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Declining recruitment and mass of Swedish moose calves linked to hot, dry springs and snowy winters

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ABSTRACT

As global temperatures continue to rise, increases in the frequency and intensity of climatic extremes will likely outpace average temperature increases, and may have outsized impacts on biological populations. Moose (*Alces alces*) are adapted to cold weather and populations are declining at the southern edge of the species' range. Moose therefore make a suitable case study to examine the relationship between population performance and both climatic averages and the frequency of rare, intense climatic events. More than twenty years of slaughter weights and moose observations collected by hunting teams across all of Sweden show that early calf recruitment has declined throughout Sweden and calf mass has also declined, particularly in central and southern Sweden. Spring weather affected mean calf mass, which declined with higher average temperatures, more frequent very hot days (days in the 95th percentile for maximum temperature) and less precipitation during this season, though in the case of hot days only when high temperatures coincided with low rainfall. This supports previous observations of moose sensitivity to both direct heat stress and the negative impacts of hot, dry spring weather on forage quality. Recruitment was similarly impacted, and the interaction between the previous year's temperature and precipitation supports a lagged effect of weather on recruitment, via female condition. Finally, cold winter temperatures and deeper snow were associated with reduced calf mass during the following autumn, while deeper snow was additionally linked to fewer calves per female. Our results suggest that similar patterns may exist for averages and the frequency of extreme values, but it is important to examine both in order to improve biological relevance. The significant and ongoing declines in calf mass in southern populations and calf recruitment throughout Sweden should serve as an early warning that Eurasian moose may suffer from climate change in similar ways to North American moose. We discuss conservation management strategies, both in terms of harvest as well as landscape management, that may help mitigate the observed patterns.

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1. Introduction

Many natural forces are only biologically relevant if a threshold is crossed leading to physiological impairment or death, in which case maximum and minimum values, and the frequency that these thresholds are crossed are more vital than means and variance (Gaines and Denny, 1993; Meehl et al., 2000). Unlike changes in averages, extremes are typically short and infrequent, but compared to average trends may disproportionately challenge an organism's ability to acclimate (Gutschick and Bassirirad, 2010), leading to large changes in ecosystem structure and function (Parmesan et al., 2000). It has been proposed that the mechanistic basis of gradual long-term biotic changes (e.g., range shifts) may be responses (stress, physical harm, death, extirpation) to a few, brief, intense events (Easterling, 2000; Parmesan et al., 2000). Compounding the potential relevance of extremes for biological populations, small changes in climatic means (e.g., temperature, precipitation) may correspond to much larger changes in the frequency of extremes (Meehl et al., 2000; Beniston et al., 2007; Gutschick and Bassirirad, 2010). Extreme weather and associated fires, floods, and droughts have increased in both frequency and intensity over the last 50 yr (IPBES, 2019). At higher latitudes, warming rates are expected to surpass the global average (Hoegh-Guldberg et al., 2018), and precipitation patterns are forecasted to change, with heavy precipitation increasing in the winter months but water availability declining in the growing season (Belyazid and Zanchi, 2019). Considering the frequency of unusually hot temperatures and days with deep snow in addition to the typically used averages may therefore increase the relevance of studies relating climatic changes to biological phenomena.

Moose (*Alces alces*) is a good model system for which to examine the relevance of extreme weather events to population performance. It is a species with a broad, circumboreal, geographic range and has been studied in many locations and contexts over several decades (e.g., Cederlund et al., 1991; Ericsson and Wallin, 1999; Keech et al., 2000a; Herfindal et al., 2006a; Murray et al., 2006; Wattles and DeStefano, 2011; Dou et al., 2013; Jensen et al., 2020; Laforge et al., 2016; Weiskopf et al., 2019). Additionally, moose populations are declining at the southern edge of the species' range (Murray et al., 2006; Dou et al., 2013; Monteith et al., 2015; Schrempp et al., 2019), and this decline has been associated with rising temperatures, particularly in summer, possibly via increased thermoregulation costs (Murray et al., 2006; Lenarz et al., 2009). While North American moose appear to be expanding north (Rempel, 2011), under current climate change scenarios, moose populations at the southern distribution boundary are projected to continue their decline (Rempel, 2011; Weiskopf et al., 2019). The same might be true for Eurasian moose (Dou et al., 2013; Malmsten, 2014), although this is currently less clear. Most current studies have linked moose populations and climate change through analysing mean changes in temperature. Given the increase in the frequency and intensity of extreme weather (IPBES, 2019), and the expected outsized increase in the frequency of extreme events compared to climatic averages (Meehl et al., 2000; Beniston et al., 2007; Gutschick and Bassirirad, 2010), moose conservation may benefit from additional knowledge of how these weather events may impact population trends. This will bolster proactive population management, for example through adjusting harvest quotas or by using adaptive land management to partially mitigate the negative effects of heightened heat or drought.

There are numerous mechanistic pathways through which temperature and precipitation may impact moose populations. Some of the best understood mechanisms involve effects on calf mass and/or recruitment (Fig. 1). The first is direct heat stress to the calf itself (or interactions between weather and latent biological processes affecting calves or females; e.g., Kock et al., 2018). Moose may lose energy through both physiological (e.g., increased respiration, heart rate and metabolic rate; panting) (Renecker and Hudson, 1986; McCann et al., 2013) and/or behavioural thermoregulation (e.g., reduced forage intake due to increased resting in thermal shelters) (Van Beest and Milner, 2013; Ditmer et al., 2018; Græsli et al., 2020). However, foraging activity may only be reduced when maximum temperatures near their seasonal upper limits, as is the case for kudu (*Tragelaphus strepsiceros*), for which foraging is restricted only 15% of the time (Owen-Smith, 1998). Weather also likely impacts moose through effects on both quantity and quality of forage. Energy intake is likely limited by forage quantity at low biomass levels, but by digestible energy and protein content at intermediate availability (Hebblewhite et al., 2008; Parker et al., 2009). Small improvements in vegetation quality can have large consequences for ungulate mass and reproduction (White, 1983). Diet may impact calves indirectly via their mothers' milk, or directly as they increase their dependence on forage and reduce consumption of milk throughout the summer (Parker et al., 2009).

