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Wolf predation risk and moose movement in eastern Finland

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Grey wolf *Canis lupus* is often the main predator of moose *Alces alces*. Therefore it can be expected that moose are able to recognize the presence of wolves and react to them to avoid predation. We examined the effect of predation risk by wolves on movement patterns by moose in eastern Finland where moose and wolves have co-existed for centuries. The level of wolf predation risk experienced by 20 radio-collared adult moose was classified according to the proportion of their fixes in wolf territories. Our results suggest that moose adjust their movement speed according to the degree they are exposed to the presence of wolves. The adjustment occurred in summer but not in winter. In summer the moose more exposed to wolves moved faster than the moose less exposed to wolves. Season and the structure of the surrounding forests also affected moose movement patterns. Both movement speed and the linearity of movement decreased in winter and with increasing canopy cover. We suggest that by increased moving when exposed to higher risk of predation moose try to keep distance to the predator and/or try to keep themselves spatially and temporally unpredictable to their predator. Our results differ from those obtained in Scandinavia where no response of moose movement to predation risk by wolves has been detected. It might be that wolves' continuous presence in eastern Finland compared to Scandinavia provide a reason why moose in our study area reacted to the presence of wolves.

Keywords: moose, movement, predation risk, wolf

Prey animals often respond to the presence of their predators or cues indicating their presence such that the risk to become killed will be decreased. These responses include e.g. seeking for safer habitats, increased vigilance and increased or decreased mobility (Lima and Dill 1990, Laundre et al. 2001, Pusenius and Ostfeld 2002, Latombe et al. 2014). The antipredator behaviors may impose tradeoffs for the prey animals such as forcing prey to forage in safer but possibly nutritionally lower quality habitats and decreasing the time spent foraging. As a consequence the energy intake and condition of the prey animals may decrease (Ditmer et al. 2018). When affecting the amount and distribution of plant consumption, the behavioral modifications of foraging prey may have effects also on community level i.e. causing behavioral trophic cascades (Ripple and Beschta 2004, 2012).

Grey wolf *Canis lupus* is often the main predator of moose *Alces alces* (Gervasi et al. 2012, Jonzen et al. 2013). Therefore moose are likely capable of recognizing the presence of wolves and reacting to them to avoid predation. Studies from North America have indicated that moose show different antipredator behaviors in the presence of wolves. Antipredator behaviors include e.g. increased use of safer habitats, increased vigilance, aggression toward wolves and increased mobility (Edwards 1983, Stephens and Peterson 1984, Berger 1999, White and Berger 2001, Mech and Peterson 2003, Ditmer et al. 2018). However, several studies from Scandinavia have failed to show any behavioral responses of moose to the presence of wolves (Sand et al. 2006, Eriksen et al. 2011, Gervasi et al. 2013, Nicholson et al. 2014, Wikenros et al. 2016). It has been suggested that because wolf has been long absent from Scandinavia and meanwhile moose hunting by humans has been the main mortality factor of moose, the antipredator behavior towards wolves by moose has become weak or absent (Sand et al. 2006, Wikenros et al. 2016). On the other hand, many of the findings of moose antipredator behavior in North America are from protected areas where human influence on moose mortality has been absent (Wikenros et al. 2016).

In the present study we examine the effect of predation risk by wolves on moose mobility and movement pattern in eastern Finland where moose and wolves have continuously coexisted for centuries, possibly over most of the post glacial era i.e. thousands of years (Ukkonen 1993). Therefore, even

if the human impact on moose mortality is strong in this area, the moose have regularly encountered wolves and similar loss of antipredator behavior towards them than in Scandinavia may not have occurred. We hypothesize that moose change their mobility and type of movements with increasing proximity to wolves. Specifically we examined whether movement speed and linearity among moose is related to the degree of seasonal home range overlap with wolves. We also hypothesize that females with calves have especially strong tendency to react to the risk of wolf predation as wolves depredate mainly calf moose (Kojola 2000). Therefore we separately analyzed the effect of predation risk on the movement behavior of all adult moose and the females with calves. Our hypothesis concerning moose mobility is two way: the moose could increase their rate of movement to escape predators or decrease the time spent in risky situations. On the other hand moose could decrease their movements to avoid to be detected. The hypothesis concerning the type of movement is one-way: increased linearity of movement might indicate avoidance of predators whereas winding movements might be more related to foraging behavior and less to predator avoidance (Fryxell et al. 2008, Wikenros et al. 2016). The movements of moose are likely affected by several other factors besides predation risk. Season affects movements as snow constraints them in the winter (Melin et al. unpubl.). The density of vegetation likely affects the potential speed of the movements. Therefore we included the effect of season into our analysis of movement and controlled also for the density of vegetation surrounding the moose.

Material and methods

Study area

The study was conducted in Kainuu, eastern Finland (63°7′N–65°5′N, 27°3′E–30°0′E), located in the boreal zone. The landscape is characterized by a varying topography with ridges, ravines and small hills. Forests cover 83% of the land area. Fifty-seven percent of the forests are on mineral soil and 43% are on peatlands. Lakes, rivers and small ponds are also typical to this area. The amount of agricultural land is small and human population density is low (3.6 inhabitants km^{-2}). The forests are coniferous dominated, the main tree species are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch *Betula* sp. Of the peatlands, ca 60–65% were drained (METLA 2010). The moose density after hunting was between 0.30 and 0.35 moose km^{-2} (Pusenius et al. 2017). The grey wolf densities (0.51/1000 km^2) were among the highest in Finland. The area also hosts brown bear *Ursus arctos*, which occur at fairly high densities, as well as wolverines *Gulo gulo* and lynx *Lynx lynx*. The climate is continental with average temperature of −11°C in January and +16°C in July. Snow cover usually lasts from the middle of November to the beginning of May. The maximum snow depth ranges between 50 and 80 cm (Kersalo and Pirinen 2009).

