tick habitat in terms of forest type,
179 aspect and altitude. For some variables, low discriminatory power and the limited sample size
180 of seronegative individuals led to non-convergence in multivariate models so their potential
181 importance could only be assessed by univariate models. Furthermore, collinearity between
182 use of mature coniferous forest and use of young coniferous forest was high so we used the
183 one with the greatest explanatory power.

184

185 **Results**

186 Tick abundance

187 The abundance of questing nymph and adult ticks sampled in mid-August in the
188 Telemark study area ranged from 0-18.5 per 100 m², with a median of 0.5 per 100 m².
189 Nymphs were on average 1.3 times more numerous than adults. We found a marked negative
190 effect of altitude such that few ticks were found above 350 m (maximum altitude 619 m),
191 regardless of forest type (Fig. 2, Table 1). Tick abundance was higher in deciduous than
192 coniferous forest, particularly in mature forest, although an interaction with altitude
193 suggested that tick numbers would be highest in young coniferous forests at the lowest
194 altitudes (Fig. 2). East-facing slopes had significantly higher tick numbers than other aspects
195 (Table 1; Fig. 2). Our best fitting model explained 59.3% of the deviance in tick abundance.

196

197 *Anaplasma* prevalence and moose reproductive success

198 Seroprevalence to *A. phagocytophilum* infection was 78.8% in Telemark ($n=33$) and
199 0% in Hedmark ($n=21$). In Telemark, over half of the females sampled and 73% of those that
200 were seropositive had an antibody titre $\geq 1:640$ (Fig. 1).

201 Within females from Telemark, seroprevalence tended to be higher among pregnant
202 than non-pregnant females (0.85 vs. 0.50; $\chi^2=3.136$, $P=0.076$; Fig. 1e and Fig. 3) and was
203 significantly higher among females that successfully calved in spring than those that did not
204 (0.93 vs. 0.62; $\chi^2=4.076$, $P=0.044$; Fig. 1f and Fig. 3). Of 6 seronegative females, 3 were not
205 pregnant and only 1 calved successfully compared with 2 non-pregnant and 11 successfully
206 calving out of 20 seropositive females. We found that pregnant females experiencing prenatal

207 or perinatal losses were no more likely to be seropositive or have a high antibody titre
208 (seropositive-high) than females in other reproductive classes (Fig. 3).

209 There were no significant differences in either January body mass or relative over-
210 winter mass change between seronegative, seropositive-low and seropositive-high individuals
211 (Fig. 1b-c). Among pregnant females, there was a significant interaction between serostatus
212 and relative over-winter mass change ($\chi^2=4.873$, $P=0.028$). The probability of successful
213 calving was positively related to winter mass change in seropositive females but negatively
214 related to winter mass change in our small sample of seronegative females. While age did not
215 differ between serological classes (Fig. 1d), pregnant females with a high antibody titre were
216 significantly older than other pregnant females ($\chi^2=4.385$, $P=0.036$).

217

218 Factors affecting seropositivity

219 Use of habitats associated with high tick abundance was a risk factor for anaplasmosis
220 seropositivity among moose. Use of mature deciduous forest was positively associated with
221 seropositivity ($\chi^2=8.969$, $P=0.003$) despite overall low usage. Five out of 6 seronegative
222 individuals did not use mature deciduous forest at all and the sixth individual spent 0.02% of
223 its time in this habitat, while median use among seropositive individuals was 0.25%. Fitting
224 problems prevented the inclusion of mature deciduous forest in our multivariate model.

225 The probability of seropositivity decreased significantly with the proportion of time
226 an individual spent above 350 m altitude ($\chi^2=3.849$, $P=0.050$). This relationship was more
227 pronounced when comparing females with a high titre against other females ($\chi^2=5.945$,
228 $P=0.015$). However there was relatively little individual variation in altitude use, with all but
229 3 individuals (all of which were seropositive-high) spending over 80% of their time between

230 April and October above 350 m. Neither mean altitude used nor migration strategy had
231 significant explanatory power.