As phenology progresses through the spring and summer, plant digestibility and protein decrease, lowering vegetation quality (Albon and Langvatn, 1992; Hebblewhite et al., 2008). May and June may be critical months as these encompass parturition and early survival for moose calves (Neumann et al., 2020). Synchrony of this energetically expensive lactation period with peak vegetation quality may be particularly important for offspring survival and mass (Couturier et al., 2009; Parker et al., 2009; Plard et al., 2014). Early onset of spring green-up, thereby increasing forage quantity, may occur with higher early spring temperatures (Doi and Katano, 2008; Douhard et al., 2018). However, rate of phenology progression also increases with warmer spring temperatures (Pettorelli et al., 2005a, 2005b, 2007; Houle, 2007; Campbell et al., 2013; Lesica and Kittelson, 2010). Both factors may be important for moose; years with an early onset of spring have been associated with heavier calves and yearlings, but lower May/June temperatures and slower plant development have also been linked to heavier yearlings (Herfindal et al., 2006a). Similar temporal associations between mass and green up have been seen in other ungulates (Pettorelli et al., 2005b, 2007; Couturier et al., 2009; Garel et al., 2011). High levels of spring precipitation may also lower plant quality by increasing the rate of phenology progression (Loison et al., 1999a; Pettorelli et al., 2007). However, very low water availability limits both the quantity and quality of vegetation (White et al., 2014; Deléglise et al., 2015). Lagged effects are also possible, with climate or summer dietary intake negatively relating to birth mass or fecundity in later years (Couturier et al., 2009; Parker et al., 2009),

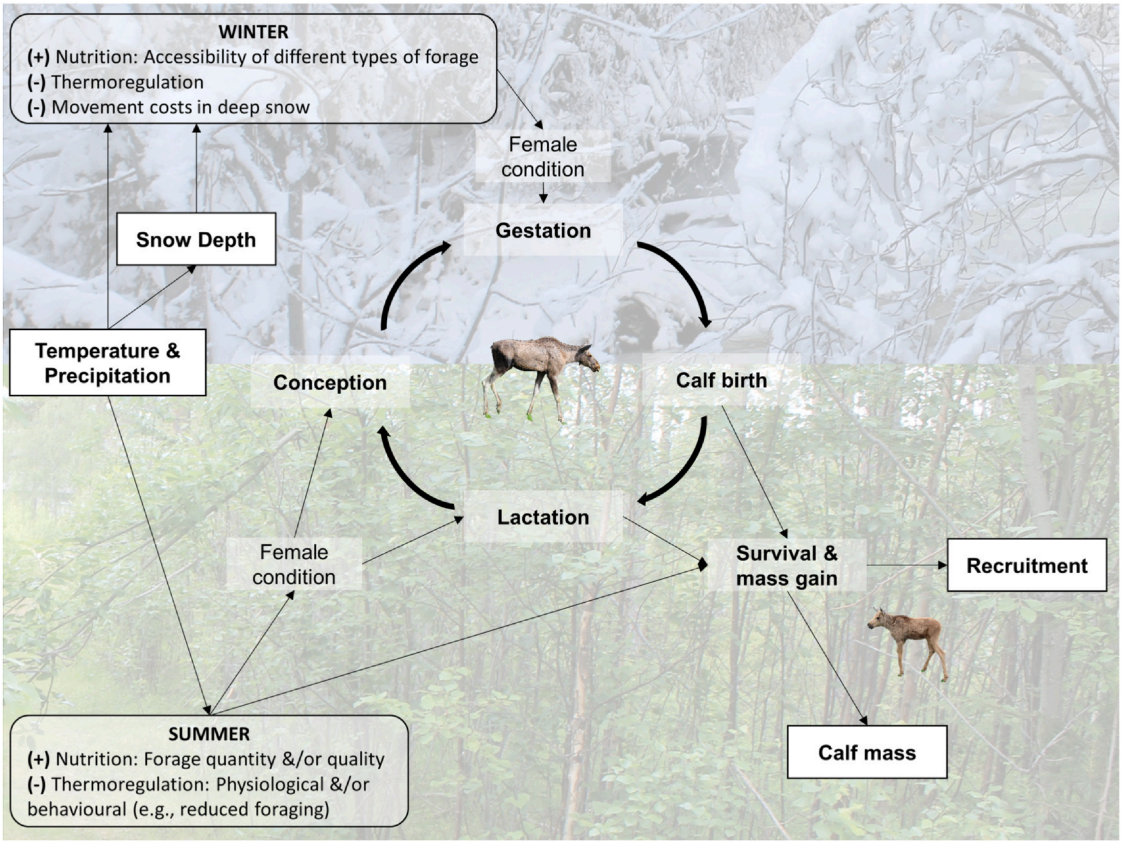

Fig. 1. Mechanisms linking seasonal temperature and precipitation to early recruitment and calf mass in moose. Stages in the life and reproductive cycle of moose are shown in relation to major seasons, with rounded boxes indicating the potential mechanisms by which temperature and precipitation may influence those stages in that season. A (+) indicates an expected energy/nutrient input and therefore positive relationship with mass gain and/or recruitment, while a (-) indicates an energetic cost, resulting in an expected negative relationship. Variables included in models for this study are shown in opaque white boxes.

likely via maternal body condition (Monteith et al., 2015) and/or delayed parturition (Testa and Adams, 1998; Solberg et al., 2007).

The impacts of winter temperature, precipitation, and snow depth on mass, fecundity, and abundance vary geographically and across species (Forchhammer et al., 1998; Post and Stenseth, 1999; Couturier et al., 2009; Ozgul et al., 2009). For example, though ungulate calf, yearling, and adult masses tend to be lower following winters with deeper snow (Cederlund et al., 1991; Loison and Langvatn, 1998; Couturier et al., 2009), for some species only exceptionally heightened snowfall may impact survival (Loison et al., 1999a). Late winter snow may also be linked to moose population growth via reduction of winter tick abundance in North American populations (Ruprecht et al., 2020). Winter weather likely impacts fecundity, mass and survival via the cumulative costs of thermoregulation, limited access to high quality forage, and/or the increased energy requirements of movement in deep snow on the body condition of gestating females (Sand, 1996; Loison et al., 1999a; Post and Stenseth, 1999).

Previous ungulate studies have mainly focused on climatic averages, and their impact on average mass. Here, we extend this approach by also examining the relationship between population performance of moose and the frequency and/or severity of rare, intense climatic events. Moreover, we apply the “extreme event approach” not only to climatic predictors but also to our moose life history and demographic variables. One study on red deer (*Cervus elaphus*) found a lower mass threshold beyond which nearly all calves died and an upper threshold above which nearly all survived (Loison et al., 1999b). This suggests that the proportions of moose calves in the heaviest and lightest size classes could be more relevant for population demographics than the average mass alone. We determine whether variability in moose calf mass and the number of calves observed per female are associated with deviations of average temperature, average snow depth, and total precipitation from the mean, as well as the frequency of very hot days or days with very deep snow in Sweden. We predict lighter calves and lower recruitment (encompassing both fecundity and summer survival of calves) in years with higher temperatures and low water availability during the start of the growing season, as well as years with deeper snow during gestation. Our study provides novel insights into the importance of infrequent, intense weather events for population performance.

2. METHODS

2.1. Study region

Sweden contains one of the densest moose populations in the world, (Jensen et al., 2020), with a large latitudinal range where moose appear to be under climatic stress in the south (Allen et al., 2017; Malmsten, 2014). Southern Sweden has also experienced critically low groundwater levels in recent years (SGU, 2020), and water deficiency is expected to be greatest in this region in the coming decades (Belyazid and Zanchi, 2019).

Our study rests on available long-term management data from all of Sweden where moose occur, encompassing 20 out of 21 counties (all, except the island of Gotland). The area stretches from approximately 55.36°N to 68.86°N and covers six different vegetation zones (alpine, mountain birch, northern boreal, middle boreal, southern boreal, nemoral). Conditions vary latitudinally, with deeper winter snow (average maximum snow depth in the normal period 1961–1990: 0 cm on southern tip to 130 cm in northern mountains), cooler temperatures (annual average temperature in 1961–1990: 8 to −3 °C south to north), and a shorter growing season (average for 1961–1990: 220 days to 100 days south to north) at higher latitudes (SMHI, 2020). More than half of Sweden's land area is covered by forest, most of which is managed for production of timber and pulp (Skogsdata, 2020). Swedish forests consist of approximately 40% Norway spruce (*Picea abies*) and 40% Scots pine (*Pinus sylvestris*) (Skogsdata, 2020). However, the proportion of land covered by old forest (> 140 years) decreases and agriculture and urban land use increase from northern to southern Sweden (Skogsdata, 2020).