Animal collaring

Collaring of moose was conducted during winters 2008–2009 and 2009–2010 by Natural Resources Institute Finland and the Finnish Food Safety Authority. The moose were located from helicopter from where they were immobilized with a dart gun by using medetomidine (50 mg) – ketamine (500 mg) solution. The reversal of immobilization after collaring was made by atipamezole (125 mg i.m. and 125 mg s.c.) The collaring was made in accordance with all regulations regarding animal safety and handling specified in the permit issued by the regional state administrative agency of Southern Finland (ESLH-2008-00177/Ym-23). The used GPS–GSM (Global System for Mobile Communications) collars (GPS Plus, Vectronic Aerospace GmbH, Berlin, Germany) stored positions on an hourly basis, together with the date, time, temperature and other auxiliary information on the animals' position. Every fourth hour, the collars sent the collected information to a database at Swedish University of Agricultural Sciences via a GSM-network. The average fix rate of GPS-positioning was ca 99%. The times of no fix seemed to happen with no reference to season or time of day.

Wolves were captured and collared in late winter or early spring (between February and April) in the years 2008 and 2009 (Kojola et al. 2006). Individuals were captured using snowmobiles when the snow was soft and at least 80 cm deep. Snowmobiles were driven alongside wolves, which were looped using a neck-hold noose attached to a pole. The wolves were placed in a wooden box that had been strengthened with a metal grating around the outside and had doors at both ends. Wolves were kept in the box for at least 30 min before being injected with a mixture of medetomidine and ketamine with a dose ratio of 1:20 (Jalanka and Roeken 1990). The wolves were equipped with collars that contained global positioning system receivers (GPS Plus 2, Vectronic Aerospace GmbH, Berlin, Germany) and Very High Frequency (VHF) radio beacon transmitters (Televilt, Lindesberg, Sweden). The collars were set to store wolf positions every fourth hour. Capture, handling and anesthetizing of the wolves met the guidelines issued by the Animal Care and Use Committee at the University of Oulu and permits provided by the provincial government of Oulu (OLH-01951/Ym-23).

Data on forest structure

The possibility that moose movements were further affected by structure of the surrounding forest was taken into account with variables available from the multi-source Finnish National Forest Inventory. The data are available as rasters (GeoTiff, EPSG:3067) with a 16 m cell size, and they have been produced with the field measurements of the National Forest Inventory and Landsat satellite images. The data include cell-level key metrics of forest structure (volume, height, biomass, canopy cover, dead wood etc.) and cover all of Finland. The data are described in detail in Mäkisara et al. (2019).

The data were linked to the moose locations with bilinear interpolation where the value of the forest variable linked to each moose location was an average calculated from the four nearest adjacent cells around the moose location. Of the available variables, volume (m^3 ha^{-1}), basal area (m^2 ha^{-1}) and canopy cover (0–100%) from the year 2013 were first chosen, but due to strong correlations between the variables, only canopy cover was eventually included in the final models. Canopy cover well reflects also the density of the vegetation

under the canopy (Melin et al. 2017) and we thus assume it to be relevant to the movements of moose.

Measuring predation risk

We assume that all wolf packs and pairs were known and at least either of the adult wolves of a given pack/pair in the study area was collared in winter and summer during year 2010. This was confirmed by intensive snow tracking and also utilizing observations of local hunters in the area (Kojola unpubl.). Therefore we could determine the spatial relationship between collared moose and wolf territories simultaneously occurring in our study area during that period. Wolf territories were determined using minimum convex polygon method (MCP, Fig. 1). We measured the predation risk to which the moose were potentially exposed to as the proportion of fixes of a moose that occurred in a wolf territory. As the predation risk may increase with decreasing distance to the core area of wolf territory, we used both the proportion of moose fixes 1) within the 100% MCPs of wolves and 2) within the 80% MCPs of wolves as the criterion of risk. Because the movement behavior of moose seems to depend on season (Wikenros et al. 2016), we split the data according to seasons winter (January–April) and summer (May–September). To simplify the analyses we recoded predation risk to two distinct classes with 1) less than half of the fixes within a wolf territory and 2) more than half of the fixes within a wolf territory.

Measures on moose movement

The measures of moose movement we used were those used by Wikenros et al. (2016); 1) travel speed (TS) measuring the distance moved by moose between two consecutive fixes as well as 2) the degree of linearity versus meandering of moose movement (LM). These measures were calculated as: $TS = (d_{1-2})/(t_2 - t_1)$ and $LM = d_{1-3} / (d_{1-2} + d_{2-3})$, where d is the distance, t is the elapsed time and the subscripts (1, 2, 3) represent consecutive locations (see also Wikenros et al. 2016). The interpretation of variable TS is straightforward – as the geographical difference of two locations it is the hourly minimum travel speed for a given individual. The values of variable LM vary between zero and unity. These extreme values reflect the moose behavior in the two consecutive hours as follows: 1) an arbitrary drift of location during the first hour, and a precise return to the starting point in the second hour; resulting $LM = 0$ and 2) a move from a starting point in the first hour, and another move in the second hour ending up to the same line but further away from the starting point of view; resulting $LM = 1$. The values between zero and unity reflect the linearity of movement such that the higher values represent more linear movements.