232 Reproductive status was a strong predictor of seropositivity and, in our multivariate
233 model, pregnancy status was the term with the greatest explanatory power ($\chi^2=19.45$,
234 $P<0.001$). Pregnant females, and particularly those that calved successfully, had a tendency to
235 use areas below 350 m more than non-pregnant females. We found a significant negative
236 effect of use of mature coniferous forest ($\chi^2=7.991$, $P=0.005$; Fig. 4), the least preferred tick
237 habitat, on seropositivity while the proportion of time spent on east-facing slopes
238 significantly increased the probability ($\chi^2=4.527$, $P=0.033$; Fig. 4). Proportional use of east-
239 facing slopes ranged from 0.05 to 0.72, with medians of 0.14 and 0.28 among seronegative
240 and seropositive females respectively. Together these terms explained 81.9% of the deviance
241 in seropositivity.

242

243 Discussion

244 We found a high seroprevalence to *A. phagocytophilum* infection in moose from our
245 southern study site in Telemark but no exposure in the inland study area in Hedmark where
246 sheep tick abundance is currently low (Jore et al. 2011). A comparably high seroprevalence
247 has previously been reported for moose in Telemark, being higher and with a higher end titre
248 to *A. phagocytophilum* than in moose tested from 3 other counties in Norway (Stuen et al.
249 2002). The prevalence in Telemark moose was also high compared with other wild cervids
250 elsewhere in Europe (Alberdi et al. 2000; Liz et al. 2002; Robinson et al. 2009; Veronesi et
251 al. 2010; Stefanidesova et al. 2008).

252 Although TBF in domestic ruminants may cause abortion (Woldehiwet 2008), we
253 found no evidence to suggest that reproductive losses in Telemark moose were associated
254 with the presence of antibodies to *A. phagocytophilum*. Poor autumn recruitment, a feature of
255 our Telemark population, was primarily due to pregnancy failure during mid- to late gestation
256 rather than summer calf mortality (Milner et al. 2013). It therefore seemed unlikely that
257 anaplasmosis was a contributing factor to the declining calving rates observed in Telemark
258 (Grøtan et al. 2009). Early winter body mass and over-winter mass change were unrelated to
259 serostatus. The higher body mass and lower over-winter mass change observed in Hedmark
260 than Telemark reflected large-scale geographic variation in moose body mass across Norway
261 (Herfindal et al. 2006) and poorer winter foraging conditions in Telemark (van Beest et al.
262 2010; Milner et al. 2013). High titre moose tended to be older than other moose, which was
263 consistent with a higher probability of seropositivity among older sheep (Ogden et al. 2002).

264 While we have shown that moose in our Telemark study area had a high exposure to
265 anaplasmosis and mounted an immune response to it, a limitation of our study is that we did
266 not know whether animals were clinically infected. Given the high prevalence and tick
267 abundance, it seems likely that moose in Telemark faced repeated tick-borne challenges. In
268 sheep, resistance to experimental re-infection increased with increasing frequency of
269 challenge, but under natural conditions sheep nonetheless showed persistent partial
270 susceptibility to re-infection (Ogden et al. 2002). However, the effects of re-infections are
271 typically less severe than the primary reaction (Stuen et al. 2011). The high *A.*
272 *phagocytophilum* antibody titre in many of our sampled moose 2-3 months after the end of
273 the tick season, together with the higher seroprevalence among pregnant than non-pregnant
274 females and an absence of effects on body mass, were consistent with persistent subclinical
275 infection, possibly due to re-infection. As conception occurs close to the end of the season of
276 tick activity, the higher seroprevalence among pregnant females was probably not due to a

277 higher probability of infection. Instead suppressed immunity during pregnancy likely meant
278 that pregnant females experienced a more persistent infection or a recurrence of a latent
279 infection. Latency and persistence are features of *A. phagocytophilum* infection due to its
280 ability to infect white blood cells and survive within apparently immune hosts (Woldehiwet
281 2008). The time seropositive moose take to revert to seronegativity is unknown. In domestic
282 livestock, antibodies to *A. phagocytophilum* generally wane rapidly in cattle, although about a
283 quarter of individuals can remain positive throughout winter (Lempereur et al. 2011).
284 Similarly, TBF can persist from one grazing season to the next in sheep housed indoors over
285 winter (Stuen et al. 2001a).