2.2. Data

Sweden has a well-developed system for monitoring and managing moose (Singh et al., 2014). As a result, we have access to unique long-term and nationwide data on moose reproductive performance (calf mass and number of calves per female) spanning more than 2 decades.

2.2.1. Calf mass

Reporting the number of moose shot to the relevant County Administrative Boards is mandatory in Sweden, while reporting slaughter weights (as per Langvatn, 1977) is voluntary. Prior to 2012, slaughter weights could be reported to the Swedish Association for Hunting and Wildlife Management (SAHWM; 'Svenska Jägareförbundet'), which holds a public commission to monitor game in Sweden. The Swedish moose management system was reformed in 2012. Currently, slaughter weights can be entered in an official management database ('Älgdata'; www.algdata.se) run collectively by the 21 Swedish County Administrative Boards. We obtained data on slaughter weights from SAHWM for the period September 1995 to February 2012 and from Älgdata for the period September 2012 to February 2020.

We cleaned slaughter weight data for entry errors by omitting individuals weighing less than 10 kg or more than 120 kg as these are unrealistic masses for moose calves in Sweden. As we were interested in the proportion of very light and very heavy individuals, we used conservative cut-offs. As moose calves continue to grow during September, we adjusted mass to October 1 for all calves harvested in September, using county-, year-, and sex-specific regression coefficients, similar to methods used in other studies (Pettorelli et al., 2005b; Herfindal et al., 2006a, 2006b). As regression coefficients were sensitive to sample size, calves shot in September were omitted if the number of individuals per county, year, and sex (prior to October 1) was below 10 individuals to ensure accurate adjustment. Post-adjustment, our final dataset was composed of 184906 calf masses (Fig. S.1).

2.2.2. Calves per female

In 1985, a system for monitoring moose through hunters' observations was developed from an existing Norwegian method (Ericsson and Wallin, 1999) and it was improved in 1997 after a Swedish-Norwegian evaluation (Engen et al., 1998). The improved system was launched across Sweden from 2000 and has since been operating successfully (Singh et al., 2014). In addition to hunting team ID, location (parish, commune, and county), date of hunt, number of hunters, and number of hours spent hunting, hunters record the number of moose males, females and calves seen during the first seven hunting days of the first 30 days of the hunting season. Studies have carefully evaluated the limitations of the data, and have indicated a high reliability of the observation data to reveal changes in population size, particularly over large areas (> 50,000 ha) (Singh et al., 2014). Collecting moose observations is not mandated by law, but many management units and major land owners require that hunting teams collect such data. There are several interconnected systems for reporting observations; the SAHWM is the official host for all the data, which can be accessed through Älgdata. We obtained data on all moose observations collected during 1999–2019 from Älgdata.

2.2.3. Weather data

We obtained daily average and maximum temperature, precipitation, and snow depth from the Swedish Meteorological and Hydrological Institute (SMHI: www.smhi.se/) for all 1229 weather stations in Sweden throughout the study period.

2.3. Variables

2.3.1. Weather variables (predictors)

Due to limited spatial resolution of the moose data prior to 2012, changing management boundaries, and the removal and addition of weather stations over the study period, we calculated all variables on the county level for each of 20 “moose counties”. For each measurement, we therefore used the average value for all weather stations in a given county.

While there is currently no consistent definition or standardised measure of climatic extremes (Easterling, 2000; Bailey and Van De Pol, 2016), there is general consensus that the occurrence must be rare and the value must deviate strongly from the mean (Beniston et al., 2007; Hoegh-Guldberg et al., 2018). Percentiles (e.g., 5th, 95th) of daily minimum, maximum, and/or total values conform to these conditions (Bonsal et al., 2001). For each day of the year in each county, we calculated the 95th percentile maximum temperature across years. We were then able to calculate the proportion of days in May for each county in a given year where the maximum temperature exceeded the day- and county-specific value of the whole time period (e.g., if the county-averaged maximum temperature exceeded 13.9 °C for the county of Västerbotten on May 1). We repeated this calculation to gain the proportion of days where temperature exceeded the 95th percentile maximum temperature (hereafter ‘hot days’) in June, and again across the winter months (December-March). We also calculated the proportion of days across the winter months (December-March) where the snow depth exceeded the 95th percentile for that county and day of year (hereafter ‘deep snow days’).

To account for general trends in temperature and precipitation, we used mean-centred values for each county. For example, we calculated the yearly deviations from the mean total precipitation in May and June for each county by subtracting the mean total May and June precipitation for that county over all years from the respective May and June precipitation for each year. We also calculated the yearly deviations of mean May, June and winter (December-March) temperatures from the mean temperature in each county, and the mean winter snow depth.

2.3.2. Moose calf variables

We examined trends in four different variables related to moose calf mass and early recruitment (fall calf – adult female ratio). First, we took the mean of the individual calf masses for each year in each county. As sample size varied across counties and years, we used sample sizes as weights in our models. To improve precision, we limited this dataset to mean values derived from a minimum of 20 calves per county and year. We then calculated the yearly deviations in mean mass for each county.

We next calculated the proportion of calves above the county-specific 95th percentile for mass. For each county, we calculated the 95th percentile for all calf masses from all years. We then calculated the proportion of calves each year that were above that mass threshold (hereafter ‘heavy calves’). To improve both accuracy and precision of this variable, we limited this dataset to proportions derived from a minimum of 50 calves. We followed this procedure again to calculate the proportion of calves below the 5th percentile mass for the county they were harvested in (hereafter ‘light calves’). Finally, for each county and year, we extracted the total number of observed calves and females as reported in the moose observations by hunters.

To enable comparison of trends across northern, central, and southern Sweden, we took the average and standard deviation of each variable (weather and moose calf) for all counties in each of the three regions of Sweden each year. We then plotted these with a linear trend line to see the temporal patterns of weather and moose performance in each region better over time.

2.4. Models

We used Variance Inflation Factors (VIF) to identify situations where variables were correlated to a degree that models gave unreliable results (Thompson et al., 2017). As several average and extreme temperature and snow variables were highly correlated (VIF values > 5; Kutner et al., 2004), we elected to run these in separate models and to qualitatively compare the outcomes. As temperature effects may interact with those of precipitation, we elected to include precipitation and interaction terms in both ‘average’ and ‘extreme’ models. To avoid overparameterizing models we further separated winter and summer analyses. We standardised (z-scored) all weather variables using the function ‘standardize’ from the ‘effectsize’ package in R. All models included county as a random factor with a continuous AR(1) correlation structure to account for spatial and temporal autocorrelation in the data. Models 1 through 4 were linear mixed models (lmm) with yearly deviation in mean moose calf mass as the dependent variable, weighted by sample size. Model 1 included the proportion of ‘hot days’ in May and in June, total precipitation in May and June, and the interaction between the proportion of ‘hot days’ and precipitation for each of these two months. Model 2 replaced the proportion of ‘hot days’ with mean temperature in May and June. Likewise, while Model 3 included the proportion of ‘hot days’ in winter and the proportion of ‘deep snow days’, Model 4 included the mean temperature and mean snow depth for the same period. Models 1–4 used the ‘nlme’ function from the ‘nlme’ package. The function ‘intervals’ was used to calculate 95% confidence intervals.