Statistical analysis

We performed analyses at first for all moose with fixes during winter and a major part of them with fixes also during summer 2010 (Table 1), and then separately for females confirmed to have a calf at heel during the summer 2010 (Table 1). The first analysis included measures of moose movement (TS or LM) as a dependent variable moose identity as a random predictor and season (winter and summer), the dichotomous predation risk, covariate canopy cover and all their interactions as fixed factors. The second analysis was similar but without the effect of season. The models were reduced using stepwise method based on AIC and starting from the highest level interactions. The reference level for predation risk was low predation risk, for season it was winter and for canopy cover zero canopy cover. Dependent variables TS and LM were respectively log and exp-arcsine-square root transformed prior to analyses to improve the assumption of normality of residuals of the linear mixed models. We performed analyses separately using 1) the recoded proportion of moose fixes within the 100% MCPs of wolves and 2) the recoded proportion of moose fixes within the 80% MCPs of wolves as a measure of predation risk. The results of these analyses were mostly similar and we report mainly the results from analyses using the proportion of moose fixes within the 100% MCPs of wolves as the measure of predation risk. We report the results of the analyses using the proportion of moose fixes within the 80% MCPs of wolves as the measure of predation risk only when they markedly differ from those obtained in the analyses using the 100% MCP criterion. The alpha was set to 0.05 for the analyses. All analyses were performed with package lmerTest (Kuznetsova et al. 2017) of software R (<www.r-project.org>).

Results

Travel speed

Based on descriptive statistics the median travel speed between consecutive locations (TS) was highest in summer among the moose exposed to higher wolf predation risk (Table 1) and somewhat lower in summer among the moose exposed to lower predation risk. The lowest TS occurred in winter irrespective of the level of risk of predation (Table 1). The differences and similarities in the TS data patterns are illustrated in quantile-to-quantile plots in Fig. 2. Among the females with calf/calves at heel the TS seemed to be higher among the animals exposed to higher predation risk compared to those exposed to lower predation risk (Table 1).

The results of the linear mixed model assessing the effects of season and predation risk, canopy cover and their interactions on log-transformed TS are presented in Table 2. The best model indicated significant main effects of season and canopy cover and interactions predation risk × season and canopy cover × season (Table 2). The main effect of season indicates, based on its parameter estimate ((exp(0.7647) − 1) × 100%) and standard error (Table 2), that TS was 114.8% (± 2 SE: 81.4–154.4%) higher in summer than in winter. The main effect of predation risk was not significant, reflecting that in the wintertime the predation risk did not have an impact on TS. Instead, the observed significant interaction effect of predation risk × season (Table 2) indicates that the TS in the summertime was 19.9% (± 2 SE: 3.6–38.8%) faster among the moose exposed to higher predation risk compared to those exposed to lower risk. The main effect of canopy cover (Table 2) indicates that TS decreased with increasing cover (a 1% increase in cover decreased TS by 0.42%; ± 2 SE: 0.07–0.77%). In addition, the canopy cover × season interaction indicates that the decrease in TS with

