Breeding phenology of a semi-domesticated reindeer (*Rangifer tarandus*) population in response to climatic variability

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ABSTRACT

Breeding phenology of a semi-domesticated reindeer (*Rangifer tarandus*) population in response to climatic variability

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The timing of reproduction in plant and animal species is a strong determinant of offspring viability and reproductive success. The large changes in climate reported the last decades could therefore have unprecedented consequences on population dynamics. The breeding time of many species have changed over the past two to three decades in response to climate change, and a developing trophic mismatch between the peak of energy demands by reproducing animals and the peak of forage availability has caused many species' reproductive success to decrease. The main aim of this thesis was to determine how reproductive phenology of reindeer (*Rangifer tarandus*) responds to the changes in its environment and whether there could be resulting fitness consequences. Using long-term datasets of 45 years of birth dates, 13 years of mating behaviors and 14 years of copulation dates of a semi-domesticated reindeer population in Kaamanen, northern Finland, I showed that both the reindeer timing of mating and timing of calving have occurred earlier over time, in response to climate. Climatic variables at four key periods in the reproductive cycle of reindeer were identified as driving the changes in reindeer breeding phenology: winter, late winter/early spring, summer and autumn. Those phenological changes allowed reindeer to keep track of its changing environment, leading to an improvement in females' reproductive success. I also found a "head-start" benefit with some females always doing better than others do. However, a later vegetative senescence in autumn negatively affected females' physical condition in winter and the subsequent calf's birth weight and calf's first-summer survival. If climatic changes were to exacerbate, the population dynamics of several ungulate species will certainly be affected.

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Contribution of Authors

I was the principal investigator for all the research work and as first author, I was responsible for the data analyses, the writing of manuscripts related to this thesis and the writing of this thesis. The manuscripts were all co-authored by Dr. Robert Weladji, Dr. Øystein Holand and Dr. Jouko Kumpula. Dr. Robert Weladji advised on the interpretation of the results, reviewed and corrected the manuscripts. Dr. Øystein Holand and Dr. Jouko Kumpula both reviewed and corrected the manuscripts.

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Reindeer females with ear tags and colored collars, Kaamanen, Finland, 2016 © Paoli A

Chapter 1 General Introduction

Among the environmental, phenotypic, and genetic factors affecting reproductive success of many species, the timing of reproduction appears to be a strong determinant of offspring viability and therefore reproductive success [animals (birds: Verhulst et al. 1995; Verhulst and Nilsson 2008, fish: Wright and Trippel 2009, mammals: Clutton-Brock et al. 1982; Bowyer et al. 1998; Holand et al. 2006), plants (Harper 1977; Dieringer 1991)]. For animals living in seasonal environments in particular, the timing of reproduction is a key step in the annual breeding cycle, as being strongly associated with fitness (Daan and Tinbergen 1997; Houston and McNamara 1999) and as environmental conditions (e.g. food supply) are favorable only for a limited period. Indeed, the timing of reproduction evolves for a balance between probability of offspring survival and future reproductive success of females (Clutton-Brock 1988). Juvenile survival, more specifically, was shown as being the most critical component of mammal reproductive success (Clutton-Brock 1988) and of large herbivores' population dynamics (Gaillard et al. 2000). Thus, large herbivorous mammals are expected to maximize their reproductive success and recruitment rate by adjusting their timing of reproduction accordingly, to favor juvenile survival.

The immature stage is the most vulnerable time in the life of animal species (Gaillard et al. 2000), affected primarily both by food resources and predation. A review made by Linnell et al. (1995) showed that predation accounted for an average of 67% ± 33 of neonatal mortality of northern and temperate ungulates in areas with predators whereas mortality rates due to predation for adults caribou (*Rangifer tarandus caribou*) in Alberta, Canada was around 9.8% (McLoughlin et al. 2005). In a context of predation risk, two types of young can be found in ungulate species: the 'hiders' remain hidden and largely immobile during the first few days/weeks after birth whereas the 'followers' accompany their mothers as soon as they are able to stand (Estes 1976; Rutberg 1987). In a context of seasonality in the availability of the resources, the mating phenology as a precursor of the calving phenology is a key mechanism to insure that young are born in the period of the year most suited for their development and survival (Rachlow and Bowyer 1991; Suttie and Webster 1995; Bronson 2009). Consequently, breeding phenology resulting from thousands of years of evolution is expected to reflect the species' adaptation to its environment. For instance, the synchrony of births after years of high dry season rainfall was higher in both topi (*Damaliscus korrigum*) and warthog (*Pharcocoerus aethiopicus*) in Mara-Serengeti, equatorial

Eastern Africa (Ogutu et al. 2010) but their calving synchrony was still much lower than temperate ungulates inhabiting highly seasonal environment, such as the Norwegian roe deer (*Capreolus capreolus*) (Linnell and Andersen 1998), Scottish red deer (*Cervus elaphus*) (Clutton-Brock et al. 1982), Alaskan moose (*Alces alces gigas*) (Bowyer et al. 1998), Alaskan caribou (Adams and Dale 1998) and American mountain goat (*Oreamnos americanus*) (Côté and Festa-Bianchet 2001). The phenology can be defined as the study of periodic biological events of plants and animals such as flowering, breeding and migration in relation to biotic and abiotic factors causing their timing (Leith 1974). Although the fitness consequences of variation in phenology of reproduction and its related seasonal patterns in reproductive success have been described extensively (e.g. for birds: Perrins 1970), the causes of these seasonal patterns are still poorly understood.

1.1 Mating phenology

The mating phenology is defined in this research as both the timing and the synchrony, i.e. the length of the mating season. The mating season of ungulates starts when males exhibit all behaviors and activities associated with the rutting season (e.g. holding and defending a harem of females in red deer; Moyes et al. 2011) and is regulated by climatic conditions both directly (i.e. as proximate factors) through influencing rut and estrus, and indirectly (as ultimate factors) through survival of the young.

1.1.1 Timing of mating

The proximate causes of the timing of the mating season were documented to be (1) external factors such as phenology and abundance of plants (Bunnell 1982; Cook et al. 2004), photoperiod in autumn as a cue to entrain the circannual program governing reproductive function (Thompson and Turner 1982; Suttie and Webster 1995); and (2) internal factors such as pheromones and social cues which probably synchronize gonadal cycles among deer males (Suttie and Webster 1995; Whittle et al. 2000), different sex ratios (Holand et al. 2002), age structure with large males initiating earlier ovulation in females (Noyes et al. 1996, 2002; Weladji et al. 2002a; Røed et al. 2007), and pre-rut physical condition linked to body reserves of individuals (Reimers 1983, 1997; Lenvik 1988; Barboza et al. 2004). For females in particular, the variation in conception time is related to their age and weight (Ropstad 2000), which represent the maternal nutrition and body condition (Cameron et al. 1993). For instance, older and heavier reindeer females mated earlier in Kaamanen, Finland (Mysterud et al. 2009), but when the physical

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condition of females was reduced, estrus and subsequently conception date were delayed or gestation length prolonged (Flydal and Reimers 2002). In summary, the timing of the mating season appears to be mainly related to (1) the individuals' physical condition dependent on forage resources in spring/summer before conception and (2) to day length as photoperiod is an important environmental cue for deer species to trigger their reproduction, while ambient temperature, nutrition state and behavior exert a modulator effect (Rosa and Bryant 2003; Williams et al. 2017). Unlike temperature, however, day length is a stable, abiotic environmental factor that does not change with climatic variation (Saikkonen et al. 2012). Consequently, photoperiod will not be considered in this study. The ultimate cause of the mating time is exerted by a genetic control where mating is precisely timed so that young are born at the period of the year maximizing their chances of survival (Rachlow and Bowyer 1991; Suttie and Webster 1995; Bronson 2009), balancing adequately the population's recruitment rate with the adults' probability of survival to the next breeding season (Clutton-Brock 1988; Skogland 1989). The action of climate will therefore result in the evolution of mating at the optimal time for survival and recruitment of young.

1.1.2 *Mating synchrony*

Reproductive synchrony acts as a strategy that animals adopt to maximize reproductive success (Ims 1990). It has been defined as the "tendency of individuals to carry out some part of the reproductive cycle at the same time as other members of the population" (Ims 1990). Depending on the sociobiological and ecological conditions in which populations reproduce, however, the best strategy might be asynchronous reproduction (Ims 1990). For instance, in species where paternal investment is unimportant, asynchronous breeding might allow receptive females to attract more males and therefore optimize mate choice than when other receptive females are around (Ims 1990). An asynchronous reproduction in plant species might also promote outcrossing in animal-pollinated plants and is predicted to be the best strategy for maximizing visitation rates of pollinators and seed dispersers (Young 1988). Sociobiological factors might, on another hand, induce reproductive synchrony. For example, social stimuli exchanged between neighboring females in birds (Gochfeld 1980) and mammals (including humans) (Estes 1976) induce synchronous reproduction. As such, just before the mating season, the gregarious migratory behavior of caribou forms large herds of hundreds or thousands (e.g. caribou in Newfoundland,

Lent 1965) and brings the males and females together which allows external proximal factors to synchronize mating (Lent 1966; Dauphiné and McClure 1974). In a bird population, female European starlings (*Sturnus vulgaris*) synchronized their clutch initiation dates in response to the presence of conspecifics (Evans et al. 2009). The biostimulation (sight, sound, odor or touch) provided by the male presence in ungulates can synchronize females' heats with those of adjacent females and thus have a synchronizing effect on ovulation (Langvatn et al. 2004) and mating (Lent 1965; Fraser 1968). When reindeer males are herded in a compact group and that density increases, the level of sexual excitement increases, as well as the intensity of the rut because of mutual stimulation (Lent 1965; Baskin 1970), leading to earlier and more frequent copulations than when animals are not herded together (Dauphiné and McClure 1974).

Ultimately, the mating synchrony reflects the need for mammals in highly seasonal environments to synchronize their births at a period of the year when environmental conditions are optimal for reproductive success of females and survival of young (Sadleir 1969; Rachlow and Bowyer 1991; Bronson 2009). The mating period genetically fixed in the individual genotypes will ensure that the birth period is concentrated to this favorable time (Sadleir 1969; Clutton-Brock 1988). The length of the mating season is thus influenced by sexual biostimulation directly linked to population density and constrained by the length of the calving season.

1.2   Calving phenology

As ultimate cause of the mating phenology, calving phenology is the most important and studied part of the ungulates reproduction and is one of the principal factors affecting calf survival and female fitness in ungulates (Bunnell 1982). Calving phenology includes timing of birth and calving synchrony.

1.2.1   Timing of births

The timing of the calving season is the most studied parameter of the reproductive phenology in ungulates. Indeed, many factors have been reported to influence timing of births: photoperiod (Goldman 2001), latitude (Thompson and Turner 1982), forage availability and quality (Festa-Bianchet 1988; Bowyer et al. 1998), plant phenology (Bunnell 1982; Thompson and Turner 1982; Post et al. 2003; Cook et al. 2004), snowfall and snow cover (Thompson and Turner 1982; Adams and Dale 1998), population density (Forchhammer et al. 2001; Nussey et al. 2005a),

male age structure and population sex-ratio (reviewed in Mysterud et al. 2002), pre-rut body weights and body conditions (Reimers 1983; Lenvik et al. 1988; Cameron et al. 1993; Flydal and Reimers 2002), conception date (Holand et al. 2002; Clements et al. 2011), gestation length (Mysterud et al. 2009; Clements et al. 2011), predation (Post et al. 2003).

Maternal condition plays an important role in the timing of parturition and includes, among other factors: winter and spring nutrition (Parker et al. 2009), body mass (Reimers et al. 1983; Cameron et al. 1993; Flydal and Reimers 2002), body protein level (Barboza and Parker 2008), age and previous year reproductive status (Guinness et al. 1978; Clutton-Brock et al. 1982; Coulson et al. 2003) and social rank (Holand et al. 2004). In species with behavioral dominance, the factors linked to maternal condition can also interact together since older and heavier females can have a higher social rank in the hierarchy, more access to forage resources and consequently a better reproductive status with early births (Ropstad 2000; Holand et al. 2004). The conception date is another important determinant for birthdate in ungulates, which is in turn determined by the timing of estrus and the ovulation rates (Holand et al. 2002; Langvatn et al. 2004; Clements et al. 2011). Ovulation rates are also related to females' body weight reflecting their nutritional status at the mating season (Langvatn et al. 1996). As a consequence, all environmental factors acting on forage availability and therefore on pre-rut maternal condition of both caribou (Bergerud 1975; Cameron et al. 1993; Adams and Dale 1998) and reindeer (Reimers et al. 1983) may determine indirectly timing of births. It could be the amount of snowfall the winter prior to conception (Adams and Dale 1998), or the wind chill and insect harassment (Weladji et al. 2002a, 2003a). Despite maternal condition having an influence on parturition date and subsequent female's reproductive success (through a maternal-offspring inheritance of genetic and phenotypic components), studies quantifying the relative influence of female conditions early in life on birth dates of mammalian species are still missing.

The onset of the plant growing season is likely the best factor determining the timing of births in ungulates, as has been shown for different North American Mountain sheep species (Bunnell 1982). An adequate timing between births and the start of the vegetative growth season will enhance (1) the survival and growth of offspring as well as (2) the survival and reproductive success of their mother (Rutberg 1987). Individuals born outside the optimal period for births will have lower probabilities to survive (Bunnell 1982; Gaillard et al. 1993) because (1) they will be

more vulnerable to predation by bears, golden eagles and other predators (Eloranta and Nieminen 1986; Nieminen et al. 2013), (2) if born too early, mothers can be in negative energy balance therefore producing a low-quality milk before food availability increases during spring (Guinness et al. 1978; Rachlow and Bowyer 1991) and (3) if born too late, young will be more susceptible to insect harassment and summer heat (Kumpula and Nieminen 1992; Weladji and Holand 2003b) and will not accumulate enough resources; ultimately reducing their survival rate during summer season, and during their first winter thereafter (Festa-Bianchet 1988; Côté and Festa-Bianchet 2001). Hence, the timing of the calving period has been intensively studied and is affected by both external and internal factors.