We used a glmm with negative binomial family for Models 5–10, which had the number of calves observed in a given county and year as the dependent variable, offset by the number of adult females observed in a given county and year. This effectively turns the dependent variable into the rate of calves per female. Models 5–8 incorporated the same fixed factors as Models 1–4. To investigate the potential for lagged effects of spring weather on reproduction the following year, Models 9 and 10 used spring/summer weather variables from the prior year (proportion of ‘hot days’, precipitation, and their interaction in May and June, t-1, and mean temperature, total precipitation and their interaction for Models 9 and 10, respectively). Models 5–10 used the ‘glm.nb’ function to determine theta levels and ‘glmmPQL’ to run the full model with random effects and correlation

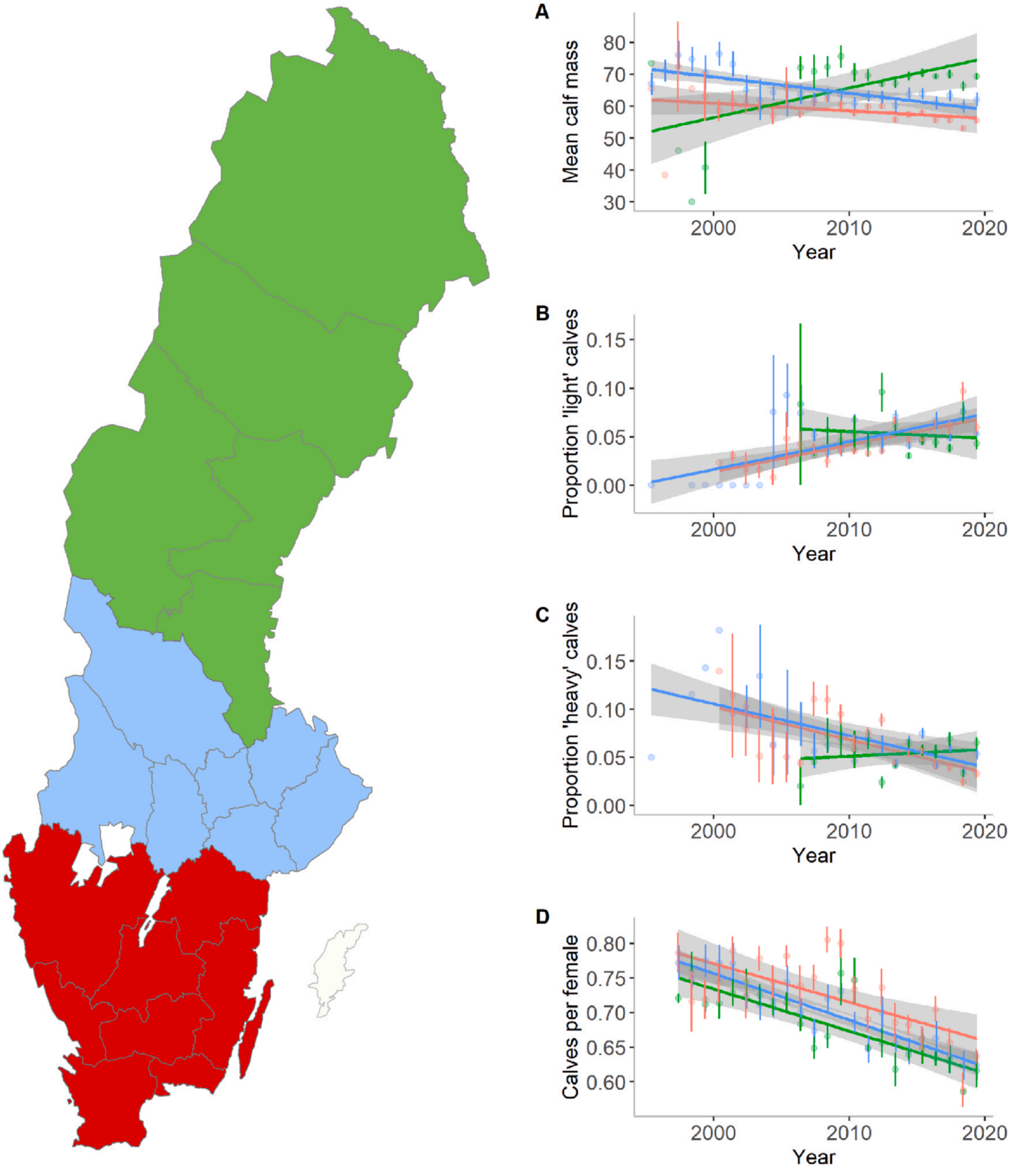

Fig. 2. Annual trends in calf mass and early recruitment for moose across the three regions of Sweden. Norrland is represented by green, Svealand by blue, and Götaland by red. Regions are denoted in matching colours on the map of Sweden, to the left. Points represent the average value across counties (denoted by lines on the map) within a region, and linear regression lines and standard error bars are included. Mass variables were restricted to counties and years with at least 20 calf masses to reduce the likelihood of spurious values. See Methods for calculation of the proportion of 'light' and 'heavy' calves, and calves per female. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structure, both in the 'MASS' package. All analyses were conducted in R version 3.6.3 (The R Foundation for Statistical Computing, 2020). Models are summarised in the supplementary materials (S.1).

3. RESULTS

Early calf recruitment, measured as the number of moose calves observed per adult female in the fall after birth, has declined in all three regions over the past two decades (Fig. 2). Calf mass has also declined in central and southern Sweden, though a steady decline is only evident for southern Sweden (Fig. 2). As the patterns in 'light' and 'heavy' calves did not differ markedly from those of mean calf mass, only mean calf mass was used in models going forward. Weather trends are somewhat less clear, and there is an exceptional amount of interannual variability (Fig. 3). Long-term trends in temperature and precipitation are not significant over the period of our study, although extreme deviations did occur such as during 2018 when there were exceptionally hot springs (with the exception of June in Norrland) and little precipitation. Temperature increases are more apparent in more southern counties in June. General trends for extreme temperatures appear similar, though not identical, to the trends for the average temperatures. There is less variation in the frequency of “deep snow days”, with higher frequencies limited to a few years with very deep snow (Fig. 3), indicating that snow patterns may be similar over multiple counties at any given time.

3.1. *Mean calf mass (Models 1–4)*

Mean calf mass was higher in years with fewer ‘hot days’ in May, lower mean temperature in May, and in years with more precipitation in June (Tables 1 and 2). However, while higher mean temperatures in June were always associated with lighter calves, a positive interaction in Model 1 indicated that more ‘hot days’ in June only linked to lower mean calf mass when precipitation was below average (Figs. S.2 and S.3). At high levels of precipitation, more ‘hot days’ in June were linked to heavier calves. Both extreme and average models showed that warmer winter temperatures and shallower snow were also associated with heavier calves (Tables 3 and 4, Figs. S.4 and S.5).