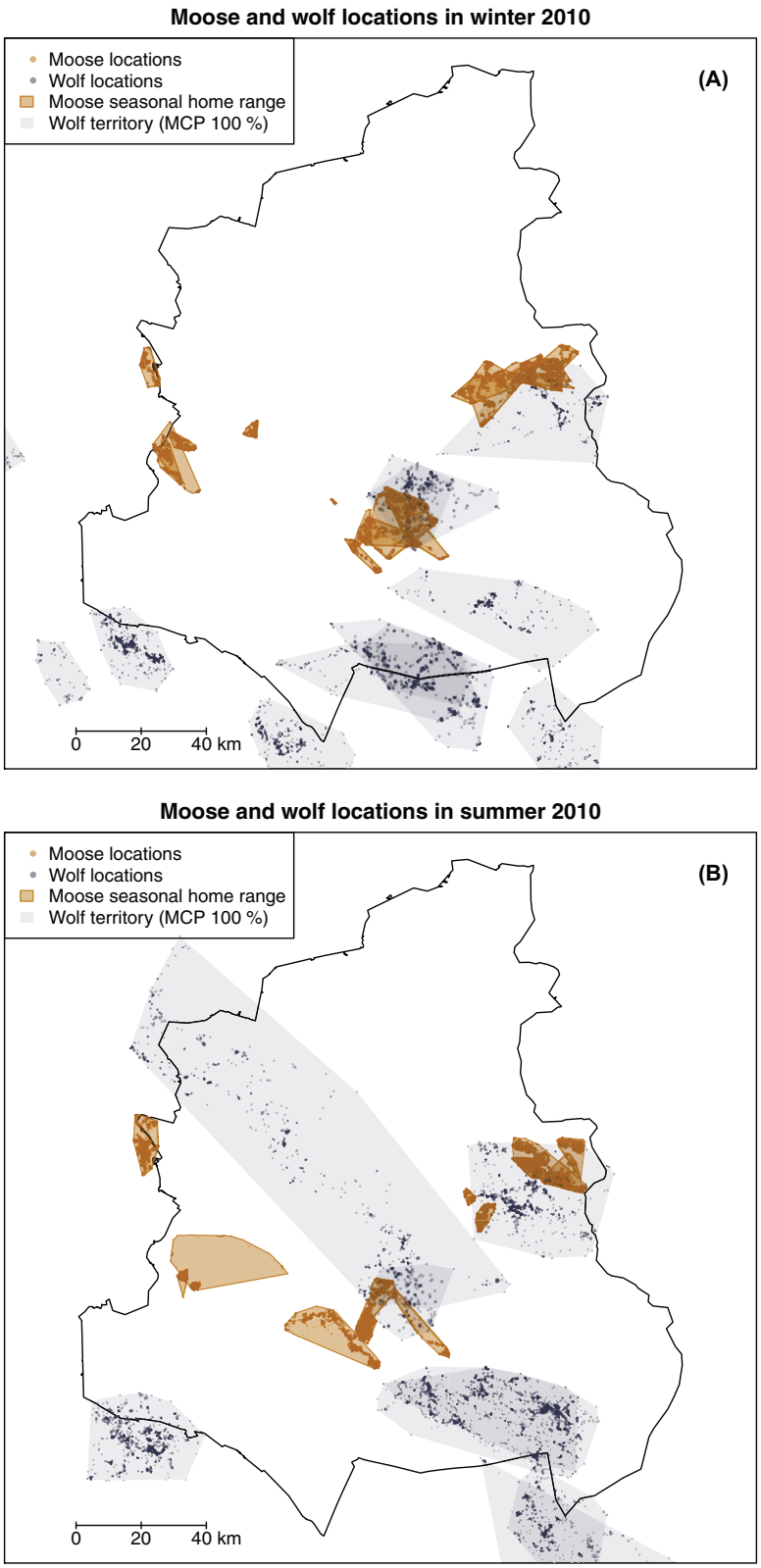

Figure 1. Moose and wolf locations, and 100% MCP home ranges (moose) and territories (wolf) in winter (A) and summer (B).

increasing canopy cover was most pronounced in summer: A 1% increase in canopy cover decreased TS by another 0.57% (± 2 SE: 0.24–0.90%) in the summertime. When using the proportion of moose fixes in 80% MCPs of wolves as the criterion of predation risk the results were otherwise the same but TS of the moose exposed to higher predation risk was 35.6% (± 2 SE: 13.5–62.0%) faster compared to those exposed to lower risk in summer (predation risk × season, parameter = 0.305, SE = 0.009, t = 3.36, df = 2327, p = 0.0008).

Table 1. Descriptive statistics of travel speed (TS) and the degree of linearity of movement (LM) for the predation risk classified based on moose overlap with 100% MCPs (A) and 80% MCPs (B) of wolves. Median and an interquartile range (IQR) are given for the different combinations of season and predation risk. N = number of gps locations.

Variable	Population	Season	Pred. risk	N	Indiv.	Median	IQR
(A)							
TS	All indiv.	winter	low	19 142	13	19.2	[7.0; 58.1]
_	_	_	high	12 211	7	19.9	[6.9; 60.6]
_	_	summer	low	25 650	9	35.1	[11.9; 97.5]
_	_	_	high	21 582	8	49.9	[13.4; 147.5]
_	Cows+calves	summer	low	22 022	8	33.1	[11.5; 89.1]
_	_	_	high	8129	3	46.8	[13.3; 143.8]
			overall	78 585	20	30	[9.6; 91.0]
LM	All indiv.	winter	low	19 142	13	0.883	[0.647; 0.974]
_	_	_	high	12 211	7	0.887	[0.658; 0.975]
_	_	summer	low	25 650	9	0.869	[0.637; 0.970]
_	_	_	high	21 582	8	0.906	[0.710; 0.978]
_	Cows+calves	summer	low	22 022	8	0.862	[0.625; 0.968]
_	_	_	high	8129	3	0.901	[0.696; 0.976]
			overall	78 585	20	0.886	[0.663; 0.974]
(B)							
TS	All indiv.	winter	low	19 142	15	19.2	[7.0; 57.2]
_	_	_	high	12 211	5	20.1	[7.0; 63.6]
_	_	summer	low	25 650	13	39.7	[12.4; 115.8]
_	_	_	high	21 582	4	44.7	[12.6; 128.0]
_	Cows+calves	summer	low	25 648	9	34.6	[11.8; 93.4]
_	_	_	high	4503	2	49.2	[12.7; 166.8]
			overall	78 585	20	30	[9.6; 91.0]
LM	All indiv.	winter	low	19 142	15	0.883	[0.647; 0.974]
_	_	_	high	12 211	5	0.887	[0.658; 0.975]
_	_	summer	low	25 650	13	0.869	[0.637; 0.970]
_	_	_	high	21 582	4	0.906	[0.710; 0.978]
_	Cows+calves	summer	low	25 648	9	0.866	[0.633; 0.969]
_	_	_	high	4503	2	0.910	[0.713; 0.979]
			overall	78 585	20	0.886	[0.663; 0.974]