286 Despite our small sample size of seronegative individuals, we found strong evidence to
287 suggest that seropositivity was related to the use of preferred tick habitats by moose, if our
288 assumption of consistency in habitat use between years was valid. This has not been well
289 studied although Cederlund & Okarma (1988) stated that adult female moose showed strong
290 fidelity to established home ranges and habitat use was consistent among seasons. Summer
291 habitat use was also highly correlated between years for 3 moose in the Hedmark study area,
292 each with 2 consecutive years of GPS data ($r > 0.97$; B. Zimmermann unpubl. data). As
293 found in Sweden (Lindström and Jaenson 2003; Jaenson and Lindgren 2011), tick abundance
294 was highest in deciduous forest in our study. Consequently use of mature deciduous forest by
295 moose was a risk factor for seropositivity. In addition, we found marked effects of altitude
296 and aspect both on tick distribution and seropositivity which are likely to be related to the
297 microclimatic requirements of ticks (Gray et al. 2009). The relationship between altitude and
298 tick abundance is well known (Gilbert 2010). Evidence suggests that the altitudinal limit has
299 been increasing in recent years in Norway (Jore et al. 2011) and elsewhere (Daniel et al.
300 2003). In 1983, the altitudinal limit of ticks in the region of our Telemark study was believed
301 to be 150 m above sea-level (Mehl 1983), while we found ticks were abundant up to about

302 350 m and occasionally found up to 620 m. Assuming that the latitudinal and altitudinal
303 expansion of the tick range observed in Norway (Jore et al. 2011) continues, in parallel with a
304 warmer climate and longer vegetation season (Jaenson and Lindgren 2011), ticks and tick-
305 borne diseases can be expected to move into the Hedmark study area and many other parts of
306 Scandinavia in the near future.

307 A high abundance of potential hosts is an important factor both for tick expansion
308 (Scharlemann et al. 2008; Gilbert 2010) and, potentially, the spread of anaplasmosis (Alberdi
309 et al. 2000; Rosef et al. 2009). Small mammals can be important reservoirs of anaplasmosis
310 in some systems (Bown et al. 2003) although rodents are thought to play only a minor role in
311 its epidemiology in the parts of Norway where this has been investigated (Rosef et al. 2009).
312 The highest prevalence of *A. phagocytophilum* in questing ticks in Norway occurred in
313 locations with the highest cervid densities (Rosef et al. 2009). As wild cervids have increased
314 dramatically in range and abundance over recent decades and occur sympatrically with free-
315 ranging domestic livestock throughout the summer months in Norway (Mysterud 2000), there
316 is considerable scope for intraspecific disease transmission if, as suspected, cervids are
317 competent reservoirs of *A. phagocytophilum* (Alberdi et al. 2000; Liz et al. 2002;
318 Stefanidesova et al. 2008; Rosef et al. 2009). In our small sample, we found no clear evidence
319 to suggest population-level effects of anaplasmosis on moose in southern Norway. However,
320 the high seroprevalence we found in Telemark warrants further investigation of the
321 competence of moose as a reservoir of infection for domestic livestock and the strains of *A.*
322 *phagocytophilum* involved. As climate change and the expansion of the tick range continue,
323 there is a need for more detailed research across wild ruminants, and within species over a
324 wider geographical area. This would increase our understanding of the risk factors associated
325 with the transmission of anaplasmosis between wildlife and domestic livestock and improve
326 our ability to manage this widespread tick-borne disease.