3.2. *Female- calf ratio (Models 5–10)*

A greater number of calves per female was observed in years with fewer ‘hot days’ in May, but only when precipitation was very low (Table 5, Fig. S.6). Otherwise, fewer ‘hot days’ in May were associated with fewer calves per female. Contrasting this, higher mean temperatures in June were related to fewer calves per female regardless of precipitation levels (Table 6, Fig. S.7). Fewer ‘deep snow days’, and shallower snow on average were both associated with a greater number of calves per female (Tables 7 and 8, Figs. S.8 and S.9). Weather the June prior to birth also appeared to play a role in the number of calves per female. Fewer calves were observed per female the year following a relatively hot June with more ‘hot days’, but only when precipitation was very low (Tables 9 and 10, Figs. S.10 and S.11). Otherwise, more calves were observed per female the year following a relatively hot June with more ‘hot days’. VIF for all models are listed in the supplementary materials (Table S.2) and Fig. 4 summarises the main results of all ten models.

4. DISCUSSION

Early calf recruitment throughout Sweden and calf mass in southern Sweden have been steadily declining over the past two decades (Fig. 2). Despite high variability and a lack of strong visible trends, temperature, precipitation, and snow depth showed consistent relationships to calf mass and recruitment across models. In our models, higher spring temperatures and low precipitation were linked to relatively low calf mass and recruitment for moose in Sweden, though sometimes both had to coincide for these patterns to emerge. As expected, winters with more deep snow days coincided with years where fewer calves were observed relative to females and where calves were lighter on average. However, warmer winter temperatures were linked to relatively heavier calves the following spring, which was unexpected.

Referring back to the mechanistic pathways through which climate may directly or indirectly influence calf mass and fall recruitment (Figs. 1 and 4), mass is likely related both to direct heat stress and to vegetation quality. Daily fluctuations in body temperature can be strongly related to ambient temperature, among other factors (Thompson et al., 2019). The strong relationship of mass to both mean temperature and the proportion of ‘hot days’ in May could indicate that physiological and/or behavioural thermoregulation (Renecker and Hudson, 1986; McCann et al., 2013; Ditmer et al., 2018) is impacting energy balance (Murray et al., 2006). Supporting this, the lowest county-specific cut-off for the 95th percentile temperature in May was 16.9 °C. This is above or in the range of thermal thresholds at which moose have experienced physiological heat stress and/or behavioural thermoregulation in the spring/summer in other studies (Renecker and Hudson, 1986; Herberg, 2017; Ditmer et al., 2018; Fohringer, 2021; but see Melin et al., 2014). Late spring temperatures may be particularly pertinent for heat stress if moose retain their winter pelage (Lenarz et al., 2009).

Higher average temperatures are also associated with lower nitrogen (Bø and Hjeljord, 1991; Lenart et al., 2002) and low water availability with lower biomass and protein content in vegetation (White et al., 2014; Deléglise et al., 2015). Nitrogen content tends to peak during green-up or late spring (Lenart et al., 2002; Shively et al., 2019). Female moose dry matter intake also peaks at this time and then decreases in conjunction with increasing temperatures (possibly related to heat discomfort) and acid detergent fibre (Shively et al., 2019). Cool, wet spring weather may delay phenology, granting access to higher quality vegetation for longer (Pettorelli et al., 2007). Even a small increase in vegetation quality can have large consequences in weight gain and/or probability of conception (White, 1983; Cebrian et al., 2008). Additionally, leaf tannin content also tends to be lower in cool, cloudy summers, which may improve protein digestibility (Bø and Hjeljord, 1991) as tannins can reduce protein digestion by more than a third (McArt et al., 2009; Spalinger et al., 2010). This coincides with the interaction between temperature and precipitation found in both the extreme spring temperature models. Interactions between precipitation and temperature on plant growth have been demonstrated previously, with increased precipitation and warming leading to increased growth and/or reduced precipitation in combination with warming resulting in reduced productivity