1.2.2   Calving synchrony

The calving synchrony – an index of the length of the births season – has been by far less studied than the calving date. Variability in birth-season lengths is commonly invoked as an adaptation to seasonality in forage availability and predation risk (Estes 1976; Estes and Estes 1979; Rutberg 1987). Birth synchrony as a mean to reduce predation is explained by several hypotheses: first, the 'saturation hypothesis' suggests that predators will be overwhelmed if all young are born in a brief period (Rutberg 1987; Sinclair et al. 2000); second, adults breeding synchronously could use vigilance to detect predators more efficiently; third, the 'confusion hypothesis' states that a high number of young in a group will decrease the predator's capacity to pursue a specific target (Estes and Estes 1979; Rutberg 1984). Thus, predation pressure promotes a short birth peak, by selecting against calves born outside the peak of parturitions and would favor an aggregated over a dispersed spatial distribution (Estes 1976). The wildebeest (*Connochaetes taurinus*) provides the best known example of synchronized calving, where predation pressure by the hyena (*Crocuta crocuta*) results in females with small young joining herds and in synchronous calving (Estes 1976). Nevertheless, many studies on northern ungulates have shown that climatic variability and therefore plant phenology contributed more than predation in constraining timing and synchrony of births, in Dall's sheep (*Ovis dalli*) (Rutberg 1984; Rachlow and Bowyer 1991), bighorn sheep (*Ovis canadensis*) (Festa-Bianchet 1988), roe deer (Linnell and Andersen 1998), reindeer (Lent 1966) and caribou (Post et al. 2003).

A short growing season for vegetation in temperate or subarctic climates and a marked seasonality in forage availability are the main mechanisms explaining variation in synchrony of

ungulates' births (Gaillard et al. 1993) which was shown to strongly influence both perinatal and neonatal mortality of ungulates in seasonal environments (Bunnell 1982; Festa-Bianchet 1988). This is particularly evident in reindeer populations, which have to survive in the highly seasonal circumpolar environment. As an adaptation to their environment, the synchrony of their births increases significantly with a shortening of the snow-free season (Skogland 1989). To the best of my knowledge, however, no study has assessed the effects of climatic variability on calving synchrony of ungulate species, despite this question being of primary concern in a context of large changes in climate as recorded the last decades.

1.3   Climatic variability and ungulate species

Animal species have always been subjected to environmental variation which appears to be of the greatest importance in the population dynamics of large herbivores (Saether 1997; Gaillard et al. 1998; Forchhammer et al. 2001). For ungulate species in particular, climatic variability was shown to have both short- and long-term consequences. Short-term consequences could act through behavioral changes like a shift in feeding or migration strategy. At a broader time scale, climatic variation was shown to affect life history strategies generating impact years later on population dynamics of northern ungulates (Putman et al. 1996; Saether et al. 1998; Post and Stenseth 1999; Gaillard et al. 2000; Weladji et al. 2002a). For instance, red deer born following warm winters were smaller than those born after cold winters (Post et al. 1997). Such growth and development variability when individuals were *in utero* produced persistent cohort variability among adults (Post et al. 1997). Climatic effects on ungulates may also be subdivided into direct and indirect effects depending if climate acts directly on individuals' physical condition or indirectly through its effects on plant phenology.

1.3.1   Direct effects

Climatic effects on ungulates may be direct, acting on individuals' physical condition through behavior and physiology (metabolic and reproductive processes). For instance, an increase in snow depth may increase costs of locomotion (Parker et al. 1984) and severe cold may lead to higher costs of thermoregulation (Parker and Robbins 1985; Putman et al. 1996). Global climatic variation may also have direct pronounced effects on survival and reproductive success of large herbivores (Post et al. 1997). For example, the development and fecundity of red deer and Soay sheep (*Ovis aries* L.) in Norway and the UK are affected by increasingly warm winters (Post et al.

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1997; Forchhammer et al. 2001). The main negative consequences of the recent large changes in climate on ungulate species may be an increase of climatic extremes, with a negative influence on juvenile survival primarily during the winter (Kruuk et al. 1999; Milner et al. 1999; Post and Stenseth 1999), an increase in average monthly temperature leading to an increase in insect harassment in summer (Weladji et al. 2002a; Vors and Boyce 2009), a shift in distributions of species, poleward in latitude and upward in elevation (Walther et al. 2002). Increasingly warm and wet winters may, on another hand, favor large herbivorous ungulates because less snow in the low-elevation areas will decrease energetic costs of thermoregulation and movement (Mysterud et al. 2003).

1.3.2 Indirect effects

Climate may also act indirectly on ungulates through its effect on forage quality and biomass (review in Mallory and Boyce 2017 for *Rangifer*). For instance, deep snow cover or 'locked pastures' under an impenetrable layer of ice resulting from freezing rain events are an example of extreme icing event which restricts access to the field layer and to forage during winter for herbivores like *Rangifer* species (Aanes et al. 2002; Tyler 2010; Hansen et al. 2011); generating major die-offs, such as the past declines of the semi domestic Scandinavian reindeer (Tveraa et al. 2007). In an alpine reindeer, combination of icing conditions and deep snow in early winter reduced reproductive rate by 49% (Helle and Kojola 2008). Such extreme icing events are likely to cause declines in other reindeer populations across the circumpolar north (Vors and Boyce 2009; Mallory and Boyce 2017), according to the range and extent of predicted winter precipitation changes (Serreze et al. 2000; ACIA 2004). Furthermore, large changes in climate were shown to lead in the future to a changing forage quality and quantity in the summer (Epstein et al. 2000; Elmendorf et al. 2012; Pearson et al. 2013; Park et al. 2016), with poor summer forage conditions associated with reductions in life-history traits and increased overwinter mortality in caribou (Crête et al. 1993; Gerhart et al. 1996), and a changing spring phenology (Oberbauer et al. 2013; Park et al. 2016), that can lead to a 'trophic mismatch' with fitness consequences (see below). On the other hand, the timing of flowering was advanced in parallel with snowmelt (Parmesan and Yohe 2003; Menzel et al. 2006). Deep snow may also lead to an extended period of access to newly emergent high-quality forage (Albon and Langvatn 1992; Post and Stenseth 1999), favorable to

both red deer and sheep in Norway (Mysterud et al. 2003), to caribou in Greenland (Forchhammer et al. 2002) and more recently to sub-Arctic reindeer (Tveraa et al. 2013).

1.3.3   The Match-Mismatch Hypothesis

Due to the global climate change of the last decades, there is increasing evidence of a mismatch between the peak of resource demands by reproducing animals and the peak of forage availability that individuals rely on to ensure survival of the young (Post and Forchhammer 2008). The Match/Mismatch Hypothesis (MMH; Cushing 1990) as a way to estimate this time lag has been to date rarely applied on ungulates and with contradictory results (see Durant et al. 2005 and Plard et al. 2014 versus Post and Forchhammer 2008). The MMH is used to estimate the gap between the phenology of a species at the higher level (i.e. the predator) and that of species at the immediate lower level (i.e. the prey). The terms of 'predator' and 'prey' are used in the broadest sense of the words. For instance, grazers can be considered as predators and vegetation as prey. If there is a time lag between the food requirement and the food availability for the predator, i.e. a mismatch, then the survival and the reproduction of the predator are expected to be low (Durant et al. 2007). For example, the barnacle goose (*Branta leucopsis*), a long-distance migrating bird, has advanced its spring migration to match its rapidly warming Arctic breeding grounds (Lameris et al. 2018). However, a reduced offspring survival was still reported due to an increased phenological mismatch between the moment of gosling hatch and the peak in food quality (Lameris et al. 2018). In ungulates, the MMH has been first applied on the Soay sheep in Hirta, Outer Hebrides in Scotland but the temporal mismatch between vegetation peak and the average birth date did not affect the lambs' survival (Durant et al. 2005). On the same note, Tveraa et al. (2013) did not detect a negative mismatch between early spring onsets and subsequent recruitment in Fennoscandia. In the Low Arctic Greenland however, the onset of the plant growing season (accompanies warmer spring temperatures) has advanced whereas the caribou's timing of calving has not (Post and Forchhammer 2008). This 'trophic mismatch' diminishes both mother and calf's ability to exploit high-quality forage during a period of high energetic requirements (i.e. lactation, replenishing winter fat reserves, calf physical growth), thus contributing to reduced production and survival of caribou calves (Post and Forchhammer 2008). Because the parturition time of ungulates living in highly seasonal environments is timed to coincide with long-term patterns of climate and plant phenology as a way to offer a hospitable environment when rearing the young,

it would render seasonal breeders more sensitive to large changes in climate (Bowyer et al. 1998). *Rangifer* species in particular is circumpolar, usually subjected to high seasonality, and likely to be most affected by large changes in climate (Vors and Boyce 2009).

1.4 Reproductive system of Rangifer species

Rangifer species include both the caribou (North America) and the reindeer (Europe), with different subspecies found in tundra and forest habitats (Røed 2005). According to the taxonomic classification of the species, a total of eight subspecies has been described based on the ecological adaptations of reindeer/caribou: Arctic, tundra, barren-ground, woodland or forest (Røed 2005). In this thesis, the Eurasian tundra subspecies (*Rangifer tarandus tarandus*) was studied and, for ease, will be referred as reindeer. As they belong to the same species, their reproductive system is quite similar and will be detailed below, regardless of the sub-species. The reproductive system of *Rangifer* species has evolved as an adaptation to their migratory habit, a feeding specialization on graminoids, shrubs and lichens and social structure of large and mobile aggregations (Geist 1999). Specifically, the open habitats where they usually live and predation by wolves (*Canis lupus*) have promoted a gregarious instead of a solitary life (Dauphiné and McClure 1974). In contradiction, the combination of short legs, large fat depots and small neonates in reindeer present strong evidence of a long evolutionary history without predators (Skogland 1989; Geist 1999). The reindeer is also the only cerviae that has been domesticated (Røed et al. 2008) and the only one in which both sexes carry antlers (Geist 1999; Melnycky et al. 2013). Reindeer and caribou are polygynous – a male can impregnate one or several females and, like most temperate cervids, are seasonal breeders, with mating coinciding with the decreasing photoperiod in the autumn, and with calving in the spring (Ropstad 2000; Figure 1.1).

1.4.1 Mating phenology

The rut season in *Rangifer* starts in early September followed by the first copulations during the last days of September up to later October/early November (Skogland 1989; Figure 1.1). By the turn of mid-October over 90% of the females have ovulated (Eloranta and Nieminen 1986) and 90% of female reindeer are impregnated in a period from 10 to 21 days in September/October (Lenvik et al. 1988). Females that were not copulated during this period display a second estrous cycle (mean length 13-33 days, Ropstad 2000). The mating dates in caribou showed little variation from year to year (Bergerud 1975), with 80% of 64 conceptions occurring the first 11 days of a 4-

5 week mating period in the Canadian barren-ground caribou (Dauphiné and McClure 1974). In the Newfoundland caribou, the length of heat was about 48h and the estrous cycle lasted 10-12 days (Bergerud 1975). The observed gestation lengths in reindeer varied between 211 and 229 days (mean of 221 days) (Mysterud et al. 2009), after which births occur in the period from mid-May to mid-June in a highly synchronous pattern (Skogland 1989; Figure 1.1).

1.4.2 Calving phenology

The timing of births in wild reindeer and caribou is mainly determined by the conception date (Holand et al. 2002). *Rangifer* species produces 80-90% of their calves within a 10-day period and complete the calving season within 4-5 weeks (Lent 1966; Dauphiné and McClure 1974; Bergerud 1975; Figure 1.1). In the experimental reindeer herd in Kaamanen, Finland, most of the calving occurred on an average 19 days between May 10 and 29 and the peak of calving varied yearly between May the 15th and 25th (Eloranta and Nieminen 1986); after which calves are nursed by females until the next rut season in late September/early October (Figure 1.1). To maintain this highly synchronous birth season, conceptions must also occur synchronously in time during the rutting season (Skogland 1989). The polygynous mating system of reindeer is adapted to this time constraints of the conception-birth seasons with a highly effective courtship-mating system (see Skogland 1989 for further details). Reindeer is actually the species that exhibits one of the largest sexual dimorphisms among ungulates, with adult males attaining a mass up to twice that of females (Geist and Bayer 1988).
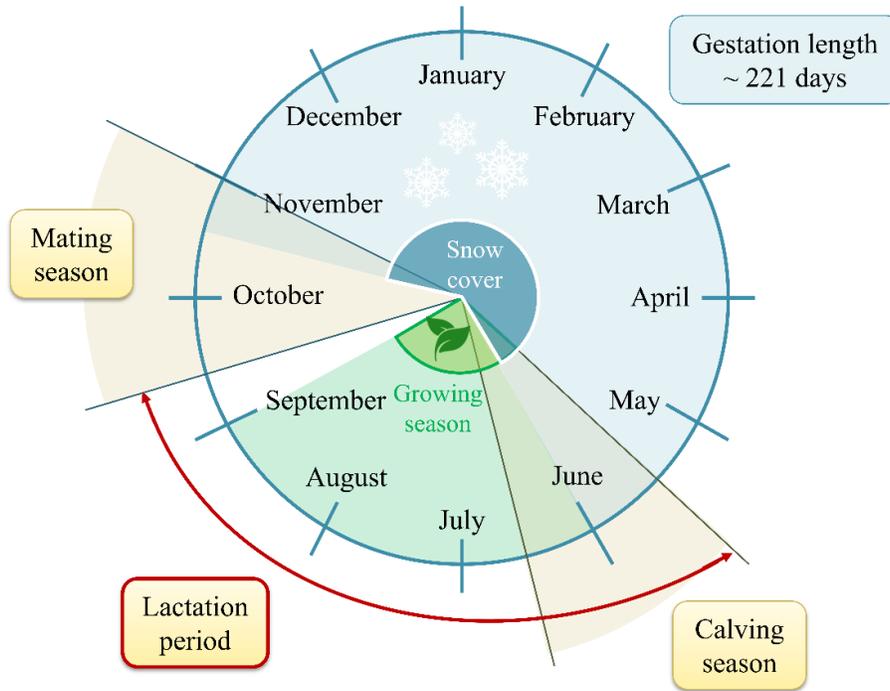
Figure 1.1 Schematic representation of the annual reproductive cycle of *Rangifer* species.