327

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338

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Table 1 Significant factors affecting abundance of *Ixodes ricinus* ticks within the Telemark study area, determined by a Poisson GLM, adjusting for overdispersion with a dispersion parameter of 2.921. Significance was assessed by change in deviance when fitted last, or immediately prior to the interaction term, using the *F*-test statistic

	df	Δ Deviance	<i>F</i>	<i>P</i>
Altitude	1	88.04	60.26	<0.001
Forest type	3	57.06	13.02	<0.001
Aspect	1	18.01	12.32	<0.001
Altitude:forest	3	15.48	3.532	0.017
Residual	120	170.4		
Null	128	418.9		

Figure Captions

Fig. 1 Titre to *A. phagocytophilum* antibodies in adult female moose in relation to ecological parameters (mean \pm se) in two study areas in southern Norway. Sample sizes are given at the bottom of bars

Fig. 2 Density of ticks (number of adults + nymphs 100 m^{-2}) in relation to altitude (m above sea level) and forest type (young coniferous, mature coniferous, young deciduous or mature deciduous) for a) slopes with an easterly aspect and b) all other aspects within the Telemark study area, August 2008. Points show observed data and lines show predictions from the Poisson GLM given in Table 1

Fig. 3 The proportion of seropositive adult female moose in Telemark in relation to their reproductive status (Not pregnant; pregnant but pre- or peri-natal mortality; successful calving). Sample sizes are given at the bottom of each bar

Fig. 4 The probability of being seropositive to antibodies to *A. phagocytophilum* in relation to pregnancy status and a) the use of mature coniferous forest and b) the use of east-facing slopes in adult female moose in the Telemark study area. Points show observed data and lines show predictions from the best-fitting logistic regression model