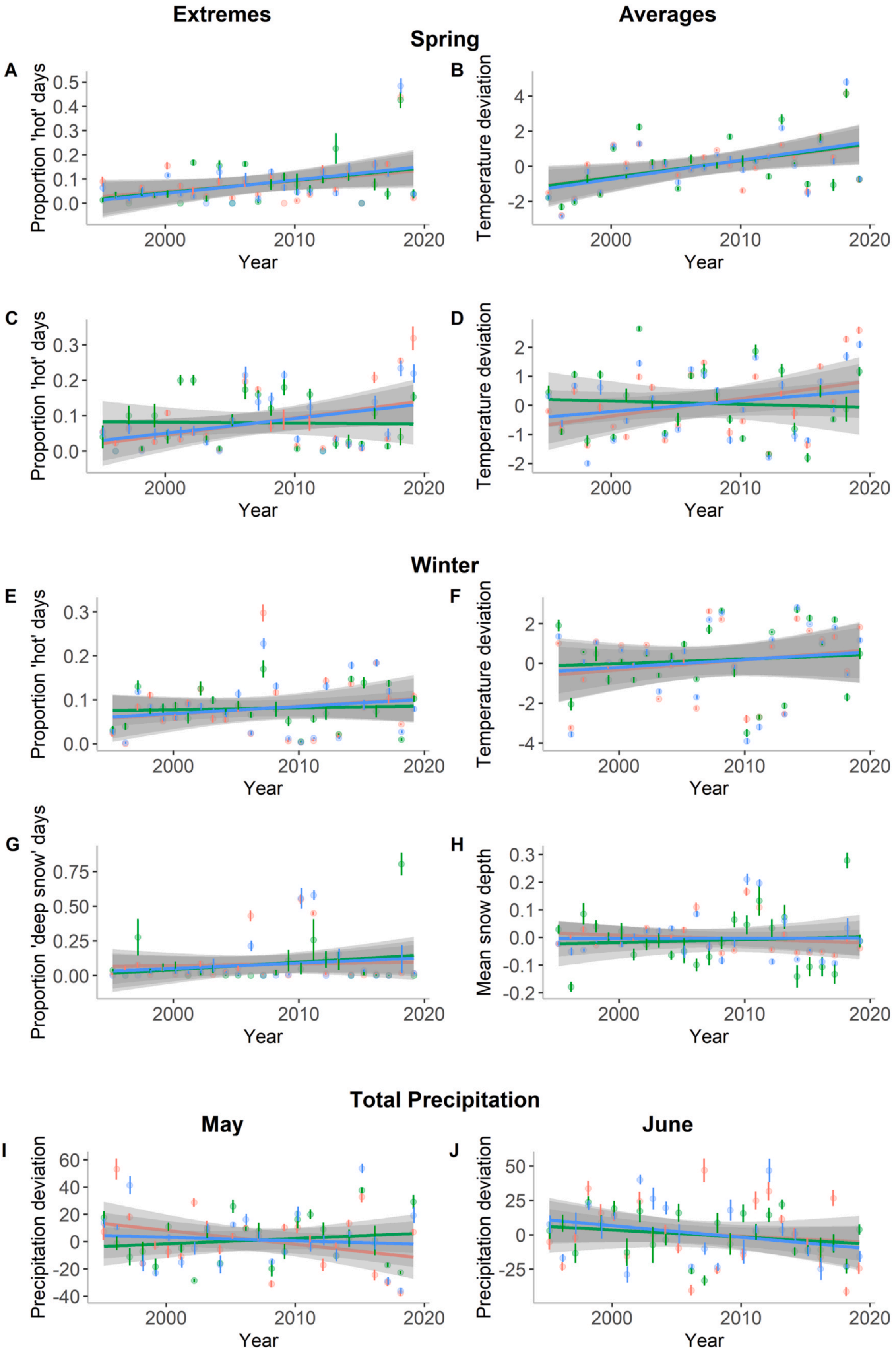

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Fig. 3. Annual trends in climatic variables across the three regions of Sweden. Norrland is represented by green, Svealand by blue, and Götaland by red. Points represent the average value across counties within a region, and linear regression lines and standard error bars are included. A,B and I depict weather in May; C,D and J represent June weather; E-H show winter (December-March) weather. See Methods for calculation of climatic variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Fixed factor estimates for Model 1 (extreme spring temperatures and precipitation on deviation from mean calf mass).

Variable	Estimate	SE	*t*-value	Confidence Interval 2.5%	Confidence Interval 97.5%
Intercept	-0.4959	0.2587	-1.9167	-1.0054	0.0135
Proportion ‘hot days’ (May)	-0.4484	0.1525	-2.9408	-0.7487	-0.1482
Proportion ‘hot days’ (June)	0.0684	0.1293	0.5295	-0.1860	0.3229
Total precipitation (May)	0.0626	0.1265	0.4950	-0.1865	0.3117
Total precipitation (June)	0.6195	0.1258	4.9229	0.3718	0.8673
May ‘hot days’ *precipitation	0.0637	0.1094	0.5825	-0.1517	0.2791
June ‘hot days’ *precipitation	0.4867	0.1494	3.2572	0.1925	0.7810

Table 2
Fixed factor estimates for Model 2 (average spring temperatures and precipitation on deviation from mean calf mass).

Variable	Estimate	SE	*t*-value	Confidence Interval 2.5%	Confidence Interval 97.5%
Intercept	-0.5422	0.2714	-1.9981	-1.0765	-0.0079
Mean temperature (May)	-0.6453	0.1123	-5.7455	-0.8665	-0.4242
Mean temperature (June)	-0.3358	0.1049	-3.2016	-0.5423	-0.1293
Total precipitation (May)	-0.1829	0.1239	-1.4759	-0.4268	0.0611
Total precipitation (June)	0.4028	0.1135	3.5484	0.1793	0.6263
May mean temperature *precipitation	0.1115	0.0718	1.5523	-0.0299	0.2528
June mean temperature *precipitation	0.1699	0.1017	1.6712	-0.0303	0.3700

Table 3
Fixed factor estimates for Model 3 (extreme winter temperatures and extreme snow depths on deviation from mean calf mass).

Variable	Estimate	SE	*t*-value	Confidence Interval 2.5%	Confidence Interval 97.5%
Intercept	-0.8836	0.2915	-3.0311	-1.4624	-0.3098
Proportion ‘hot days’ (Dec-Mar)	0.4394	0.1214	3.6187	0.1026	0.6024
Proportion ‘deep snow days’ (Dec-Mar)	-0.4069	0.1070	-3.8019	-0.6581	-0.2306

Table 4
Fixed factor estimates for Model 4 (mean winter temperatures and mean snow depths on deviation from mean calf mass).

Variable	Estimate	SE	t-value	Confidence Interval 2.5%	Confidence Interval 97.5%
Intercept	-0.9366	0.3294	-2.8430	-1.5847	-0.3459
Mean temperature (Dec-Mar)	0.6935	0.1270	5.4618	0.2284	0.7551
Mean snow depth (Dec-Mar)	-0.3524	0.1214	-2.9038	-0.7413	-0.2572

Table 5
Fixed factor estimates for Model 5 (extreme spring temperatures and precipitation on number of calves per female observed).

Variable	Estimate	SE	*t*-value	Confidence Interval 2.5%	Confidence Interval 97.5%
Intercept	-0.3496	0.0142	-24.6877	-0.3772	-0.3220
Proportion ‘hot days’ (May)	-0.0040	0.0046	-0.8850	-0.0130	0.0049
Proportion ‘hot days’ (June)	-0.0051	0.0036	-1.4119	-0.0120	0.0019
Total precipitation (May)	-0.0015	0.0037	-0.3960	-0.0087	0.0058
Total precipitation (June)	-0.0030	0.0031	-0.9838	-0.0090	0.0030
May ‘hot days’ *precipitation	0.0071	0.0031	2.2701	0.0010	0.0132
June ‘hot days’ *precipitation	0.0028	0.0031	0.8925	-0.0033	0.0089

Table 6
Fixed factor estimates for Model 6 (average spring temperatures and precipitation on number of calves per female observed).

Variable	Estimate	SE	t-value	Confidence Interval	
				2.5%	97.5%
Intercept	-0.3521	0.0141	-24.8911	-0.3797	-0.3245
Mean temperature (May)	-0.0064	0.0037	-1.7191	-0.0137	0.0009
Mean temperature (June)	-0.0129	0.0032	-4.0116	-0.0191	-0.0066
Total precipitation (May)	-0.0019	0.0035	-0.5422	-0.0088	0.0050
Total precipitation (June)	-0.0034	0.0031	-1.0860	-0.0095	0.0027
May mean temperature *precipitation	0.0030	0.0026	1.1428	-0.0021	0.0080
June mean temperature *precipitation	-0.0002	0.0030	-0.0638	-0.0061	0.0057

Table 7
Fixed factor estimates for Model 7 (extreme winter temperatures and extreme snow depths on number of calves per female observed).

Variable	Estimate	SE	t-value	Confidence Interval	
				2.5%	97.5%
Intercept	-0.3550	0.0140	-25.2897	-0.3825	-0.3275
Proportion ‘hot days’ (Dec-Mar)	-0.0030	0.0030	-1.0014	-0.0089	0.0029
Proportion ‘deep snow days’ (Dec-Mar)	-0.0183	0.0033	-5.5430	-0.0248	-0.0119

Table 8
Fixed factor estimates for Model 8 (mean winter temperatures and mean snow depths on number of calves per female observed).

Variable	Estimate	SE	t-value	Confidence Interval	
				2.5%	97.5%
Intercept	-0.3546	0.0141	-25.1472	-0.3822	-0.3269
Mean temperature (Dec-Mar)	-0.0049	0.0038	-1.2851	-0.0123	0.0025
Mean snow depth (Dec-Mar)	-0.0180	0.0040	-4.5578	-0.0258	-0.0103

Table 9
Fixed factor estimates for Model 9 (lagged extreme spring temperatures and precipitation on number of calves per female observed).