1.5 Objectives

Although phenological events in mammals can lead to wider ecological or evolutionary consequences (Réale et al. 2003), studies linking phenological changes in relation to climatic variability are limited. Furthermore, understanding what drives timing of reproduction is of primary concern for ungulate species since it determines later on individuals' reproductive success and the population's recruitment rate. The timing of births is mainly adapted to the subsequent peak of forage resources but in a context of climate change, the time lag between the birth period and the vegetative growing season is very likely to change. Mother characteristics like maternal physical condition also strongly determine the timing of births. Nevertheless, very few studies have highlighted whether the variation in birth dates of large herbivores can be explained by a maternal-offspring inheritance of such characteristics.

Rangifer is one of the two only ungulate species to have established in the highly variable Arctic environment, the other being muskoxen (*Ovibos moschatus*). *Rangifer* is the cultural and socioeconomic cornerstone of northern peoples throughout the circumpolar north and, herding and hunting have permitted these cultures to survive in a harsh and variable environment (Vors and Boyce 2009). However, the species has not received enough attention with respect to the global change debate. Body mass (Weladji and Holand 2003b) and offspring sex-ratio (Weladji and Holand 2003a) of reindeer have been investigated in relation to climatic variation, as well as caribou's timing of calving in relation to warmer spring (Post and Forchhammer 2008). Nevertheless, studies on the reindeer's mating time and calving phenology (date and season length) regarding the climatic variation are lacking. The main aim of this thesis is thus to investigate how the reindeers' reproductive phenology is affected by climatic variability.

Objective 1: The calving phenology in response to climatic variability. In Chapter 2, the direct effects of climatic variability on calving season (timing and length) were assessed using local weather variables (temperature, precipitation and snow depth). Since the timing of births is one of the most studied parameter of the reproductive phenology in ungulates, many factors were already reported to influence it. As such, after having controlled for the known effects of population parameters on calving date, I first assessed the direction and magnitude of the change over time of calving dates in the studied reindeer population. I then assessed which climatic variables would best explain the variation in calving time.

Objective 2: The mating time in response to climatic variability. Environmental conditions have a great impact on ungulates mating time: winter weather in elk (*Cervus canadensis*) (Cook et al. 2004); plant phenology in northern ungulates (Bunnell 1982) and resource availability in sheep (Rachlow and Bowyer 1991) acting through its effects on individuals' physical condition (Flydal and Reimers 2002; Barboza et al. 2004; Mysterud et al. 2009). However, to my knowledge, effects of climatic variation on reindeers' mating time have not been studied. To do so, the temporal trend of the mating season was first determined by quantifying the rate of change over time of its timing in Chapter 3. Then, how this temporal trend was explained by climatic variables was assessed.

Objective 3: The effects of conditions early in life on variation in calving date and plastic response to climatic variability. Maternal characteristics have been shown to exert a great influence on calving timing through maternal nutrition (Rowell and Shipka 2009); body weight (Reimers 1983, 1997; Cameron et al. 1993; Adams and Dale 1998; Flydal and Reimers 2002), body protein stores (Barboza and Parker 2008); physical condition (Cameron et al. 2005); age (Reimers 1983; Garel et al. 2009; Mysterud et al. 2009); reproductive status the previous year (Guinness et al. 1978; Feder et al. 2008); and social rank (Holand et al. 2004). For example, 90% of body fat depletion in female elk delayed calving date on average of 34 days (Cook et al. 2004). A maternal-offspring inheritance of genetic and phenotypic components (Weladji et al. 2006; Muuttoranta et al. 2013) could therefore provide a head-start benefit to females early in their reproductive life. However, in a context of global climate change where the timing of reproduction of many species was shown to have changed, the causes of the between-individual differences in phenotypic plasticity are still poorly understood. In Chapter 4, and based on conclusions drawn in Chapter 2, I tested whether an inter-individual heterogeneity in the plastic response of females' calving date to climatic variability was detected and further if conditions early in life could influence a female's calving dates throughout her reproductive life and the magnitude of her plastic response to climatic variability.

Objective 4: Applying the match-mismatch hypothesis on reindeer in Finnish Lapland. An earlier onset of the spring snowmelt and plant green-up have been predicted as an indirect consequence of climate change (Post et al. 2009; Park et al. 2016). To match this advanced peak of forage availability and to have access to high-quality vegetation to meet the energetic

requirements that the lactation involves (Clutton-Brock et al. 1989), reindeer's females are expected to give births earlier with climate change. However, Visser (2008) and Post and Forchhammer (2008) found that the shifts in phenological events in several bird species and in caribou respectively are insufficient to match the overall advancement of spring season across the northern hemisphere. By accelerating the rate at which spring advances, the climate warming may thus exacerbate the trophic mismatch between food requirements of predators and peak of its prey availability (Visser et al. 1998; Visser and Holleman 2001; Durant et al. 2007). Furthermore, the reindeer females give birth two to four weeks prior to snow melt and spring onset (Tveraa et al. 2013) for the lactation period to match the availability of high-quality forage (Kojola and Eloranta 1989; Reimers 2002), meaning that the peak of the calving season occurs before the peak of forage availability. In Chapter 5, the match-mismatch hypothesis was thus applied on reindeer to test the assumption that the trophic mismatch or time lag between the calving season and the plant growing season (the start in spring and the end in autumn) was changing over time.

Chapter 2 Winter and spring climatic conditions influence timing and synchrony of calving in reindeer

2.1 Abstract

In a context of climate change, a mismatch has been shown to occur between some species' reproductive phenology and their environment. So far, few studies have either documented temporal trends in calving phenology or assessed which climatic variables influence the calving phenology in ungulate species, yet the phenology of ungulates' births affects offspring survival and population's recruitment rate. Using a long-term dataset (45 years) of birth dates of a semi-domesticated reindeer population in Kaamanen, North Finland, we show that calving season has advanced by ~ 7 days between 1970 and 2015. Advanced birth dates were associated with lower precipitation and a reduced snow cover in April and warmer temperatures in April-May. Improved females' physical condition in late gestation due to warmer temperatures in April-May and reduced snow conditions in April probably accounted for such advance in calving date. On the other hand, a lengthening of the calving season was reported following a warmer temperature in January, a higher number of days when mean temperature exceeds 0°C in October-November and a decreasing snow cover from October to November. By affecting the inter-individual heterogeneity in the plastic response of females' calving date to better climatic conditions in autumn and winter, climatic variability contributed to weaken the calving synchrony in this herd. Whether variability in climatic conditions form environmental cues for the adaptation of calving phenology by females to climate change is however uncertain, but it is likely. As such this study enhances our understanding on how reproductive phenology of ungulate species would be affected by climate change.

2.1 Introduction

Reproductive synchrony is the tendency of individuals to carry out parts of their reproductive cycle at the same time as other members of the population (Gochfeld 1980; Findlay

and Cooke 1982). In natural populations of either plant or animal species, reproductive synchrony is the result of natural selection when a reproductive advantage (e.g. reduced predation) is conferred to individuals breeding in a synchronous pattern (Ims 1990). Being the main ultimate factor of reproductive synchrony, offspring survival can be affected by multiple factors, such as climate, predation and sociobiological. Reproductive synchrony as a mean to reduce predation is explained by several hypotheses: first, the 'saturation hypothesis' suggests that predators will be overwhelmed if all young are born in a brief period (Rutberg 1987; Sinclair et al. 2000); second, adults breeding synchronously could use vigilance to detect predators more efficiently; third (Estes and Estes 1979; Ims 1990), the 'confusion hypothesis' states that a high number of young in a group will decrease the predator's capacity to pursue a specific target (Rutberg 1984, 1987). The wildebeest provides the best known example of synchronized calving, where predation pressure by the hyena has promoted a short birth peak and an aggregated over a dispersed spatial distribution of individuals in order to ensure the survival of the young (Estes 1976; Sinclair et al. 2000).

Several studies on northern ungulates have shown that climatic variability contributed more than predation in constraining timing and synchrony of births: bighorn sheep (Festa-Bianchet 1988), caribou (Post et al. 2003), Dall's sheep (Rutberg 1984; Rachlow and Bowyer 1991), reindeer (Lent 1966) and roe deer (Linnell and Andersen 1998). In temperate and subarctic climates, a marked seasonality in forage availability has been shown to strongly influence both perinatal and neonatal mortality of ungulates (Bunnell 1982; Festa-Bianchet 1988) and thus explains variation in synchrony of ungulates' births (Gaillard et al. 1993). Individuals born outside the optimal period for births will have lower probabilities to survive (Bunnell 1982; Gaillard et al. 1993) because (1) they will be more vulnerable to predation by bears, golden eagles and other predators (Eloranta and Nieminen 1986; Nieminen et al. 2013), (2) if born too early, mothers can be in negative energy balance therefore producing a low-quality milk (Guinness et al. 1978; Rachlow and Bowyer 1991) and (3) if born too late, young will be more susceptible to insect harassment and summer heat (Kumpula and Nieminen 1992; Weladji and Holand 2003b) and will not accumulate enough resources; ultimately reducing their survival rate during summer season, and during their first winter thereafter (Festa-Bianchet 1988). The calving phenology resulting from thousands of years of evolution is thus expected to reflect the species' adaptation to its environment.

In a context of the worldwide global warming recorded the last decades, a mistiming has been shown to occur between species' reproductive phenology and their environment leading to a decrease in their recruitment rate: in great tits (*Parus major*) (Visser et al. 1998), several species of birds (Visser et al. 2004), caribou (Post and Forchhammer 2008), reindeer (Veiberg et al. 2016), Columbian ground squirrel (*Urocitellus columbianus*) (Lane et al. 2012). Determining the relationship between reproductive tactics and a species environment and understanding the role of phenotypic plasticity on reproductive traits are therefore crucial to predict how climate change will affect species' viability. Ungulates with highly synchronized births in particular are of primary concern because they are more susceptible to climatic variation than asynchronously breeding ungulates that are better adapted to large changes in climate (Bowyer et al. 1998). *Rangifer* species (including both caribou and reindeer) in this context is certainly the most vulnerable species since: (1) this is one of the two ungulate species to have successfully colonized the highly variable Arctic environment and (2) *Rangifer* species has been shown to produce 80-90% of their calves within a 10-day period and complete the calving season within 4-5 weeks (Lent 1966; Dauphiné and McClure 1974; Bergerud 1975). Moreover, herding and hunting of *Rangifer* allowed northern peoples in the Arctic Circle to survive in a harsh and austere environment (long, cold winters and short, cool summers), and constitute the cultural and socioeconomic pillar of these cultures (Vors and Boyce 2009). Surprisingly, reindeer has not received enough attention with respect to the global climate change debate (but see Weladji et al. 2002a; Weladji and Holand 2006; Vors and Boyce 2009; Tyler 2010). Our aim here is thus to investigate how the reindeers' calving phenology is affected by climatic variability by using a long term dataset of birth dates recorded since 1970 in a semi-domesticated reindeer population in Northern Finland. In this study, the calving phenology will be assessed using both the date when births occur and the length/synchrony of the births season.

Since births in ungulates have been reported to occur later following winters with colder temperatures (Thompson and Turner 1982), higher amounts of snowfall (Bergerud 1975; Skogland 1983) and deep snow cover (Adams and Dale 1998), females are expected to present a plastic response in calving date according to the severity of winter and consequently the calving season is expected to occur earlier with a reduced snow cover, and an overall warmer and wetter climate as predicted over Northern Hemisphere (Serreze et al. 2000; IPCC 2007). Such climatic changes, by contributing to the lengthening of the vegetative growing season (Serreze et al. 2000; Post et

al. 2009), would release selective pressure to having births highly concentrated in time to match the forage resources (Rutberg 1987) and a lengthening of the calving season would result. The aims in the present study are to: (1) quantify rates of temporal change of reindeer reproductive phenology (date and length) and of climatic variables for our study site and (2) assess whether phenological changes in reindeer reproduction can be explained by the variation in local climatic condition.