The linear mixed model assessing the effect of predation risk on the summertime TS of females with calf/calves at heel had only two regressors: level of predation risk and canopy cover. The interaction was excluded from the best model, which showed only significant main effects of predation risk (parameter = 0.293, SE = 0.127, t = 2.32, df = 8.80, p = 0.047) and canopy cover (parameter = −0.009, SE = 0.002, t = −4.98, df = 1818, $p < 0.0001$). The females exposed to higher predation risk moved 34.1% (± 2 SE: 4.6–71.9%) faster than the ones exposed to lower risk. In addition, a 1% increase in canopy cover decreased TS by 0.89% (± 2 SE: 0.54–1.24%). When using the proportion of moose fixes in 80% MCPs of wolves as the criterion of predation risk the results were otherwise the same but the increase in TS of the females with calf/calves exposed to higher predation risk was only marginally significant (parameter = 0.307, SE = 0.160, t = 1.92, df = 10.33, p = 0.083).

Linearity of movement

Descriptive statistics of the linearity of movement suggest rather linear movement patterns and a slight increase in LM due to high predation risk (Table 1, Fig. 3). However, the results of the best linear mixed model assessing the effects of season, predation risk, canopy cover and their interactions on exp-arcsine-square root transformed LM revealed only significant main effects of season (parameter = 0.085, SE = 0.022, t = 3.87, df = 7695, $p < 0.0001$) and canopy cover (parameter = −0.003, SE = 0.001, t = −4.53, df = 8316, $p < 0.0001$). The movements were more linear in summer than in winter. In addition LM decreased with increasing canopy cover. No significant main effect or interactions containing the predation risk were observed.

The linear mixed model assessing the effect of predation risk, canopy cover and their interaction on the transformed LM of the females with calf/calves at heel indicated only the main effect of canopy cover (parameter = −0.004, SE = 0.001, t = − 3.01, df = 2003, p = 0.0026). The LM decreased with increasing canopy cover.

The results concerning LM did not change when using the proportion of moose fixes in 80% MCPs of wolves as the criterion of predation risk.

Discussion

Our results suggest that moose react to wolves by adjusting their movement speed according to the degree they are exposed to the presence of wolves. However, the response to wolf predation risk appeared to depend on season; movement speed was related to wolf presence in summer but not in winter. In summer the moose more exposed to wolves moved faster than the moose less exposed to wolves, the results thus supporting our hypothesis concerning movement speed. Also female moose with calf/calves increased the speed of their movement when exposed to higher risk of wolves. The effect size of predation risk seemed to be somewhat larger among the females with calf/calves