Variable	Estimate	SE	t-value	Confidence Interval	
				2.5%	97.5%
Intercept	-0.3507	0.0142	-24.6682	-0.3784	-0.3230
Proportion ‘hot days’ (May)	-0.0022	0.0047	-0.4812	-0.0113	0.0068
Proportion ‘hot days’ (June)	0.0078	0.0035	2.2540	0.0011	0.0146
Total precipitation (May)	-0.0004	0.0039	-0.0935	-0.0079	0.0072
Total precipitation (June)	0.0022	0.0031	0.7302	-0.0038	0.0082
May ‘hot days’ *precipitation	0.0011	0.0035	0.3243	-0.0057	0.0079
June ‘hot days’ *precipitation	0.0067	0.0029	2.3089	0.0010	0.0123

Table 10
Fixed factor estimates for Model 10 (lagged average spring temperatures and precipitation on number of calves per female observed).

Variable	Estimate	SE	t-value	Confidence Interval	
				2.5%	97.5%
Intercept	-0.3552	0.0142	-24.9712	-0.3830	-0.3275
Mean temperature (May)	-0.0003	0.0042	-0.0758	-0.0086	0.0079
Mean temperature (June)	0.0002	0.0032	0.0690	-0.0060	0.0065
Total precipitation (May)	-0.0021	0.0037	-0.5692	-0.0094	0.0052
Total precipitation (June)	0.0021	0.0033	0.6488	-0.0042	0.0085
May mean temperature *precipitation	-0.0034	0.0029	-1.1833	-0.0090	0.0022
June mean temperature *precipitation	0.0063	0.0030	2.0990	0.0004	0.0121

(Wu et al., 2011; Hoeppner and Dukes, 2012). This indicates that at least some of the relationship between spring climatic factors and calf mass and recruitment may occur via variation in vegetation quantity.

While heavier calves were associated with shallower snow, as expected, counter to our predictions, heavier calves were associated with warm winters. Despite the negative impact on neonatal survival, warm, wet winters tend to be followed by earlier, longer, and more spatially variable growing seasons with increased forage availability and quality, promoting compensatory growth (Post and Stenseth, 1999; Forchhammer et al., 2001; Kreyling, 2010). This may be the case in the south of Sweden, where winter precipitation more likely falls as rain. Biomass and/or digestibility may be higher for some forage when

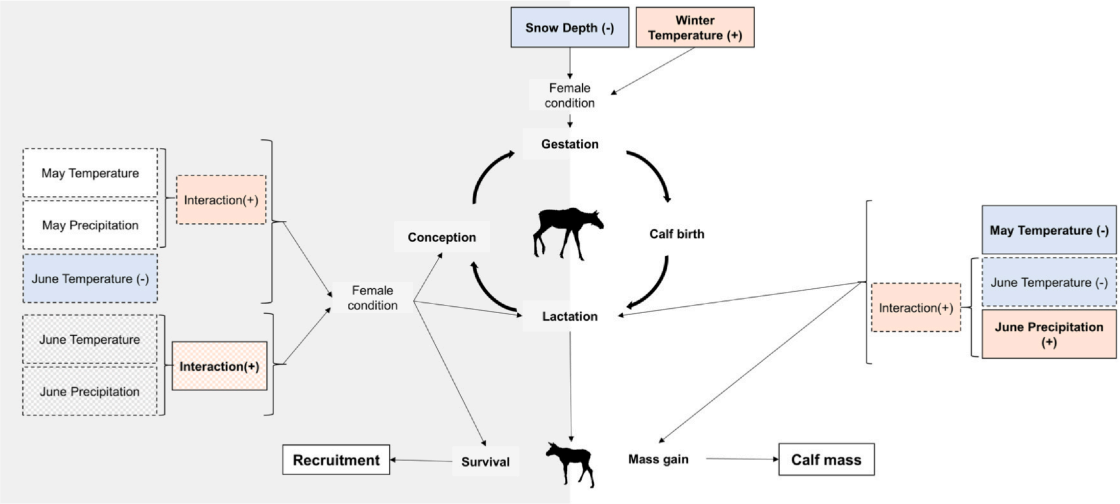

Fig. 4. Summary of results for models one through ten, relating weather to calf mass and recruitment (based on the number of calves per female). A dashed box and plain text denotes a variable that was included in either the extreme weather or the average weather models but not both. Bold text and solid box indicate a variable that was consistent across extreme and average models. A (-) next to a factor and a blue background reflects a negative relationship between that factor and the response variable throughout the 95% confidence interval for that factor. A (+) next to a factor and an orange background reflects a positive relationship, and no sign indicates that the variable itself was not included in any models without an interaction effect. A chequered background refers to a lagged effect from weather the previous spring. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

snowmelt is earlier, for example (Van der Wal et al., 2000; Cebrian et al., 2008). On the other hand, deep snow in higher altitudes or latitudes is more likely to delay vegetation emergence in the spring (Pettorelli et al., 2005b; Lesica and Kittelson, 2010) and result in a shorter vegetation period (Ericsson et al., 2002). It may therefore be useful to examine regional differences in both climatic and moose population trends (see below for further discussion).

In contrast to the main factors influencing mass, the number of calves per female may rely mainly on female body condition at conception and through gestation. Studies suggest that neonatal survival in ungulates is impacted by poor female condition when gestating in deep snow (Post and Stenseth, 1999; Forchhammer et al., 2001). Indeed, ‘deep snow’ years, and years with deeper snow on average, were associated with fewer calves in this study. This corresponds with deep snow limiting female access to forage in the field layer (Månsson, 2007) and restricting movement, particularly at depths over 70 cm (Sweanor and Sandegren, 1989), constraining allocation of energy and nutrients to foetal growth (Post and Stenseth, 1999). Winter conditions preceding birth may also have a strong influence on calf survival in the period of lactation, potentially via low birth mass or poor nutrition (Allen et al., 2017). Females that lost less mass over winter were more likely to give birth, but also to have calves survive to autumn in one Norwegian study (Milner et al., 2013).

While vegetation quality and female energy balance at parturition are likely important for early calf survival via lactation, the relatively strong relationship of recruitment to the interaction between temperature and precipitation the previous June suggests that female body condition at the start of pregnancy could also be very important to fecundity and early calf survival the following spring/summer. The effect of food availability during lactation on next year’s reproductive performance via female condition has been suggested previously (e.g., Festa-Bianchet, 1998; Ericsson et al., 2001; Parker et al., 2009). Moose are considered capital breeders (Ericsson et al., 2001) with pregnancy rates, calving rates, calf mass, and early survival relating positively to pre- and mid-winter female condition (Sand, 1996; Testa and Adams, 1998; Keech et al., 2000b; Milner et al., 2013). A similar pattern was seen in several populations of Shiras moose (Monteith et al., 2015). Recruitment declined the year after warm annual temperatures and/or a dry spring/summer, likely due to high thermoregulatory costs or reduced nutrition due to shortened high-quality forage availability (Monteith et al., 2015). It is worth noting that even though the weather trends observed in this study were not strong, the high variability that we see across years (predicted to increase with climate change; Hoegh-Guldberg et al., 2018) could negatively impact moose populations if it results in more hot, dry springs or winters with deeper snow.