2.2 Material and Methods

2.2.1 Study area and reindeer population

The data collected come from the Kutuharju field reindeer research station in Kaamanen, northern Finland (69°N, 27°E). The area is characterized by open birch *Betula spp.* and pine *Pinus sylvestris* forests with many bogs and lakes and the landscape varies between 185-370 m above the sea level. We studied a semi-domesticated reindeer population constituted of about 100 animals every year. All animals were marked with ear tags from birth, allowing their age to be known, while being individually recognizable thanks to the long term book-keeping of the herd demography. Reindeer are free ranging most of the year, excluding the calving period. In summer and during the rut, reindeer use two large fenced enclosures, the north-west section (Lauluvaara ~ 13.8 km²) and the south-east section (Sinioivi ~ 15 km²). After the breeding season in late October, the animals are gathered and taken to a winter grazing area (15 km²) where they can graze freely on natural pastures. Only in late winter and especially after harsh winters, animals receive in addition supplementary feed (pellets and hay). In late April, females are gathered into a calving enclosure (approximately 0.5 km²) where newborn calves are captured, weighed, sexed and marked with ear tags (L'Italien et al. 2012). The enclosure is surveyed daily, so that calving date is known for all individuals and has been recorded since 1970.

2.2.2 Calving season

All calendar dates were converted into Julian days since 1 January for analysis purposes. Assuming that the calving dates follow a bell curve, the synchrony – or length – of the calving season (when 95% of births occurred) was estimated as the width of the 95% confidence interval around the peak date of each period, a function of the within-year variance used by Loe et al. (2005) and calculated as two times twice the standard deviation ($2 \times 2\sigma$) of the whole calving

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season in any given year. In total, 45 years of data were available for both the calving date and the length of the calving season.

2.2.3 Population variables

Being a research herd, several experiments have been conducted on this reindeer population for different purposes. Thanks to the book-keeping of the herd, the identity of the animals involved in any experiment was known. Experimental animals were excluded from our analyses when: (1) males or females isolated for experimental purpose could have been subjected to other factors and do not reflect the overall trend of the herd and (2) an artificial feeding could have buffered climatic effects on females' body condition and therefore on calving date. Indeed the calving date has been shown to be strongly influenced by female's body weight at different periods of the year (Reimers 1983, 1997; Cameron et al. 1993; Adams and Dale 1998; Flydal and Reimers 2002; Cook et al. 2004). Because artificial feeding in 2009 was done more than would be expected in a normal year, we excluded the data for year 2009 from the analyses since earlier calving dates could just be the result of females being heavier that particular year, independently of climatic conditions. Given the great variability within and between years in females' body weight (see Figure 2.1), we believe that regular level of supplemental feeding alone could not buffer climatic effects by keeping up females' body weight at a stable level, hence our decision to remove year 2009.

To control for the effect of proportion of males on breeding time and thereafter on birth dates (Flydal and Reimers 2002; Holand et al. 2002; Mysterud et al. 2002), the proportion of males was estimated as the number of males divided by the number of females present in a specific enclosure during the breeding season. Between 1996 and 2011 (except 1998), the herd was separated in the two large enclosures, Sinioivi and Lauluvaara and consequently the proportion of males was estimated per enclosure for those years. Using the identity of the females present in each enclosure, the calving date of a specific female was related to the proportion of males estimated in that enclosure the past breeding season. The effect of proportion of males on breeding time and consequently on calving date (Flydal and Reimers 2002; Holand et al. 2002; Mysterud et al. 2002) was thus controlled for in the analyses.
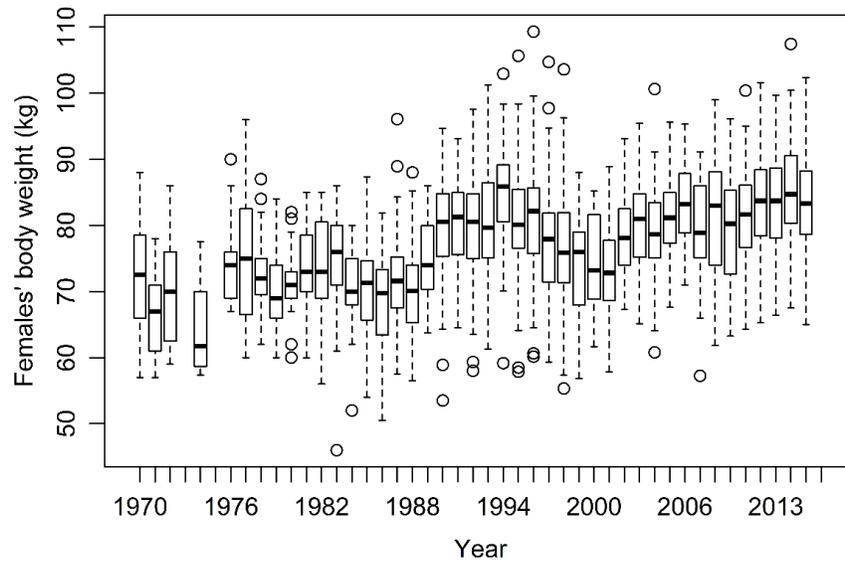
Figure 2.1 Within and between year variability in adult females' body weight of the Kutuharju field reindeer research station herd between 1970 and 2015 in northern Finland. Each female's body weight per year was calculated as the average value of the recorded body weights for that female from June to December the precedent calendar year and from January to May the same calendar year as the female's calving season.

2.2.4 Climatic data

Local climatic data (daily recorded values for temperature, precipitation and snow cover) from 1970 to 2015 have been obtained from three different weather stations (Utsjoki, Ivalo airport and Nellim) in north Finland (68°N, 27°E) from the Finnish Meteorological Institute, Helsinki, Finland. The weighted mean by the distance from the weather station to our study site was used to estimate the local weather at our study site with as much reliability as possible. A Great Circle longitude-latitude calculations tool (http://www.cpearson.com/excel/LatLong.aspx) was used to assess precisely the distance between our study site and each of the weather stations, based on the GPS coordinates of the two locations. All the weather variables were considered on a monthly basis. Monthly average temperature was the average of the mean daily temperatures recorded over a month whereas the sum was used for precipitation and snow depth. Precipitation includes rain and/or snow depending on the temperature. Snow depth index (SDI) was calculated as the cumulative sum of daily snow depths on the 15th day in each month. Moreover, the following temperature parameters for each month were used to reflect the climatic variation: number of days when the mean temperature exceeds 0°C and 5°C (Kumpula and Colpaert 2003) and number of days when the mean temperature goes below -10°C. All the weather variables used in the analyses for calving date and synchrony and the references justifying their use are summarized in Table 2.1. The temporal trend was assessed using linear models with *Year* considered as a continuous variable and entered as a fixed-effect factor in the models.

Table 2.7 Summary of all the weather variables used to analyse the influence of climatic variability on both the calving date and calving synchrony of a semi-domesticated reindeer population for the study area of the Kutuharju field reindeer research station in Kaamanen, northern Finland (69°N, 27°E).

Month	Local weather variables					
	Temperature				Precipitation	Snow cover
	Mean T°(°C)	Number of days when mean T° >		Number of days when mean T° <	Sum (mm)	Snow depth index – SDI (mm)
		0°C	5°C	-10°C		
January	×	×		×	×	×
February	×	×		×	×	×
March	×	×		×	×	×
April	×	×	×	×	×	×
May	×	×	×		×	×
June	×		×		×	
July	×				×	
August	×		×		×	
September	×	×	×		×	
October	×	×	×	×	×	×
November	×	×	×	×	×	×
December	×	×		×	×	×
References	(Thompson and Turner 1982; Cook et al. 2004)	(Kumpula and Colpaert 2003) (Kumpula and Colpaert 2003)			(Nussey et al. 2005a)	(Bergerud 1975; Thompson and Turner 1982; Skogland 1983; Adams and Dale 1998; Feder et al. 2008)

The availability of each weather variable depending on the month is indicated by an "×". The significant influence of each weather variable on parturition date for different ungulate species is referred in the last line.

2.2.5 Statistical analyses

The following statements apply to the analyses for both calving date and calving synchrony. Since phenological variation in calving period (timing and synchrony) could be independently influenced by the previous year's climatic conditions and conditions in the beginning of current year, we performed models using current year calving data (t), and climatic data for both current year from January to May (t) and precedent calendar year ($t – 1$) from June to December. Calving dates and calving synchrony were used as response variables in the analyses. We centered and standardized all the predictor variables considered ($\overline{X} = 0$, SD $= 1$) to be on a comparable scale and assessed for multicollinearity among them using the Variation Inflation Factor (VIF). Predictor variables with VIF smaller than five were kept in the model (Montgomery and Peck 1992). If several consecutive months of the same weather variable significantly influenced one trait of the calving phenology (timing or synchrony) when considered separately, the mean (for temperature) or the cumulative sum (for precipitation and SDI) was calculated for the entire period. For example, if mean temperature in April and in May significantly influenced calving date when considered separately, then the mean temperature for the period from April to May was instead used in the model in order to avoid multicollinearity.

Before performing a model selection to identify which variables best explained variation in calving phenology (date and length separately), we assessed the change over time of the reindeer calving phenology using two models both with year, the predictor variable considered as a continuous fixed-effect parameter in the models. The first model, had calving date as response variable and we used a Linear Mixed-effects Model (LMM) with year and individual identity included as random factors; while the second model had calving synchrony as response variable and a Linear Model (LM) was used. These two models were not subject to model selection. A model selection was then performed to find combinations from all the explanatory variables used providing the most probable models to explain calving phenology and was based both on the Akaike Information Criterion, corrected for small sample size (AICc) and Akaike weights (AICc weights) to compare the relative performance of the models tested (Anderson et al. 2001; Burnham and Anderson 2002). The delta AICc (Δ_i) was calculated to provide a measure of each model relative to the best model (with the lowest AICc value). All models within a ΔAICc of 2 units were retained as competing models since a substantial evidence was given to the model if $\Delta_i < 2$

(Burnham and Anderson 2002). To account for model selection uncertainty and if more than one model were retained as best models in explaining the data then the estimates of the coefficients of parameters in all models with ΔAICc < 2 were averaged, following the model averaging approach (Burnham and Anderson 2002; Grueber et al. 2011; Symonds and Moussalli 2011; Mazerolle 2019). We reported the effect of each predictor variable on the response variable considered with model-averaged parameter estimates, as well as their 95% confidence intervals based on our entire list of candidate models. These estimates are weighted based on the relative importance of the models (given by the AICc weights) containing those parameters and only the 'conditional averages' were reported, i.e. the averages over the models where the parameters appeared. The variables included in the competing models were considered important if their 95% CIs excluded 0 and only the important variables were further discussed. Since our predictor variables were beforehand centered and standardized, we could directly interpret their main effects even when involved in interactions and thus avoided the potential misinterpretation of main effects between models with and without the interaction term (Gelman 2008; Schielzeth 2010; Grueber et al. 2011). Analyses were performed in R 3.3.0 (R Development Core Team 2012).

2.2.5.1 Calving date

The calving dates data was analysed using Linear Mixed-effects Models (LMMs), by running the lmer-function in the R package lme4 (Bates et al. 2015, <www.r-project.org>), and with individual identity and year of study being included in the models as random effects to control for repeated measures (Kruuk et al. 1999; Milner et al. 1999). *Year* included as a random effect also allows accounting for between-year variations. In addition, as female age (Bergerud 1975; Guinness et al. 1978; Plard et al. 2013a), female body weight (Cameron et al. 1993; Reimers 1997; Cook et al. 2004; Mysterud et al. 2009) and proportion of males (Flydal and Reimers 2002; Holand et al. 2002; Mysterud et al. 2002) are known to influence the calving date, their respective effect was controlled for in the models. Since in reindeer factors linked to maternal condition interact with each other (Ropstad 2000) so that older individuals tend to be heavier, we used a female body condition index (BCI) so that (1) effects of female body weight controlling for age be taken into account and (2) multicollinearity between these two highly correlated variables be avoided. This body condition index was estimated by a measure of female body weight the year preceding the calving season after the effect of age is controlled – the age-specific residual body mass (see Festa-bianchet et al. 1997; Weladji et al. 2003b). This age-specific residual body mass was calculated by

subtracting from each female's body weight the average body weight of all females of the same age. These population terms were included in every model and formed what we call the "basic model", i.e.: $Calving\ date \sim ♀BCI + PM + (1|ID) + (1|Year)$, with BCI the body condition index of females, PM the proportion of males, ID the individual identity of the mother, and $Year$ the year of management. The terms $(1|ID)$ and $(1|Year)$ meant that they were included as random factors in the models.

To assess which local weather variables over different months best explained variation in the calving date, the weather variables presented in Table 1 were added to the basic model. As physical condition of females can also be influenced by weather variables, the interactions between BCI and weather variables were also tested in the models. The effect size of each predictor variable was estimated by the parameter estimates from the selected model using the restricted maximum likelihood estimates as recommended for mixed effect models (Bolker et al. 2009) whereas the AICc values were calculated using the maximum likelihood methods (Anderson et al. 2001). Once the most probable models to explain variation in calving date were selected, we then assessed how the calving date was affected by the most important variables by looking at the sign of their conditional averaged slope values extracted from the entire list of our competing models. The conditional R^2 values were calculated to indicate the proportion of variance explained by both the fixed and random factors of the best-fitting models.

2.2.5.2   Calving synchrony

As the calving synchrony (length of the calving season) was estimated annually, linear models were used. The predictor variables used were the same weather variables described in Table 2.1. Because calving synchrony is estimated annually for the entire population and to control for the effects of population variables (BCI of females and proportion of males) on calving synchrony, an average value of the BCI of all the females per year, as well as an average value of the proportion of males par year was calculated. Our "basic model" for calving synchrony was thus as follow: $Calving\ synchrony \sim ♀BCI + PM$, with BCI the body condition index of females and PM the proportion of males. To assess which weather variable over different months best explained variation in the calving synchrony, the weather variables presented in Table 1 were added to this basic model. As physical condition of females can also be influenced by weather variables, the interactions between BCI and weather variables were also assessed in the models.