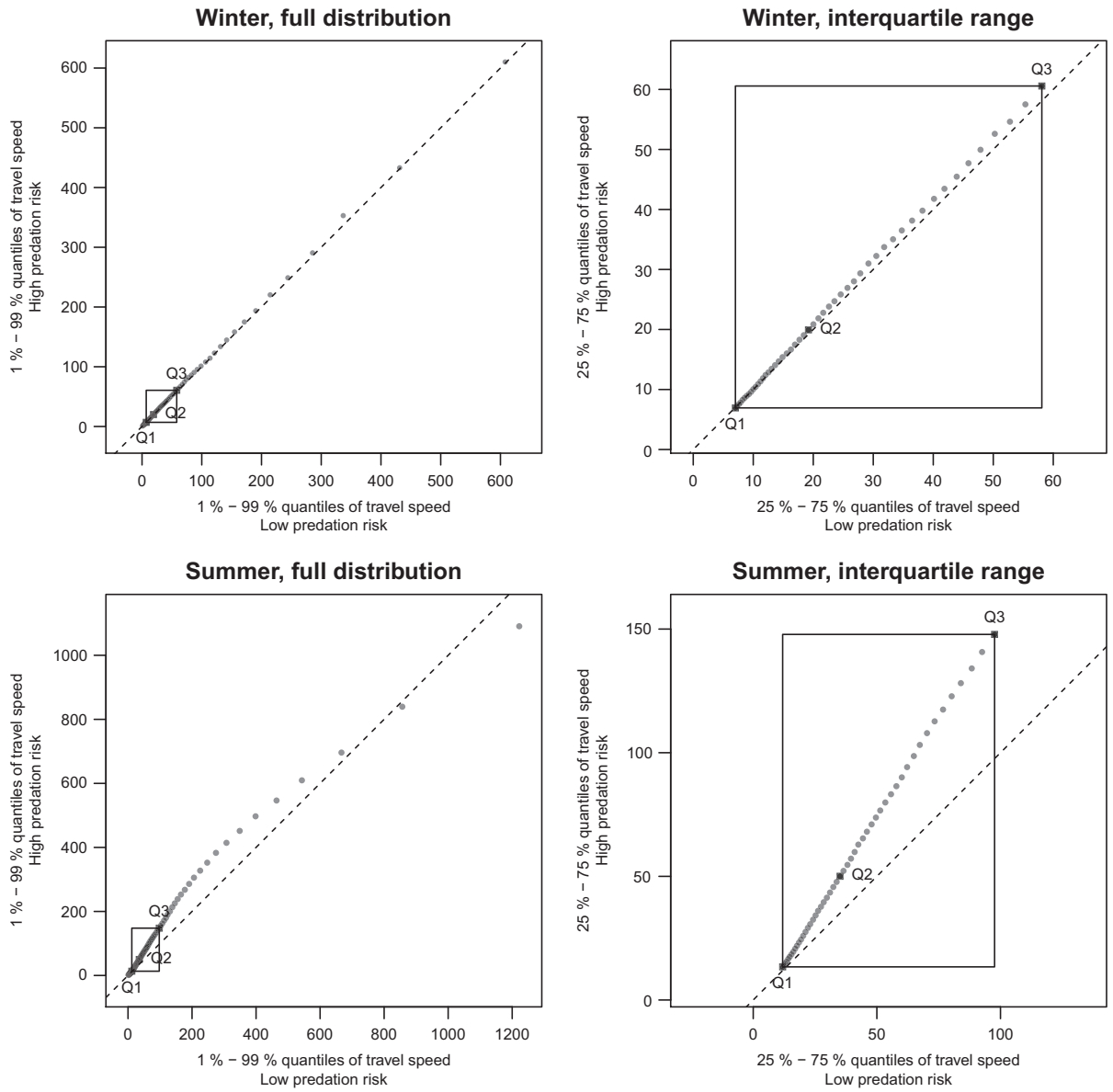

Figure 2. Quantile to quantile plots illustrating the differences in travel speed between moose exposed to higher versus lower risk of wolf predation. The level of predation risk was classified based on the proportion of fixes of moose on 100% MCPs of wolves. Left panels: 1–99% quantiles of travel speed among the moose exposed to higher predation risk plotted against 1–99% quantiles among the moose exposed to lower predation risk in winter (above) and summer (below). Right panels: 25–75% quantiles of travel speed among the moose exposed to higher predation risk plotted against 25–75% quantiles among the moose exposed to lower predation risk in winter (above) and summer (below). The dashed lines represent equal mobility. Lower quartiles, medians and upper quartiles of the distributions are labeled by Q1, Q2 and Q3, respectively.

compared to all adult moose. However, the hypothesis that female moose with calves would especially strongly react to predation risk by wolves was not clearly supported. Neither did our results support the hypothesis that the linearity of movement would increase with increasing risk of predation.

The results indicating increased movement speed among moose with more spatial overlap with wolves suggest that these moose were more likely to end up in situations where they perceived the presence of wolves and subsequently attempted to move away of the predator. Probably these moose, more exposed to the presence of wolves and likely also to cues indicating their presence, e.g. scent-marking and vocalizations, were also more alerted and stressed. Therefore they might have had less the courage to settle to slow movements indicating e.g. foraging (Fryxell et al. 2008, Wikenros et al. 2016).

An alternative explanation to the increased moving in the presence of predation risk is provided by Mitchell and Lima (2002). They modeled a predator–prey interplay, and concluded that if the predator is capable to spatially learn from the prey searching trials and cannot kill a large proportion of prey encountered, the prey should attempt to be spatially and temporally unpredictable and thus increase moving. That is, the prey should move away from a spot where the learning predator is likely to return. This mechanism might apply to moose wolf system where wolf patrols

Table 2. The results of fixed effects of mixed effects models testing the effects of predation risk, season, canopy cover and their interactions on log – transformed moose traveling speed (m h^{-1}). Results of a model reduced using stepwise (AIC) method are shown.

Effect	Estimate	SE	df	t	p
Intercept	3.116	0.0672	138.9	46.383	<0.0001
Predation risk (P)	0.0107	0.0590	294.3	0.181	0.857
Season (S)	0.7647	0.0863	7104	8.858	<0.0001
Canopy cover (C)	−0.0042	0.0018	8407	−3.522	0.0004
P × S	0.1817	0.0746	2125	2.435	0.0150
S × C	−0.0057	0.0017	8504	−3.299	0.0010

its home range attempting to localize potential prey but may not attack all of them and even in cases where attacks it is able to kill only a subset of them, e.g. 25% in the study of Wikenros et al. (2009).

The reactions of moose to increased wolf predation risk occurred in summer but not in winter. Also the movement speed was higher in summer than in winter. These results are most likely associated to the presence of snow cover in winter that impeded movements (Lundmark and Ball 2008, Melin et al. unpubl.). The thick snow cover prevailing in Kainuu obviously increased the costs of movements to an extent that moose living in the more risky environments could not change their movements.

The degree of change in the movement speed due increased exposure to predator was only slightly larger among the females with calf/calves at heel compared to all adult moose. It can be speculated that the calves at heel constrained the way these females could move. Also costs of lactating probably moderated the tendency to increase movement due to predation risks.

The linearity of movement was not affected by predation risk, but changed due season and changes in the canopy cover. The less linear movements during winter compared to summer are probably related to the snow cover in winter. In deep snow moose tend to forage in a very small area which likely yields a slow and winding movement pattern (Fryxell et al. 2008, Wikenros et al. 2016). Also increasing canopy cover increased winding of the movements and decreased movement speed among both all moose and those with calf/calves at heel. Among all moose the effect on movement speed was pronounced in summer. These observations could have been because moose chose to spend more time e.g. foraging in thick vegetation especially in summer. Alternatively thick vegetation resisted movements and thus affected both movement speed and linearity.

We used the overlap of moose with both 100% and 80% MCPs of wolf territories as a measure of predation risk. The results of both approaches were very similar. The effect size of predation risk on traveling speed of all moose seemed to increase somewhat when using the 80% MCP criterion. So it might be that the effect of predation risk on moose behavior increased when moose were closer to the core area on wolf territories.