The effects of temperature may depend in part on precipitation type or vegetation phenology (Loison et al., 1999a). This may be particularly relevant in Sweden as the start of the growing season can vary by up to a month along a north to south gradient (Neumann et al., 2020). The effects of precipitation also vary across latitude, with differences between northern and southern counties in water deficiency (Belyazid and Zanchi, 2019) and the proportion of precipitation accumulating as snow depth. This climatic and phenological variation suggests that region-specific patterns may be worth examining. This is further supported by our observation that the proportions of light and heavy calves in Norrland show contrasting trends to those in Götaland and Svealand (Fig. 2). Northern populations calve prior to green-up (Neumann et al., 2020), and contain more migratory moose (Allen et al., 2016), both of which may buffer populations against the indirect effects of weather via forage quality (Mysterud et al., 2001a; Pettorelli et al., 2005a; Hebblewhite et al., 2008; Neumann et al., 2020). Examining differing trends across a large latitudinal gradient may be particularly relevant for addressing the widespread declines in southern moose populations globally (Murray et al., 2006; Dou et al., 2013; Monteith et al., 2015; Schrempp et al., 2019).

It is important to note that there are many non-climatic factors that can influence mass, fecundity, and/or survival in ungulates, some of which may interact with climatic factors (e.g., Herfindal et al., 2006a). These include population density (Forchhammer et al., 1998; Kjellander et al., 2006; Tveraa et al., 2013), maternal effects (age, previous reproduction, cohort effects) (Forchhammer et al., 2001; Feder et al., 2008; Bårdsen and Tveraa, 2012), birth date (Feder et al., 2008), topography (Mysterud et al., 2001a, 2001b; Pettorelli et al., 2005a), latitude (Sæther, 1985; Sand et al., 1995), and harvest rate (Proaktor et al., 2007; Sand, 1996). While we do not have the detailed data to account for many of these, age structure of hunted females is similar both across our study regions and over time (Fredrik Widemo, unpublished data). Additionally, the current population density of moose in Sweden is less than half as compared to the peak in the early eighties and the population has decreased by 15% during our study period (Älgdata, 2020). Thus, we think it is unlikely that decreasing recruitment or calf weights are due to density dependent effects. Predation in Sweden disproportionately impacts central (grey wolf and brown bear) and northern (brown bear) populations (e.g., Swenson et al., 2007; Sand et al., 2008), therefore the apparently similar recruitment that we see across Sweden (Fig. 2) suggests that other factors (e.g., climate) may act disproportionately on southern populations.

We have focused on moose calves as a single stage in the life cycle of moose. While other life history stages may also be impacted by climatic factors, this stage is highly relevant for the relationship between climate and demography, as calves show increased susceptibility to environmental conditions due to small size, lack of reserves, and high metabolism (Parker et al., 2009). Further, early growth can influence juvenile overwinter survival (Parker et al., 2009), as well as adult size and reproduction (Albon et al., 1987; Festa-Bianchet et al., 1997; Gaillard et al., 1997, 2003; Keech et al., 2011). Such cohort effects, where conditions in the spring/summer of birth have lasting impacts on adult mass and reproductive success (Albon et al., 1987; Solberg et al., 2008), demonstrate that both gradual trends and rare, acute weather events can have time-lagged impacts on population demography several years into the future, and are thus important to monitor and counteract, if possible.

While we were not able to compare extreme weather and averages directly, we found many similarities across paired models, particularly for winter effects and lagged effects. Given the similar trends between extreme and average temperature values, it may be difficult to disentangle the effects of these variables on coarse-scale factors like annual demographics. Such effects may need to be traced to changes in individual condition over a shorter timescale. There were, however, a few disparities between models with extreme versus average weather. Interactions, for example, were more common between ‘hot days’ and precipitation than between mean temperatures and precipitation. This could relate to the fact that elevated mean temperatures could result from a few very ‘hot days’ or from several above average days but no ‘hot days’. As noted, high temperatures combined with low precipitation are known to reduce productivity, likely due to water stress (Hoeppner and Dukes, 2012). If there is a temperature threshold above which evapotranspiration strongly increases, reducing water availability for food plants, this could explain why this interaction shows only in the extreme temperature models. Alternatively, given that ‘hot days’ were based on daily maximum temperatures instead of daily averages, more rainfall could be associated with shorter hot periods in the day and greater cooling periods associated with rain, reducing the direct thermoregulatory stress of these periods of maximum temperature. Such differences suggest that for future studies it may be valuable to investigate not only averages, but also the frequency of rare, intense events when considering declines in mass or recruitment. It is also possible that important biological thresholds, such as physiological and behavioural responses to heat stress (Renecker and Hudson, 1986; Owen-Smith, 1998; Melin et al., 2014; Herberg, 2017; Ditmer et al., 2018) may better capture moose responses to climate change. Studies have shown that, despite individual variation, biological thresholds may still be apparent when using pooled population data (Lenarz et al., 2009; Melin et al., 2014). Additional thresholds that may be relevant include snow depth thresholds for limiting browsing or movement (Sweanor and Sandegren, 1989; Månsson, 2007) and water availability thresholds for reduction in protein or biomass of food plants (e.g., tree mortality due to hydraulic failure during severe drought; Urli et al., 2013; Choat et al., 2018). Note that some of these thresholds may not have been identified yet, and studies will require data on a finer spatial (and ideally temporal) scale, to pinpoint locations and times when a threshold is crossed.

The moose is an iconic species and culturally important for communities across the northern hemisphere. Moose is also the dominant ungulate across the world’s boreal zone and plays a central role in the functioning of boreal ecosystems (Pastor et al., 1988). Declines in moose populations will thus have a major impact on the socio-ecological systems of the northern latitudes. In contrast to North American moose, we have not yet observed serious declines in populations of Eurasian moose. However, the significant and ongoing declines in calf mass in southern populations and calf recruitment throughout Sweden should serve as an early warning. This leads to the question: what can (Swedish) moose management do to counteract declining calf mass and early recruitment? We identify two main avenues, some of which may reinforce strategies already in place. First, we showed that spring conditions may affect calf recruitment the next year. This gives management the time to adjust harvest quotas. Concretely, our results would argue for reduced harvest of reproductive females subsequent to hot and dry springs. Secondly, we showed that spring conditions affect calf mass the following autumn and discussed that this is likely, at least partly, due to effects of spring weather on forage plants. Moose management may thus also need to ensure “foodscapes” that support moose populations through harsh years. This could include maintaining landscapes with both food (e.g., young successional forest with a well-developed field layer; Van Beest et al., 2012) and thermal shelter (e.g., mature conifer forest with dense canopy cover; Van Beest et al., 2012) to facilitate an energy-maximising strategy by moose under heat stress (Van Beest and Milner, 2013). Wetland areas may also provide important thermoregulatory benefits for moose as temperatures rise (Laforge et al., 2016) and forage quality could also be increased through retaining more water at the landscape level, especially during dry years. While well-drained areas may be more valuable in wet years and wet areas more important in dry years (Campbell et al., 2013), we see that recruitment and mass are currently lower following hot, dry years so increasing the proportion of wet areas may better balance forage availability and quality across years to support stable moose populations. Water deficiency during the growing season is forecasted for all of Sweden, posing future challenges for the forestry industry (Belyazid and Zanchi, 2019) so increasing water availability may benefit forestry efforts in the future. Additionally, managing forests to have a rich field and shrub layer has been shown to positively impact calf body mass in southern Sweden (Felton et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01594.

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