How the calving synchrony was affected by a weather variable was assessed with the conditional averaged slope values extracted from the most important variables of our competing models. Adjusted R^2 values were calculated to indicate the proportion of variance explained by the best-fitting models.

2.3 Results

After the exclusion of the birth dates coming from artificially fed females for specific experiments, of females with unknown body weight (as we wanted to correct for the mothers' physical condition influence on calving date), and of calving dates with unknown related proportion of males, 2,137 birth dates in total were available over 45 years (minus years 1973, 1975 and 2009 because not enough data were available, see Figure 2.5) for a total of 482 mothers, corresponding on average to 50 births per year. The mean calving date was 19-May and the average length of the calving season was 25 days (Figure 2.6).

2.3.1 Temporal trends in calving season

Between 1970 and 2015, calving date significantly advanced by an estimated 0.15 days per year (95% CI [-0.24, -0.07]; Figure 2.2a). Across the 45-year study period, calving dates in female reindeer were estimated to have advanced by 6.8 days (Figure 2.2a). There was a tendency for the duration of the calving season to lengthen over time, i.e. a tendency for calving synchrony to weaken along the study period (b = 0.06; Figure 2.2b) but this temporal trend was not statistically significant (95% CI [-0.08, 0.21]).
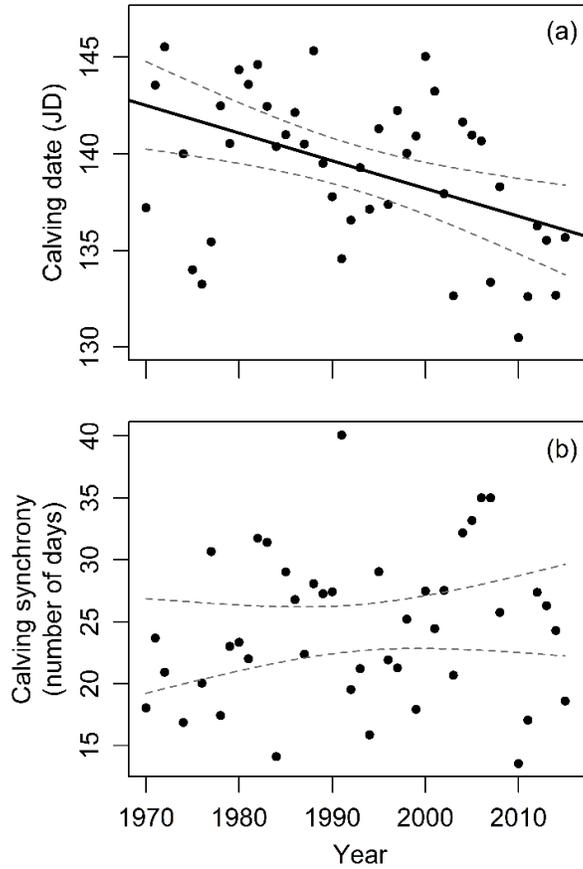
Figure 2.2 Variation of (a) mean calving date and (b) calving synchrony of a semi-domesticated reindeer population between 1970 and 2015 in Finnish Lapland. The fitted line and the 95% confidence interval band are provided.

2.3.2 Temporal trends in climatic data

Among all the weather variables used in this study and described in Table 2.1, 16 significant changes over time out of 55 were found (see Table 2.2). The most noticeable changes being (1) a warming trend from April to May and from August to November, mainly triggered by an increasing number of days when temperature exceeds 0°C in April, an increasing number of days when mean temperature exceeds 5°C in April and in May, and a decreasing number of days when mean temperature goes below -10°C in November; (2) a reduced snow cover from December to February as well as in May and October characterized by a decreasing SDI and (3) an increasing amount of precipitation in May.

Table 2.8 Parameter estimates (with SE) for the linear models with the year of management included as a covariate to assess the temporal trends in all the weather variables for the Kutuharju field reindeer research station, northern Finland.

Weather variables		Estimate	SE	t-value	P	Total change over the study period
Mean temperature (°C)	*April*	0.066	0.019	3.44	< 0.01	+ 3.1 °C
	May	0.046	0.016	2.89	< 0.01	+ 2.1 °C
	August	0.028	0.014	2.04	< 0.05	+ 1.3°C
	September	0.051	0.015	3.34	< 0.01	+ 2.3°C
	October	0.047	0.023	2.02	< 0.05	+ 2.2°C
	November	0.09	0.033	2.75	< 0.01	+ 4.1°C
Number of days when mean T° > 0°C	*April*	0.19	0.058	3.30	< 0.01	+ 8.9 days
Number of days when mean T° > 5°C	*April*	0.037	0.017	2.16	< 0.05	+ 1.7 days
	May	0.15	0.056	2.71	< 0.01	+ 7.0 days
Number of days when mean T° < -10°C	*November*	-0.15	0.051	-2.94	< 0.01	- 6.9 days
Precipitation (mm)	*May*	0.49	0.18	2.72	< 0.01	+ 22.7 mm
Snow depth index (mm)	*January*	-3.95	1.80	-2.19	< 0.05	- 182 mm
	February	-4.03	1.98	-2.04	< 0.05	- 185 mm
	May	-6.99	2.95	-2.37	< 0.05	- 321 mm
	October	-0.52	0.22	-2.43	< 0.05	- 24.1 mm
	December	-3.76	1.68	-2.24	< 0.05	- 173 mm

Only the significant changes over time (either positive or negative) of the weather variables over different months are presented in this table. The last column indicates the estimated change over time of each climatic variable over the study period, i.e. from 1970 to 2015.

2.3.3 Climatic effects on calving date

After comparison of models including local weather variables over different months, three competing models were found to be within 2 AICc of the model with the lowest AICc, i.e. $\Delta_i < 2$ (see Table 2.3). These three best models indicated that the most important variables given by the model averaging approach and explaining variation in calving date (in order of effect size) were: the females' body condition index, the proportion of males in the herd, the amount of precipitation in April, the mean temperature in May, the mean temperature in the period from April to May and the SDI in April (Tables 2.3, 2.4). The three best models showed that calving dates were affected by (1) the female BCI (Table 2.4, Figure 2.3a) and (2) the proportion of males in the herd (Table 2.4, Figure 2.3b). Accordingly, earlier calving dates were observed with females in better physical condition the year preceding calving (heavier and older; Figure 2.3a) and in years with a higher proportion of males present in the herd (Figure 2.3b). The best models also revealed that earlier calving dates were observed following a decreasing amount of precipitation in April (Figure 2.3c), a warmer climate in May (Figure 2.3d) and in April-May (Figure 2.3e), as well as a decreasing snow depth index in April (Figure 2.3f). These models explained around 44-45% of the variation in calving date.
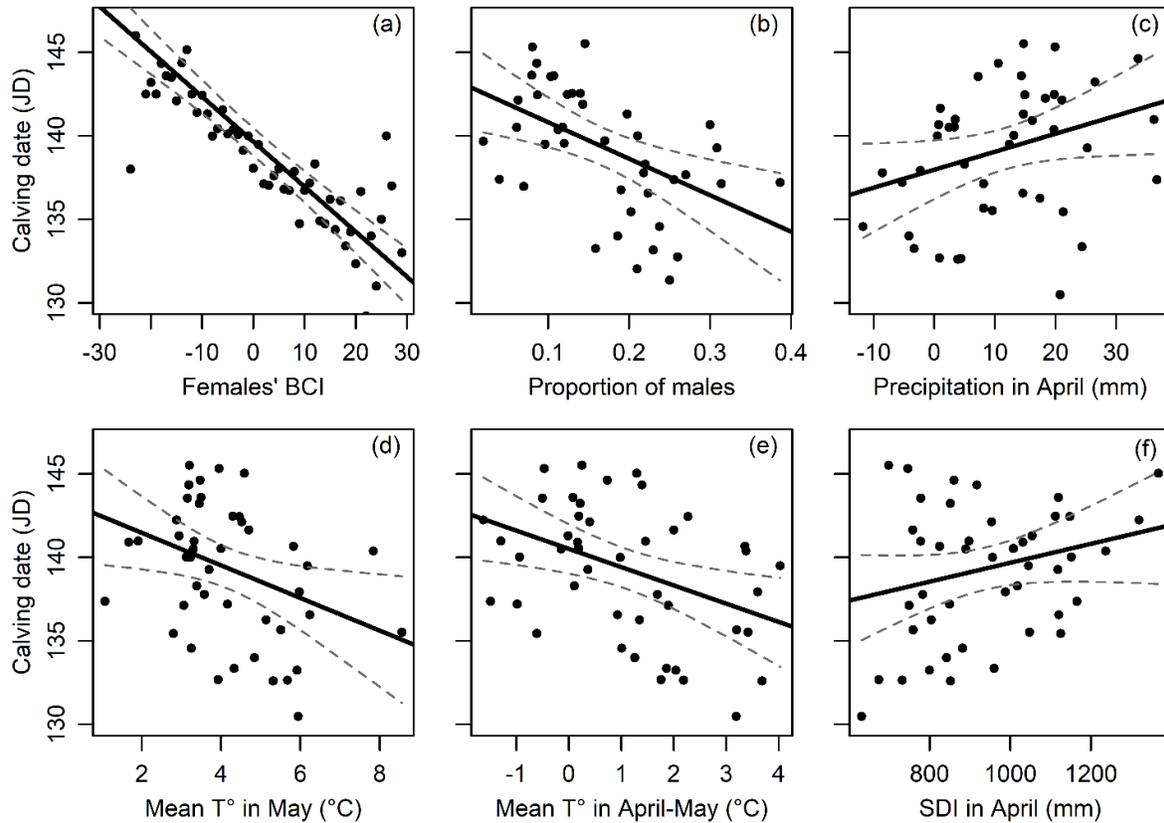
Figure 2.3 Relationship between reindeer calving date from the Kutuharju field reindeer research station herd from 1970 to 2015 and (a) females' body condition index (BCI), (b) proportion of males in the herd the precedent breeding season, (c) amount of precipitation in April, (d) mean temperature in May, (e) mean temperature in April-May and (f) snow depth index (SDI) in April. The 95% confidence interval band around the fitted line is provided. The calving date is expressed in Julian day (JD) starting January 1st. Each point represents the average value of the predictor variable for a specific calving date.

Table 2.9 AIC table presenting comparative models for calving date of a semi-domesticated reindeer population in Kaamanen, northern Finland, including different weather variables over different periods of the year.

Models	Fixed covariates		Mean T°		Precipitation	Snow depth index	Calving date				
Rank	♀ BCI	Proportion of males	April-May	May	April	April	AICc	df	AICc weights	ΔAICc	R^2
1	×	×		×	×		13894.9	8	0.42	0.0	0.44
2	×	×	×		×		13895.3	8	0.36	0.4	0.45
3	×	×		×		×	13896.2	8	0.22	1.3	0.44

All linear mixed-effects models for calving date included female's body condition index and proportion of males as fixed effects and female identity and year as random factors. The models presented in the table are the three competing models retained in explaining calving, i.e. with ΔAICc < 2 (see text for details).

Table 2.10 Model-averaged estimates of predictor variables in order of effect size based on the best models in explaining calving date of a semi-domesticated reindeer population in relation to climatic variability in Finnish Lapland.

Variable	Estimate	Unconditional SE	Nbr models	Relative importance	95% CI
Females' BCI	-1.77	0.19	3	1.00	-2.12, -1.39
Proportion of males	-1.47	0.28	3	1.00	-2.02, -0.91
Precipitation in April	0.93	0.41	2	0.77	0.12, 1.73
Mean T° in May	-1.14	0.43	2	0.63	-1.97, -0.30
Mean T° in April-May	-1.14	0.45	1	0.37	-2.03, -0.26
SDI in April	0.89	0.43	1	0.23	0.03, 1.74

All the competing models were linear mixed-effect models with calving date as our response variable and included year and individual identity as random factors. The parameter estimates are standardized effect sizes and are therefore on a comparable scale. "Nbr models" is the number of models (out of the three best models in Table 2.3) including that variable.