Our results differ from those obtained in Scandinavia where no response of moose movement, traveling speed and linearity, to the exposure to wolf predation risk was found by Wikenros et al. (2016) in an area which was relatively recently occupied by wolf population. These authors suggested that the intense moose hunting by humans during the past century and simultaneous absence of wolves as well

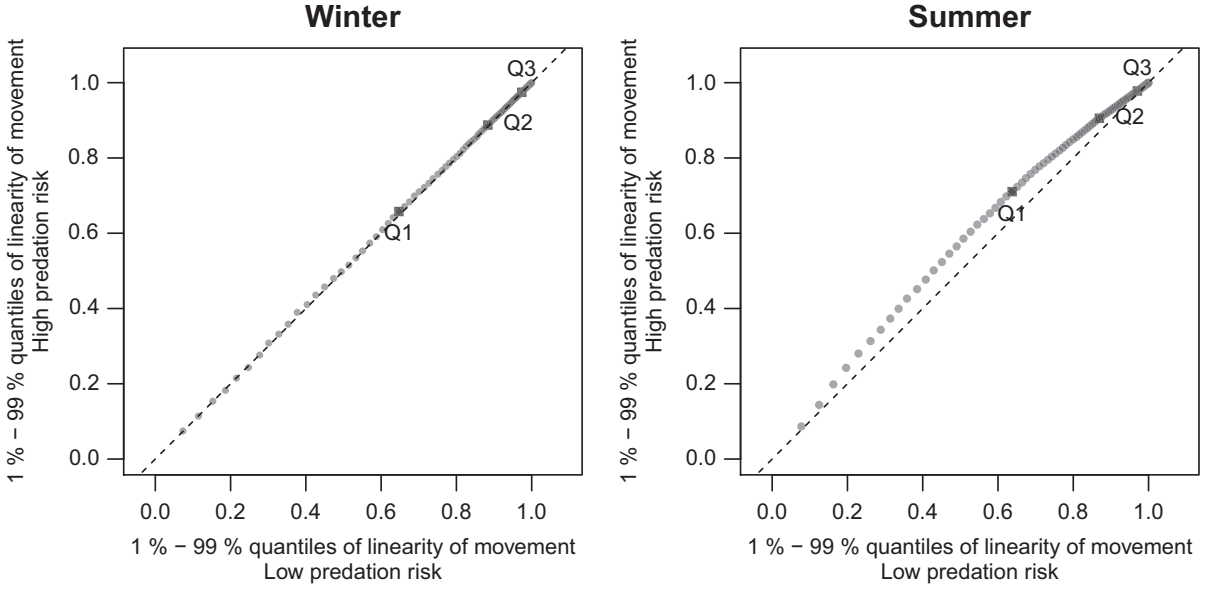

Figure 3. Quantiles (1–99%) of linearity of movement among the moose exposed to higher predation risk plotted against quantiles among the moose exposed to lower predation risk. The level of predation risk was classified based on the proportion of fixes of moose on 100% MCPs of wolves. Left panel: winter, right panel: summer. The dashed lines represent equal degree of linearity of the movement. Lower quartiles, medians and upper quartiles of the distributions are labeled by Q1, Q2 and Q3 respectively.

as high moose to wolf ratio has decreased the reactions of moose to the presence of wolves. The moose densities in Finland are half of those in Sweden (Wallgren 2016, Jensen et al. 2020), and the size of wolf territories is of the same magnitude in both countries (Johansson 2002, Kaartinen et al. 2005, Mattisson et al. 2013). Consequently the moose to wolf ratio is lower in Finland than in Sweden such that each individual moose theoretically have a higher probability to become killed by wolves in Finland. However, it seems that a wolf pack in Sweden kills substantially more moose per year than a wolf pack in Finland (Sand et al. 2008, Kojola et al. unpubl.). Therefore the probability to become killed for a moose living on a wolf territory may not be very different between these countries. The effect of humans on moose in our study area may also be comparable to that in Sweden. So, it might be that wolves' continuous presence in eastern Finland compared to Scandinavia provide the reason why moose in our study area reacted to the presence of wolves.

The results of the study of Ditmer et al. (2018) in North America were more similar with those of ours: The study found that moose moved faster in areas with a high likelihood of presence of wolves. Sand et al. (2006) stated that in North America moose have been continuously exposed to wolves and grizzly bears. Thus the situation has been similar to that in our study system.

Ditmer et al. (2018) suggested that antipredator behaviors like increased movement rates could reduce the time available to critical activities like foraging, breeding and finding thermal shelter and are therefore likely to involve costs to moose. Therefore it seems plausible that these behaviors will be preserved only in conditions where they are regularly needed. In the case of our study system the long coexistence of moose and wolf probably maintains the antipredator behavior of moose. Further studies may assess whether other antipredator behaviors like changes in habitat use occur in this system and whether the risk aversive behavior of moose causes behavioral trophic cascades as has been shown in wolf – elk *Cervus elaphus* system in North America (Ripple and Beschta 2012).

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References

Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. – Proc. R. Soc. B 266: 2261–2267.

Ditmer, M. A. et al. 2018. Moose movement rates are altered by wolf presence in two ecosystems. – Ecol. Evol. 8: 9017–9033.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. – Oecologia 60: 185–189.

Eriksen, A. et al. 2011. Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. – Anim. Behav. 81: 423–431.