Fig. 1

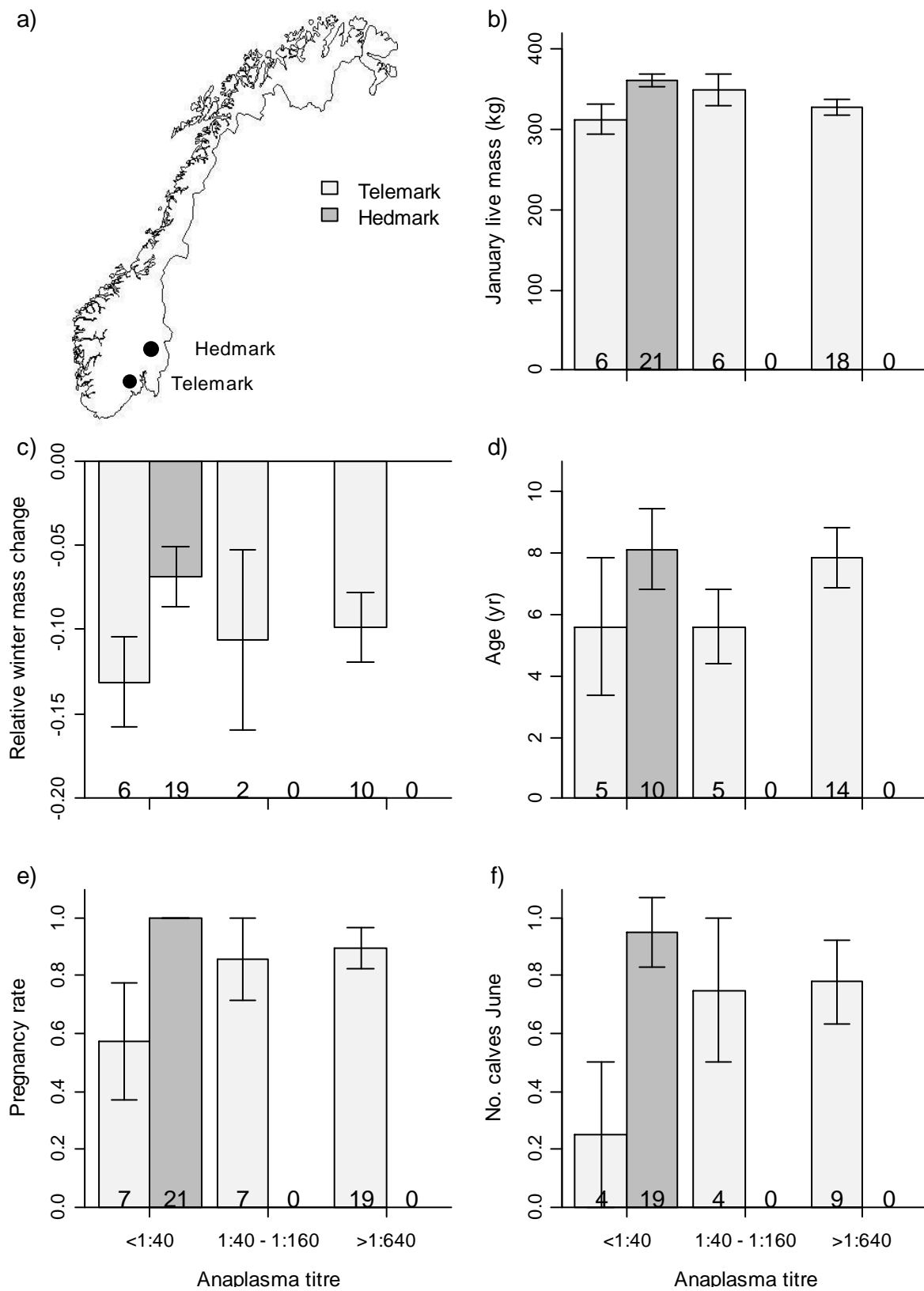


Fig. 2

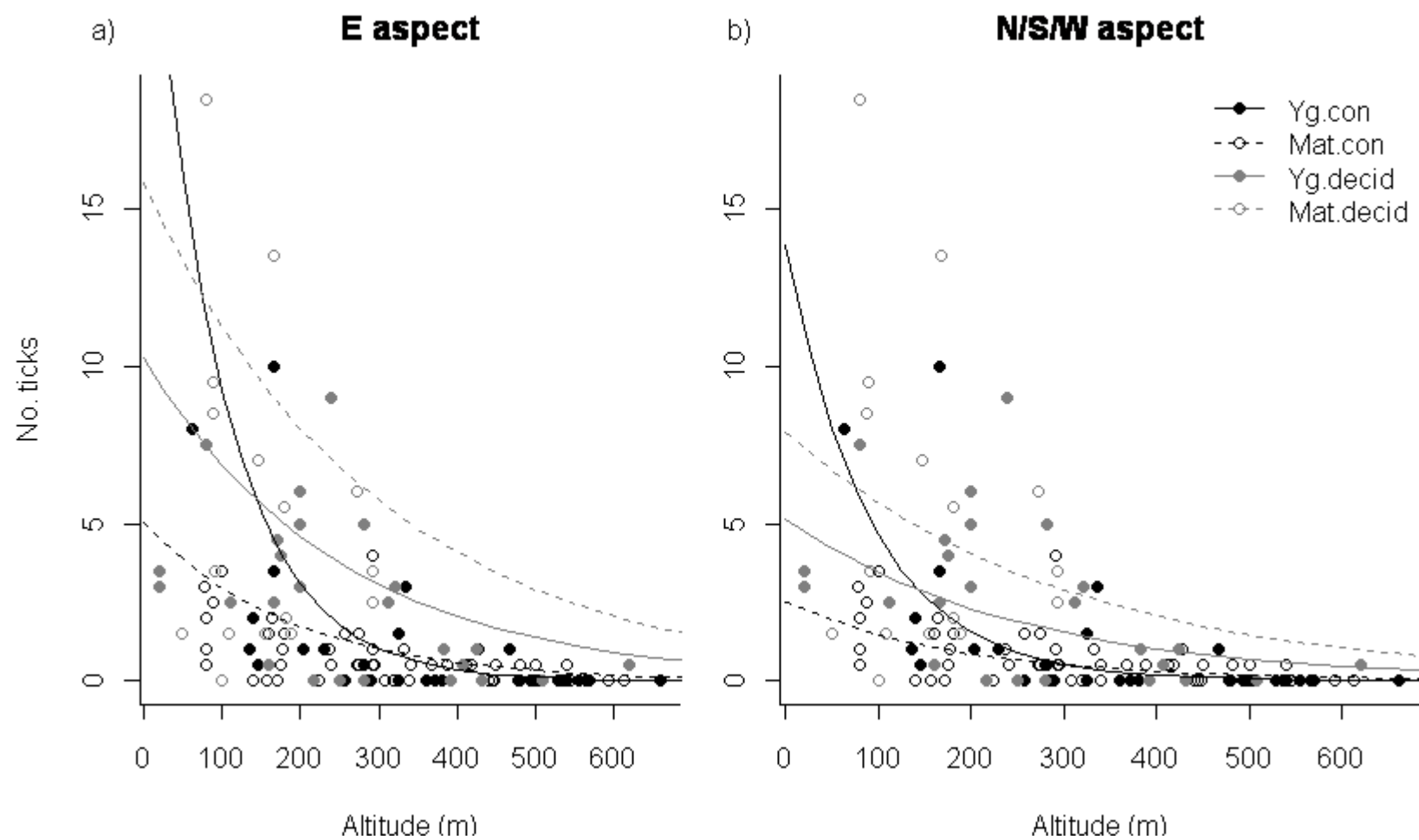