2.3.4 Climatic effects on calving synchrony

The model averaging approach applied on the best supported models to explain length of the calving season (see Table 2.5) indicated that the important variables (whose 95% CI excluded 0) were: the mean temperature in January, the sum of the snow depth indexes from October to November, the number of days when mean temperature exceeded 0°C in October-November, and the SDI in November the precedent calendar year (Table 2.6). More precisely, a lentghening of the calving season was observed following warmer temperatures in January (Figure 2.4a), a decreasing cumulative SDI for the period October-November (Figure 2.4b), a higher number of days when mean temperature exceeds 0°C in October-November (Figure 2.4c), and a decreasing SDI in November (Figure 2.4d). The best models also indicated a significant interaction between the mean temperature in January and the average body condition index of females on calving synchrony (Table 2.6). Apart from this interaction however, both the average BCI of females and the proportion of males were not important in explaing the variation in calving synchrony (Table 2.4). The competing models explained between 17-23% of the variation in calving synchrony.
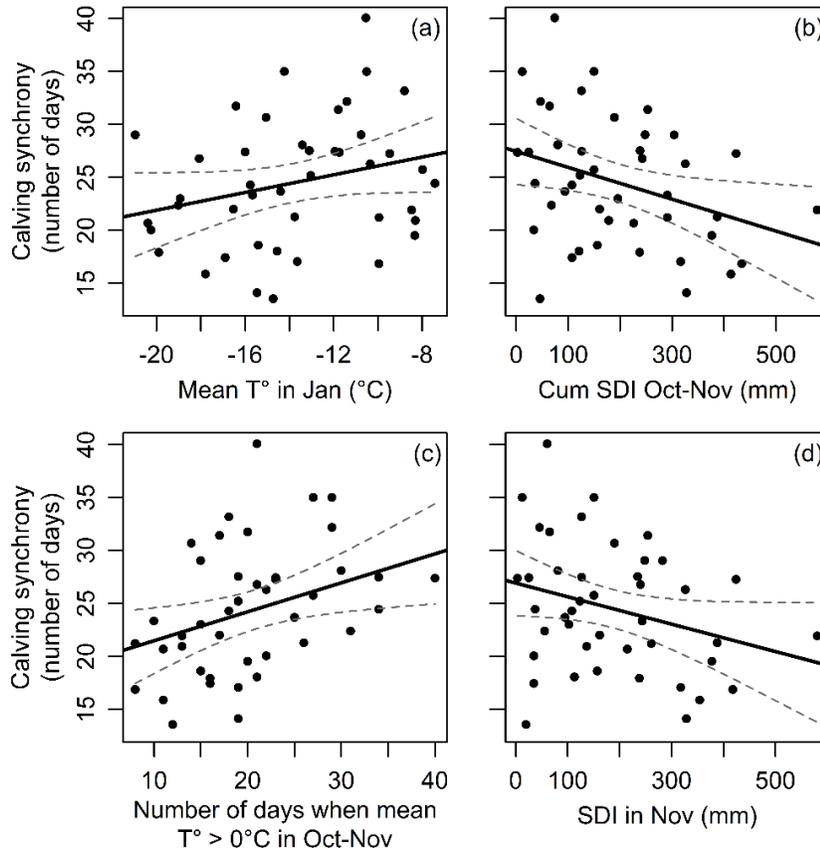
Figure 2.4 Relationship between calving synchrony of a reindeer population in northern Finland and (a) the mean temperature in January, (b) the cumulative snow depth indexes in the period from October to November, (c) the number of days when mean temperature exceeds 0°C in October-November, and (d) the SDI in November. The 95% confidence interval band around the fitted line is provided. The climatic data from October to November were from the calendar year preceding the year of the calving synchrony whereas the climatic data for January were from the same calendar year as calving synchrony. The calving synchrony was expressed in number of days as the width of the 95% confidence interval of the birth distribution. The cumulative SDI was the sum of the snow depth indexes for the period of interest.

Table 2.11 Competing linear models of calving synchrony of a semi-domesticated reindeer population in Kaamanen, northern Finland, in relation to local weather variables over different periods of the year.

Models	Fixed covariates									Calving synchrony				
Rank	♀ BCI	Proportion of males	Mean T°	Number of days when mean T°		Precipitation	Snow depth index		AICc	df	AICc weights	ΔAICc	R^2
			Jan	> 0°C in Oct-Nov	< -10°C in Dec	June	Oct-Nov	Nov					
1	(×)	×	(×)				×		276.2	7	0.34	0.0	0.23
2	(×)	×	(×)					×	277.2	7	0.21	1.0	0.22
3	×	×		×	×				277.8	6	0.16	1.6	0.17
4	×	×		×		×			278.0	6	0.14	1.8	0.17
5	(×)	×	(×)			×			278.0	7	0.14	1.8	0.20

All linear models for calving synchrony included female's body condition index and proportion of males as fixed effects. The climatic conditions in June and in the period from October to December were from the calendar year preceding the calving season whereas the climatic conditions for the month of January were from the same calendar year as the calving season. Variables with the checkmark in brackets mean that the interaction term between both was included in the model. The five models of the table were retained as our best models in explaining calving synchrony, i.e. with ΔAICc < 2 (see text for details).

Table 2.12 Model-averaged estimates of predictor variables in order of effect size based on the best linear models in explaining calving synchrony of a semi-domesticated reindeer population in relation to climatic variability in Finnish Lapland.

Variable	Estimate	Unconditional SE	Nbr models	Relative importance	95% CI
Females' BCI	0.97	1.02	5	1.00	-1.08, 3.02
Proportion of males	-0.76	0.98	5	1.00	-2.73, 1.21
Mean T° in Jan	2.13	0.89	3	0.70	**0.34, 3.93**
Mean T° in Jan X Females' BCI	1.97	0.88	3	0.70	**0.19, 3.76**
Cumulative SDI Oct-Nov	-2.06	0.83	1	0.34	**-3.75, -0.37**
Number of days when mean T° > 0°C in Oct-Nov	2.23	0.87	2	0.30	**0.46, 4.00**
Precipitation in June	-1.77	0.89	2	0.29	-3.58, 0.03
SDI in Nov	-1.91	0.84	1	0.21	**-3.62, -0.21**
Number of days when mean T° < -10°C in Dec	-1.93	0.98	1	0.16	-3.93, 0.06

The parameter estimates are standardized effect sizes and are therefore on a comparable scale. "Nbr models" is the number of models (out of the five best models in Table 2.5) including that particular variable. The variables in bold text were assumed important in explaining calving synchrony since their 95% CI excluded the value 0. The symbol "**X**" stands for "interaction".

2.4 Discussion

2.4.1 Climatic effects on calving date

The calving season of the semi-domesticated reindeer population of the Kutuharju field reindeer research station in Kaamanen, North Finland has advanced significantly over the last 45 years by almost one week. Eloranta and Nieminen (1986) already reported that most of the calving of this same herd occurred on average 19 days between May 10 and 29 and that the peak of calving varied yearly between May the 15th and 25th. Similarly, 90% of the caribou calves in North America are born in a brief 2-week period (Bergerud 1975). Therefore, our peak calving date (19-May) matched the previous findings on the same herd (Eloranta and Nieminen 1986) but an overall advancement of 6.8 days of the whole calving season represents a consequent change for the calving period in this area (see Figure 2.7). So far, very few studies have highlighted such temporal trends in the reproductive phenology of mammal populations (squirrel: Réale et al. 2003, red deer: Moyes et al. 2011). This temporal trend corroborated the overall warming of the spring period from April to May, as well as the reduced snow cover just prior to the births in May observed in the study area the last 45 years. Indeed, earlier calving dates were found following warmer temperatures in April-May, a decreasing amount of precipitation in April (mainly snowfalls at that time of the year) and a reduced snow cover in April the same calendar year. The spring period appears to be critical for ungulate species in northern latitudes, given its influence on the plant growth season pattern (Pettorelli et al. 2005) and consequently on the food availability during summer. Moreover, late winter/early spring is the most demanding period for reindeer in Arctic since individuals' body condition and fat reserves to draw upon (reindeer being a capital breeder) are at their lowest point and availability of food is difficult due to hard and thick snow cover (Tveraa et al. 2007). When temperatures rise earlier in spring, the snow starts to melt, and snow free patches will also emerge much earlier, allowing reindeer to easily have access to lichens and dwarf shrubs. Altogether, (1) a better availability of late winter food and a decreasing amount of energy spent in thermoregulation (Parker and Robbins 1985; Putman et al. 1996) and locomotion on snow (Parker et al. 1984) due to a decreasing amount of snowfalls and a reduced snow cover in April, and (2) an earlier onset of the vegetative growing season (Menzel et al. 2006) and an increased plant biomass observed in the Arctic tundra (Epstein et al. 2000; Hughes 2000) due to warmer temperatures in April-May certainly contributed to increase females' body condition in

late pregnancy. Indeed, further analyses revealed that females' BCI had significantly increased over the last 45 years in this population (Figure 2.8). Such improvement in females' physical condition will result in mothers having more resources during pregnancy, hence likely advancing the date at which the foetus is mature and resulting in an earlier birth, as compared to years with severe late winter conditions (Cameron et al. 1993). The significant advancement in calving date could thus be explained by females in better condition giving birth earlier (Baskin 1970; Cameron et al. 1993; Reimers 1997; Flydal and Reimers 2002). The large influence of female body condition on calving date has already been highlighted in numerous studies (bighorn sheep: Feder et al. 2008, caribou: Bergerud 1975; Cameron et al. 1993, elk: Cook et al. 2004, reindeer: Reimers 1997; Flydal and Reimers 2002; Mysterud et al. 2009).

An optimal timing of calving will ensure that females have access to a high-quality vegetation (i.e. higher protein content), allowing their calves to be nourished with a high-quality milk (Bunnell 1982; Chan-McLeod et al. 1994; Festa-Bianchet 1988; Parker et al. 1990) and accelerating the rate of fat accumulation for calves. Moreover, earlier birth dates will (1) provide calves with a longer period of time to sufficiently accumulate fat reserves to survive winter and therefore promoting both their survival and growth, and (2) allow mothers to recover faster from their pregnancy and lactation period and to be in good enough shape to reproduce the next breeding season, promoting both their survival and reproductive success as a result (Reimers et al. 1983; Rutberg 1987; Festa-Bianchet 1988; Parker et al. 2009). Therefore, such plastic response is essential for deer species to adapt to climate change by adjusting the period of high energetic requirements (i.e. lactation) with the period of high-quality forage and thereby ensuring offspring survival. Identifying the climatic variables that trigger a plastic response in the reproductive phenology of animal species is thus of primary concern in order to better predict their long term viability. Many species of birds and mammals have already been shown to rely on temperature to match the birth timing with the peak of resource availability (Visser et al. 2004; Caro et al. 2013). In ungulate species, females may adjust their gestation length as a strategy to give birth at the period of the year best suited for offspring survival. Such adjustment of gestation length as part of the reproductive tactic has previously been reported in reindeer (Mysterud et al. 2009; Rowell and Shipka 2009). On the Isle of Rum, Scotland, warm March temperatures were associated with shorter average gestation lengths in red deer and Clements et al. (2011) proposed that high March temperatures could act as a cue to indicate that the optimum birth date is likely to be earlier. The

females of the Kutuharju field reindeer research station also seemed to rely on temperature in April-May but also on snow conditions (amount of snowfalls and snow depth index) in April to adjust their gestation length in late pregnancy and consequently calving time within the same year accordingly. Nevertheless, the significant relation between calving dates and mean temperature in April-May do not necessarily mean that females use temperature as a predictive cue for future climatic conditions. This correlation could just be the result of an increased female's physical condition following improved climatic conditions in late winter/early spring. To demonstrate a cause-effect relationship and whether temperature has a direct signaling effect on seasonal timing, experimental approaches would be necessary but as Caro et al. (2013) mentioned, "given the scarcity of experimental approaches investigating this causal effect of temperature, especially in mammals, generalizations are not possible and additional studies are desperately needed".

2.4.2   *Climatic effects on calving synchrony*

The calving synchrony was also affected by an overall warming of the period from August to December as well as a reduced snow cover in winter from December to February reported in the study area since a lengthening of the calving season was observed following an overall warming weather in January and an increasing number of days when mean temperature exceeds 0°C in October-November. The calving synchrony was also weakened by a decreasing snow cover in the period from October to November. Moreover, females with an overall better physical condition (i.e. above the third quantile of the population distribution) delayed their calving dates following a higher number of days when mean temperature exceeds 0°C in October-November (LMM; $b = 1.31$, 95% CI [0.22, 2.39]) and warmer temperatures in January (LMM; $b = 1.36$, 95% CI [0.18, 2.53]) whereas females in poor physical condition (i.e. below the first quantile of the population distribution) showed no phenotypic plasticity in their calving dates when facing better climatic conditions in October-November (95% CI [-1.62, 0.68]) and in January (95% CI [-0.05, 2.05]). The lengthening of the calving season following better climatic conditions in October-November and warmer temperatures in January may thus reflect a reduced plasticity among low-quality mothers (young and light females), so that they are not able to respond as quickly as high-quality mothers (older and heavier females) do, to favorable climatic conditions in autumn and winter.

The onset of the rut period in deer species has been shown to be mainly triggered by a sudden drop in temperature around the breeding season (around late September/October) which trigger males' rutting behaviors to start (Marshall 1937; Amoroso and Marshall 1960; Sadleir 1969). Therefore, a higher number of days when mean temperature exceeds 0°C in October-November, highly correlated with a decreasing snow cover during the same period, would delay the time when males begin to display mating behaviors; resulting in a delay in females' estrus (Langvatn et al. 2004). Further analyses on a dataset of validated copulation dates (which led to the birth of a calf within the 211–229 days' time window for gestation lengths reported in this herd, Mysterud et al. 2009) also revealed a delay in copulation dates only for females in poor physical condition in September following a higher number of days when mean temperature exceeds 0°C in October-November (LMM; $b = 3.06$, 95% CI [1.46, 4.69]). Therefore, the delay in estrus dates following better climatic conditions around the mating time would be more pronounced for females in poor physical condition while females in good condition (old and heavy females) would still be mated earlier (Langvatn et al. 2004; Mysterud et al. 2009). As shown in many ungulate species, late copulation dates are also correlated with shorter gestation lengths (Scott et al. 2008; Mysterud et al. 2009; Rowell and Shipka 2009; Clements et al. 2011) such as females in poor physical condition not having enough reserves to buffer climatic effects and cope with gestation costs. On the contrary, females in good physical condition would be able to afford the risks of delayed calving dates (as reported above) when climatic conditions in autumn are better (Berger 1992), and afford such the corresponding gestation costs and thus lengthen their gestation lengths (Mysterud et al. 2009; Clements et al. 2011) to improve their calves' condition at birth, increasing their own reproductive success the following summer as shown in caribou and reindeer (Tveraa et al. 2003; Wilson et al. 2005; Weladji et al. 2006). The lengthening of the calving season after years with better climatic conditions in October-November (warmer temperatures and a decreased snow cover) would thus be explained by delayed calving dates from females in good physical condition.