Fryxell, J. M. et al. 2008. Multiple movement modes by large herbivore at multiple spatiotemporal scales. – Proc. Natl Acad. Sci. USA 105: 19114–19119.

Gervasi, V. et al. 2012. Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore-ungulate systems in Scandinavia. – J. Anim. Ecol. 81: 443–454.

Gervasi, V. et al. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. – Ecol. Appl. 23: 1722–1734.

Jalanka, H. H. and Roeken, B. O. 1990. The use of medetomidin-ketamine combinations, and atipamezole in nondomestic mammals: a review. – J. Zoo Wildl. Med. 21: 259–282.

Jensen, W. F. et al. 2020. A review of circumpolar moose populations with emphasis on Eurasian moose distributions and densities. – Alces 56: 1–16.

Johansson, K. 2002. Wolf territories in Scandinavia; sizes, variability and their relation to prey density. – MS thesis, Agric. Univ. of Sweden, Uppsala, Sweden.

Jonzen, N. et al. 2013. Sharing the bounty – adjusting harvest to predator return in the Scandinavian human–wolf–bear–moose system. – Ecol. Model. 265: 140–148.

Kaartinen, S. et al. 2005. Finnish wolves avoid roads and settlements. – Ann. Zool. Fenn. 42: 523–532.

Kersalo, J. and Pirinen, P. 2009. Suomen maakuntien ilmasto. – Ilmatieteen laitoksen raportteja 2009: 8. 185 p. Ilmatieteen laitos, Helsinki.

Kojola, I. 2000. Suden, hirven ja metsästyksen vuorovaikutussuhteet. – Suomen Riista 46: 76–81.

Kojola, I. et al. 2006. Dispersal in an expanding wolf population in Finland. – J. Mammal. 87: 281–286.

Kuznetsova, A. et al. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.

Latombe, G. et al. 2014. Spatio–temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. – J. Anim. Ecol. 83: 185–198.

Laundre, J. W. et al. 2001.Wolves, elk and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. – Can. J. Zool. 79: 1401–1409.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

Lundmark, C. and Ball, J. P. 2008. Living in snowy environments: quantifying the influence of snow on moose behavior. – Arctic Antarctic Alpine Res. 40: 111–118.

Mattisson, J. et al. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic and social factors. – Oecologia 173: 813–825.

Mech, L. D. and Peterson, R. O. 2003. Wolf–prey relations. – In Mech, L. D and Boitani, L. (eds), Wolves: behavior, ecology and conservation. Univ. of Chicago Press, pp. 131–160.

Melin, M. et al. 2017. Assessing the performance of aerial image point cloud and spectral metrics in predicting boreal forest canopy cover. – ISPRS J. Photogrammet. Remote Sens. 129: 77–85.

METLA 2010. Finnish statistical yearbook of forestry. – Vammalan Kirjapaino Oy, Sastamala, Finland.

Mitchell, W. A. and Lima, S. L. 2002. Predator–prey shell games: large scale movements and its implications for decision-making by prey. – Oikos 99: 249–259.
Mäkisara, K. et al. 2019. The multi-source national forest inventory of Finland – methods and results 2015. – Natural resources and bioeconomy studies 8/2019. Natural Resources Institute Finland, Helsinki, 57 p.
Nicholson, K. L. et al. 2014. Testing the risk of predation hypothesis: the influence of recolonizing wolves on the habitat use of moose. – Oecologia 176: 69–80.
Pusenius, J. and Ostfeld, R. S. 2002. Mammalian predator scent, vegetation cover and tree seedling predation by meadow voles. – Ecography 25: 481–487.
Pusenius, J. et al. 2017. Hirvikannan koko ja vasatuotto. – In: Helle, P. (ed.), Riistakannat 2016. Luonnonvara- ja biotalouden tutkimus 41/2017. Luonnonvarakeskus, pp. 7–13.
Ripple, W. J. and Beschta, R. L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems. – Bioscience 54: 755–766.
Ripple, W. J. and Beschta, R. L. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. – Biol. Conserv. 145: 205–213.
Sand, H. et al. 2006. Crosscontinental differences in patterns of predation: will naïve moose in Scandinavia ever learn? – Proc. R. Soc. B 273: 1421–1427.
Sand, H. et al. 2008. Summer kill rates and predation patterns in a wolf-moose system: can we rely on winter estimates? – Oecologia 156: 53–64.
Stephens, P. W. and Peterson, R. O. 1984. Wolf-avoidance strategies of moose. – Holarct. Ecol. 7: 239–244.
Ukkonen, P. 1993. The post-glacial history of the Finnish mammalian fauna. – Ann. Zool. Fenn. 30: 249–264.
Wallgren, M. 2016. Sverige har världens tätaste älgstam. – Skogforsk, kunskapsbanken 11. <www.skogforsk.se/kunskap/kunskapsbanken/2016/varldens-tataste-algstam/>.
White, K. S. and Berger, J. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? – Can. J. Zool. 79: 2055–2062.
Wikenros, C. et al. 2009. Wolf predation on moose and roe deer: chase distances and outcome of encounters. – Acta Theriol. 54: 207–218.
Wikenros, C. et al. 2016. Mobility of moose – comparing the effects of wolf predation risk, reproductive status and seasonality. – Ecol. Evol. 6: 8870–8880.