Fig. 3

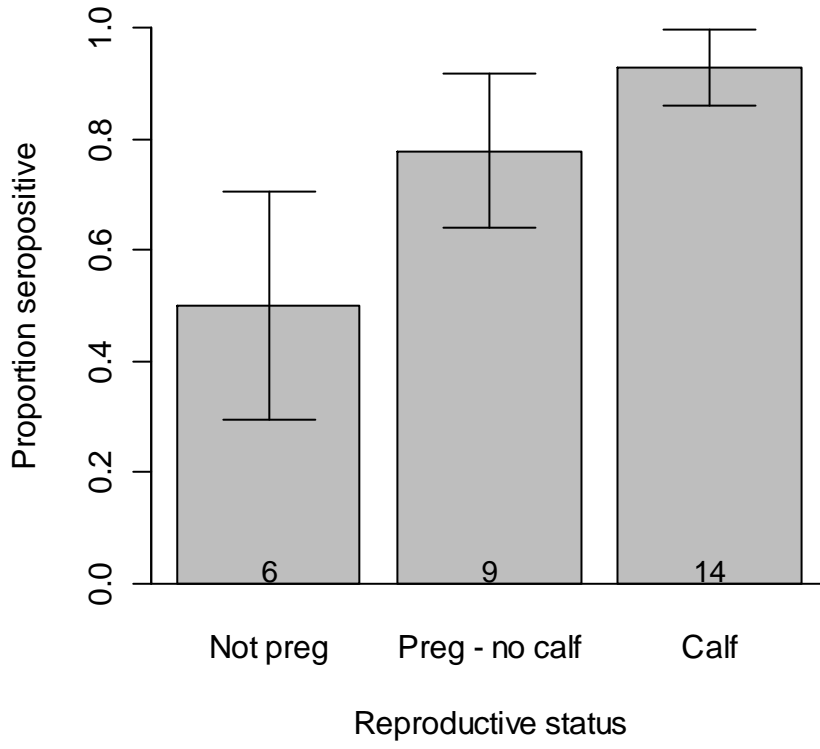


Fig. 4