The positive relationship between mean temperature in January and calving synchrony was enhanced by females BCI. Indeed, longer calving seasons were observed following warmer temperatures in January contributing to increase females' physical condition, which in turn delayed their calving dates (as described above). From the mother and offspring's points of view, delaying calving when climatic conditions in winter are favorable provide selective advantages. A longer

gestation length provides (1) the foetus a longer period for growth and development (Skogland 1984; Reimers 2002), (2) a higher offspring's birth weight (Berger 1992), ensuring a higher survival probability (Adams and Dale 1998; Cook et al. 2004; Clements et al. 2011) and (3) an enhanced fitness for the offspring (Wilson et al. 2005). A higher offspring's fitness will certainly mean improved fitness for the mother (Wilson et al. 2005; Weladji et al. 2006). However, the ability for a female to be plastic requires a higher physical condition to be physiologically able to do so (Nussey et al. 2005a; Bårdsen et al. 2008). A warming temperature in January would allow pregnant females to spend less energy for thermoregulation (Parker and Robbins 1985; Putman et al. 1996) and reduce the costs of locomotion on snow (Parker et al. 1984), thus improving their overall physical condition. However, females with an overall higher physical condition would be more able to buffer climatic effects in warmer winters and allocate more resources to growth and development of their foetus (Skogland 1984; Post and Stenseth 1999; Reimers 2002), whereas females in poor physical condition would probably prioritize the maintenance of their own body reserves over their foetus's growth and development (Skogland 1984; Reimers 2002; Fauchald et al. 2004). In warmer winters, only females in good physical condition would be able to delay their calving dates, thereby contributing to a lengthening of the calving season in those years. Such asymmetric response to improved vs. reduced winter conditions has been demonstrated in reindeer as a 'risk-averse adjustment in reproductive allocation' (Bårdsen et al. 2008).

The inter-individual heterogeneity in the response to improved climatic conditions in October-November and January would thus be responsible for the variability in calving synchrony observed in this herd. Understanding what shapes inter-individual heterogeneity in the plasticity of calving date in response to climatic variation would be a natural continuation to this study. We noted that the shift in birth synchrony has occurred in the quasi-absence of predation (20 cases of calves killed by predation out of 2,137 birth dates) so that climatic variability seemed to be one of the main driver shaping calving synchrony in this population. As the competing models explained at best 23% of the variation in calving synchrony, it suggests that other parameters could also be important in explaining variation in the length of calving season (e.g. social, physiological or behavioral cues). Whether phenological changes in calving date and/or calving synchrony have consequences for populations' recruitment rate and/or females' reproductive success is a question with contrasted answers among ungulate species. In red deer, Moyes et al. (Moyes et al. 2011) did not find a significant temporal change in either offspring birth weight or offspring first-winter

survival whereas parturition date has advanced. On the contrary, Post and Forchhammer (2008) found a reduced production and survival of caribou calves following warmer spring temperatures due to a trophic mismatch between the caribou's timing of calving and onset of the plant growing season in the Low Arctic Greenland. In this semi-domesticated reindeer population, assessing the offspring first-winter survival was not feasible because approximately one third of the calves are slaughtered every autumn for meat production. However, calves who survived the summer had earlier birth dates than calves who died either at birth, after one day, one week or later in the summer (LMM; b = -1.23, 95% CI [-1.96, -0.50]). Moreover, Holand et al. (unpublished) have found that both the calving dates and calves' birth weight of this population are under stabilizing selection with advanced birth dates and increased calves' birth weights. Whether such selection has consequences in terms of population dynamics and life history traits in this population is yet to be demonstrated but as Gaillard et al. (2000) mentioned: "the immature stage, despite a low relative impact on population growth rate compared with the adult stage, may be the critical component of population dynamics of large herbivores". Furthermore, conditions early in life has been reported to shape lifetime reproductive success (Gaillard et al. 1997; Kruuk et al. 1999). Therefore, changes in birth dates and birth weights could have major consequences on population dynamics of ungulate species like reindeer. More studies on this matter are needed with the need to disentangle behavioral/phenotypic plastic responses from microevolutionary responses and the consequences for ungulate populations (Gienapp et al. 2007).

2.5 Conclusions

The calving season of the semi-domesticated reindeer population in Kaamanen, northern Finland has occurred earlier following warmer temperatures in April-May, a decreased amount of snowfalls in April and a reduced snow cover in April and has lengthened with a warming weather in January, a higher number of days when mean temperature exceeds 0°C in October-November and a decreasing snow cover in the period from October to November. Such phenological trends have allowed this reindeer population to track at least partially the climatic changes observed in this area. The phenology of many species have changed in response to climate change, particularly at higher latitudes in the Northern Hemisphere but most evidences came from long-term studies of many taxonomic groups other than ungulate species (Visser et al. 1998; Parmesan and Yohe 2003; Root et al. 2003). As such, this study enhances our understanding of how reproductive phenology

of ungulate species would be affected by climate change. That such results on a semi-domesticated reindeer population were observed, where supplemental feeding in harsh winter years could have helped to buffer against climatic conditions, suggests that influence of climatic variation on the reproductive phenology of wild populations might be even stronger. Therefore, more ecological studies linking reproductive phenology of wild populations to climatic variation are needed. While the calving date has already been found to be influenced by temperature and snow conditions (Thompson and Turner 1982; Adams and Dale 1998; Forchhammer et al. 2001), this study is so far the first to highlight an influence of weather variables on calving synchrony in ungulates. In summary, the variability of climatic conditions in the period from October to November and in January seemed important for the variability in females' plastic response of calving dates to better climatic conditions and as a consequence in shaping calving synchrony at the population level whereas climatic conditions in early spring, just before the calving season, seemed more important in defining the calving dates at the individual level, likely because of its influence on the adjustment of each female's gestation length.

2.6 Appendices
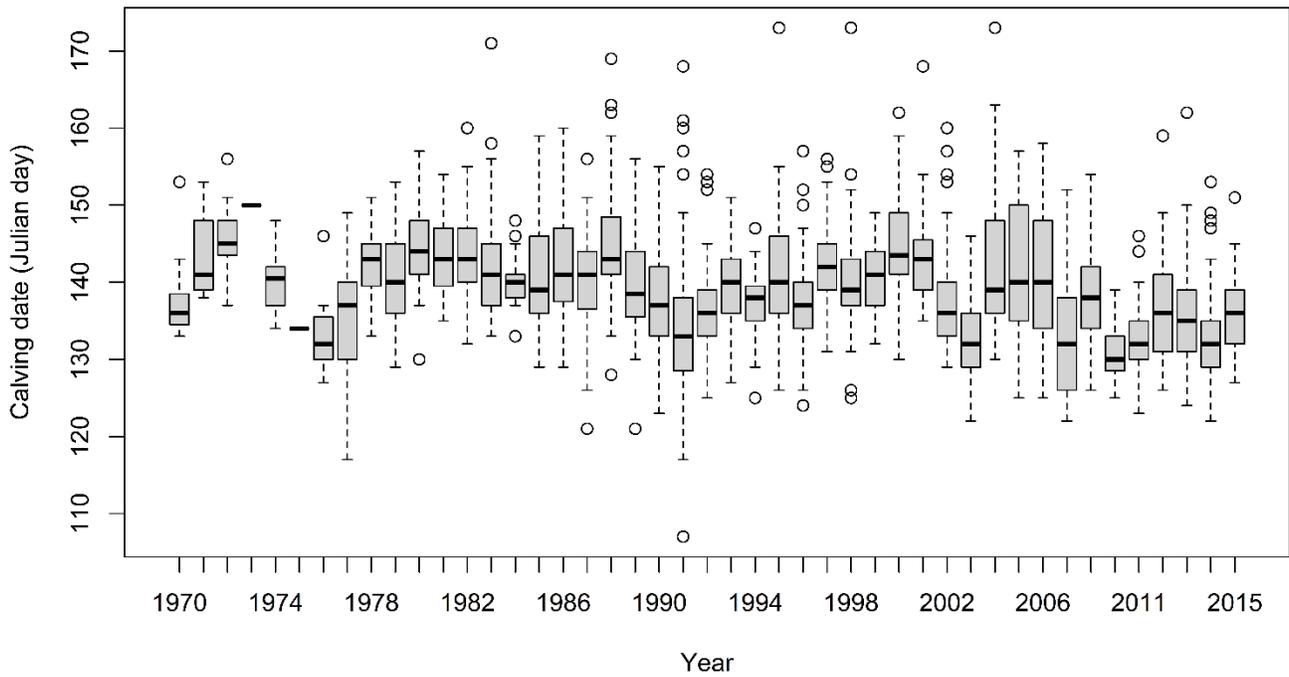
Figure 2.5 Annual distribution of calving dates from the Kutuharju reindeer herd in Kaamanen, northern Finland in the period from 1970 to 2015. The thick, solid lines represent the median and the dashed lines represent the 25th percentile for the lower part and the 75th percentile for the upper part. The empty circles represent the extreme values.
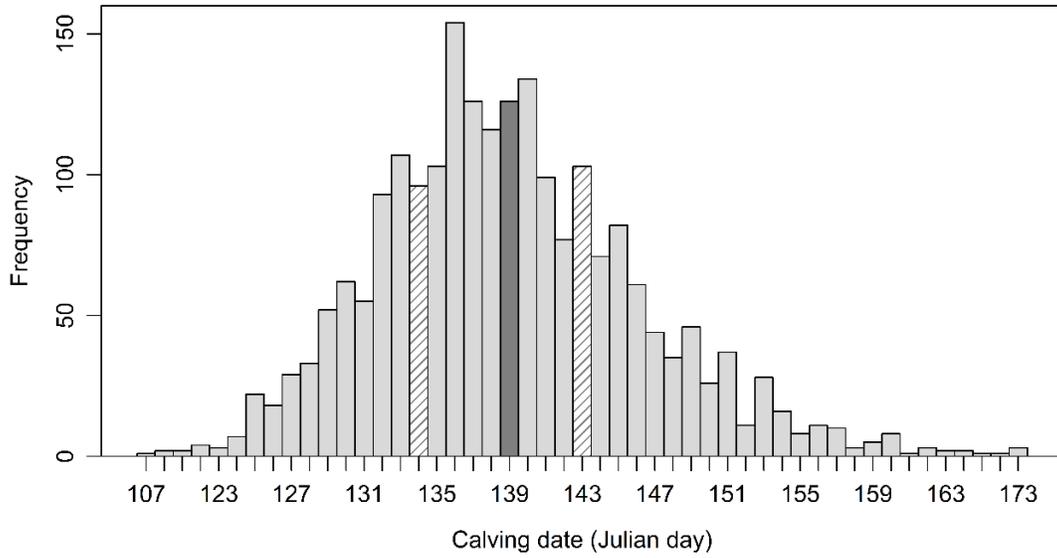
Figure 2.6 Distribution of calving dates expressed in Julian day from a semi-domesticated reindeer herd in Kaamanen, northern Finland from 1970 to 2015. The darker bar represents the mean of the distribution, while the two striped bars represent respectively the 25th and 75th percentile of the distribution.
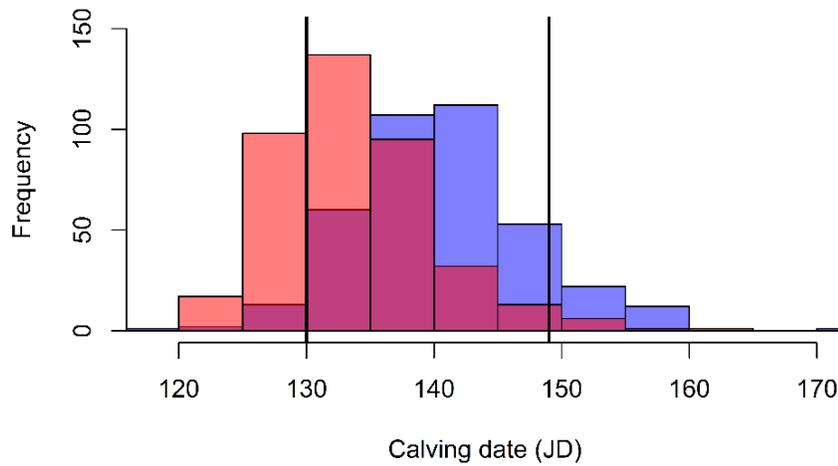
Figure 2.7 Calving dates distribution of the Kutuharju field reindeer research station herd; from 1970 to 1985 in blue color and from 2006 to 2016 in red color. The purple color represents the overlap between the two different period's distributions. The two black vertical lines represent the historical May 10 - May 29 time window for calving dates from 1970 to 1985 (Eloranta and Nieminen 1986).
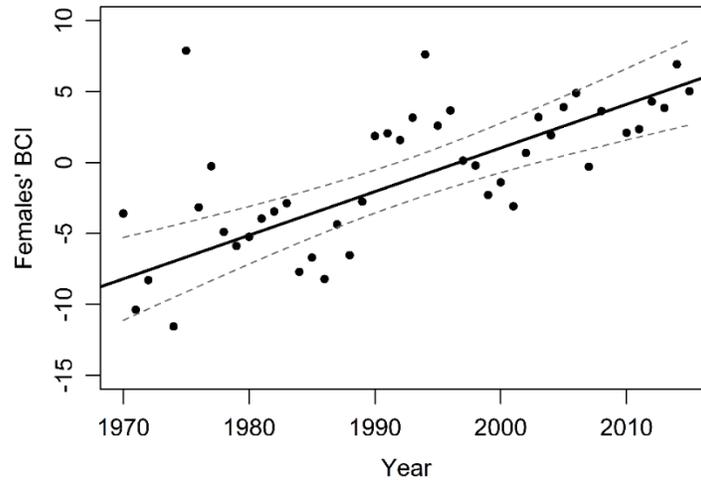
Figure 2.8 Temporal trend of an improvement of the females' body condition index (BCI) of the Kutuharju reindeer herd from 1970 to 2015. The fitted line and the 95% confidence interval band are provided. The BCI was calculated as an age-specific residual body mass – a measure of female body weight after the effect of age is controlled (see text for more details).

Chapter 3 Response of reindeer mating time to climatic variability

The following chapter is based on the manuscript: Paoli A, Weladji RB, Holand Ø and Kumpula, J Response of reindeer mating time to climatic variability. Resubmitted to *BMC Ecology* on 22/05/2019

3.1 Abstract

The breeding time of many species has changed over the past two to three decades in response to climate change. Yet it is a key reproductive trait that affects individual's parturition time and reproductive success, and thereby population dynamics. In order to predict how climate change will affect species' viability, it is crucial to understand how species base their reproductive efforts on environmental cues. By using long-term datasets of mating behaviours and copulation dates recorded since 1996 on a semi-domesticated reindeer population, we showed that males' mating behaviours and females' copulation dates occurred earlier in response to climatic conditions at different key periods in the annual breeding cycle of reindeer. Males' timing of rutting activities occurred earlier following better climatic conditions in late winter. Females' copulation dates were advanced with less snowfalls in January and colder maximum temperatures in July. The mediated effect of better climatic conditions in late winter on improving males' pre-rut body weight through a better availability of late winter food and early green-up of vegetation would explain the observed advance in males' mating time. Winter climate by acting during pregnancy through nutritional status might have helped females to shorten their gestation period and to advance their copulation date the next mating season. A lower level of insect harassment caused by colder maximum temperatures in July might also have caused an advance in copulation dates. The plastic response of reindeer mating time to climatic variability, despite supplemental feeding occurring in late April, demonstrated that environmental factors may have a greater influence on reproductive outputs than previously supposed in ungulates.

3.2 Introduction

Breeding time in animals is a strong determinant of offspring viability and reproductive success (birds: Verhulst and Nilsson 2008, fish: Wright and Trippel 2009, mammals: Clutton-Brock et al. 1982; Bowyer et al. 1998) and therefore a key component of population dynamics. Accordingly, a mismatch between species' timing of reproduction and its environment could have

major consequences on offspring production (Post and Forchhammer 2008) and could compromise the species' viability. The mating season of ungulates is regulated by climatic conditions both directly (i.e. as proximate factors) through influencing rut and estrus, and indirectly (as ultimate factors) through survival of the young, both by reducing predation risk (Rutberg 1987) and by coinciding with vegetation quality or availability (Festa-Bianchet 1988). Indeed, for animals living in seasonal environments, the breeding season is ultimately constrained by a genetic control where mating is precisely timed so that parturition is timed to coincide with long-term patterns of climate as a way to offer a hospitable environment when rearing the young (Suttie and Webster 1995; Bronson 2009), balancing adequately the population's recruitment rate with the adults' probability of survival to the next breeding season (Gaillard and Yoccoz 2003). Seasonal breeders might therefore be more sensitive to large changes in climate (Bowyer et al. 1998). If born too early, offspring would be nursed with a low-quality milk produced by mothers that are in negative energy balance due to a low-quality vegetation (i.e. low protein content; Chan-McLeod et al. 1994; Festa-Bianchet 1988; Parker et al. 1990) and if born too late, young are observed to not be able to use summer green flush up as effectively as early born calves and might therefore lack time to grow and develop sufficiently to overcome winter severity (Festa-Bianchet 1988). Small and late born calves were then shown to be more prone to (1) insect harassment and summer heat (Kumpula and Nieminen 1992; Weladji et al. 2003) and (2) predation by bears, golden eagles and other predators (Eloranta and Nieminen 1986; Nieminen et al. 2013). Consequently, individuals born outside the optimal period for births ultimately had lower probabilities to survive (Festa-Bianchet 1988; Gaillard et al. 1993), jeopardizing their survival and growth, as well as the survival and reproductive success of their mothers (Clutton-Brock 1988). In stochastic environments, a plastic response of mating time to environmental change would thus allow species to optimize their recruitment rate under changing climatic conditions.

The timing of reproduction of many taxa has changed over the past two to three decades in response to climate change (bird: Visser et al. 1998; Frederiksen et al. 2004, amphibian: Blaustein et al. 2001, fish: Asch 2015, mammal: Burthe et al. 2011; Moyes et al. 2011, marine species: review by Poloczanska et al. 2013). Such observed responses to climate change, however, appeared to be insufficient to track a rapidly changing environment and has led to reduced offspring viability and reproductive success (Post and Forchhammer 2008). The mechanisms underlying such phenological changes are still poorly understood. To understand how climate

change will affect species' viability, it is imperative to understand the link between a species' reproductive strategies and its environment and to understand how the reproductive traits are directly or indirectly affected by climatic changes. In ungulates and long-lived mammals, however, there are several challenges. First, the long overwinter gestation period of those species may render difficult to find the climatic drivers determining the timing of reproduction, because there might be a substantial time lag between those climatic drivers and the point at which reproduction occurs. Second, a certain climatic driver (e.g. temperature) might induce a plastic response in the timing of reproduction but in opposite directions, depending on the time of the year considered. For instance, warmer temperatures in spring result in an increase of vegetation productivity and lengthened growing seasons, which benefits the reproduction of *Rangifer* (Parker et al. 2009). On the other hand, warmer temperatures in summer have increased the level of insect harassment and decreased the body condition of reindeer (Weladji et al. 2003). A first step to understand the mechanisms behind phenological changes is therefore to identify the critical time windows during which the climatic drivers affect the most the timing of reproduction (van de Pol and Cockburn 2011). In most seasonally breeding mammals, however, the annual cycle of daily photoperiod has long been identified as the determinant factor of seasonal breeding, while ambient temperature, nutrition state and behaviour exert a modulator effect (Rosa and Bryant 2003; Williams et al. 2017). Unlike other seasonal breeders, Arctic species such as reindeer has recently been shown to 'lack a circadian clock' (Lu et al. 2010). As suggested by studies on mammals, species that will probably be the most affected by climate change will be the longer-lived species at the mid to higher latitudes whose reproduction is rigidly controlled by photoperiod (Bronson 2009). Decoupled from an endogenous circadian clock, the activation of the reproductive axis in reindeer might thus be more sensitive to other environmental cues than just simply photoperiodism (e.g. ambient temperature, nutritional status and behaviour).

A second step to understand the mechanisms behind phenological changes is to decouple the direct and indirect effects that the climate might have on reproductive traits. Capital breeders such as reindeer rely on body reserves to finance reproduction (Williams et al. 2017) so they could be affected both directly and indirectly by climatic conditions: directly by energetic demands (e.g. thermoregulation: Parker and Robbins 1985, locomotion on snow: Parker et al. 1984) and indirectly through plant productivity that they need to build up their endogenous reserves (Post and Stenseth 1999; Parker et al. 2009; Albon et al. 2017). Body weight of adults is a good metric

to take into consideration effects of both animals' energy requirements and feeding strategies. For this reason, many of the reproductive parameters are examined in relation to adult body weight. Reindeer's mating was previously found to be influenced by females' (Cameron et al. 1993; Flydal and Reimers 2002) and males' body weight (Barboza et al. 2004; Mysterud et al. 2004). In our study, the indirect effects of climate on mating time will therefore be examined through the pre-rut body weight of individuals (measured in September for both males and females). The Arctic surface air temperatures have warmed at twice the global rate (Weladji et al. 2002a; Post et al. 2009; Vors and Boyce 2009) and that *Rangifer* is one of the two only ungulate species to have established in the highly variable Arctic environment and was shown to complete the mating season within 4–5 weeks (Dauphiné and McClure 1974). Therefore, reindeer is an ideal candidate to answer our study question aiming at identifying the critical periods of the year during which climatic drivers affect the most mating time. This will be achieved by examining the associations between climate, population variables and mating time and using two long-term datasets, one of males' mating behaviours and the other of females' copulation dates, recorded since 1996 on a semi-domesticated reindeer population in Finnish Lapland.

From previous studies on this population, we had a priori expectations as to which periods of the year and which climatic variables are more likely to affect mating time. The NAO index in winter negatively affected the growth rate and body weight of reindeer calves in summer and early winter because of nutritional stress that may worsen the females' body condition during pregnancy (Weladji and Holand 2003b) so winter is a first key period with influences on reindeer's reproduction. Also, earlier calving dates were recorded following warmer temperatures in April-May and lower precipitation and a reduced snow cover in April (Paoli et al. 2018) so early spring appears to be a second critical period in reindeer's breeding time. Summer weather also played a detrimental role on reindeer and caribou body condition, because warm summer temperatures increased the level of insect activity and therefore insect harassment (Weladji et al. 2002a, 2003a). From those findings, specific hypotheses could be derived for both males' mating time and females' copulation dates. (1) Reindeer's mating time would be negatively affected (i.e. delayed) by winter climatic conditions (especially for pregnant females), through direct effects of temperature, snowfalls and snow cover on energetic costs of thermoregulation and movement on snow (Parker et al. 1984; Parker and Robbins 1985), and indirect effects on forage accessibility in winter (Hansen et al. 2011; Aikio and Kojola 2014), both impairing individuals' body condition.

(2) Reindeer's mating time would be positively affected by temperature and precipitation in late winter/early spring through indirect effects on spring vegetation productivity and on individuals' regain of fat reserves (Cook et al. 2004; Parker et al. 2009) but negatively by snow cover through direct effect on the energetic costs of individuals (Parker et al. 1984; Parker and Robbins 1985). (3) Reindeer's mating time would be delayed following warmer summer temperatures through indirect effect on the level of insect harassment and therefore summer foraging conditions (Weladji et al. 2002a, 2003a). Although we had clear hypotheses, and to ensure a fully objective evaluation of the potential effects of climatic variability on mating time, we considered all time windows of climatic variables (van de Pol and Cockburn 2011), varying by the start date and on a weekly basis (as in Stopher et al. 2014). Further, we also considered some population variables known to have an influence on reindeer's mating time as the changes in those variables (mainly caused by management practices) can potentially reinforce or dampen climatic effects on mating time (Ozgul et al. 2010). The population variables included population sex ratio (Holand et al. 2002; Mysterud et al. 2003; L'Italien et al. 2012), population density (Langvatn et al. 2004; Burthe et al. 2011) and male age structure (Holand et al. 2006; L'Italien et al. 2012; Tennenhouse et al. 2012). Based on all of these studies, tentative path models on how climatic variability probably affects reindeer's mating time can be built (Figure 3.1a and Figure 3.2a). To investigate the direct versus indirect effects of climate on mating time, path analysis can be employed (Shipley 2000, 2009). In the present study, we thus aimed to: (1) quantify the rate of change over time of reindeer's mating time, (2) determine whether phenological change in mating time was explained by climatic drivers, and which time windows of those climatic drivers best explained variation in mating time and (3) assess the direct and indirect (through individuals' pre-rut body weight) effects of the climatic drivers identified on mating time.

3.3   Material and Methods

3.3.1   Study area and population

The data is from the Kutuharju field reindeer research station in Kaamanen, northern Finland (69°N, 27°E). Open birch and pine forests, bogs and lakes dominate the area and the landscape varies between 185–370 m above the sea level. A semi-domestic reindeer population of about 100 animals per year was used in this study. Reindeer were all of known age and individually recognizable thanks to the long-term book-keeping of the herd demography and by marking all of

them by collars and ear tags. Since 1996, males were fitted with VHF radio collars while females were fitted with coloured collars, both with unique identification facilitating the monitoring of individual behaviour. Most of the year, reindeer were free ranging in two large fenced enclosures, the north-west section (Lauluvaara ~ 13.8 km²) and the south-east section (Sinioivi ~ 15 km²). Every day during the rut period from mid-September to mid-October the collared males and their harem were located and the group composition and all males' mating behaviours recorded. All the copulations observed in the field were also recorded. After the mating season in late October, the animals were gathered and taken to a winter area (15 km²) where they can graze freely on natural pastures. By the end of winter, females were transferred into a calving enclosure (approximately 0.5 km²) where calving dates have been recorded. In late winter and especially after harsh winters, the animals were supplementary fed (pellets and hay). Given the significant between-years variability in both males' (one-way analysis of variance, $F_{(12, 65)} = 8.97$, $P < 0.001$) and females' body weight in September ($F_{(14, 183)} = 4.20$, $P < 0.001$), we believe that regular supplemental feeding alone could not buffer climatic effects by keeping up individuals' body weight at a stable level. Unfortunately, no detailed information was available on the duration or the amount of supplemental feeding given every year to the animals.

3.3.2   Mating behaviors

Males mating behaviours were observed using the focal observation technique (Martin and Bateson 2007). Priority was given to the dominant males as they perform most of the mating behaviours during the rut period (e.g. chasing other males, grunting, herding females, etc; see Tennenhouse et al. 2011 for further details). The dominant males in reindeer can be easily identified as 'harem holders', i.e. occupying a central position in the group (contrary to the 'satellites'). One dominant male was observed for 15 minutes and every 15 seconds, the activity of that male (rest, feed, stand, and walk) was recorded as well as his mating behaviours. The mating behaviours used in this study included 'Herd', 'Chase females', 'Spar', 'Fight', 'Displace', 'Chase', 'Flehmen', 'Investigate', 'Sniff', 'Attempt copulation', 'Court', 'Follow female' (see de Vos et al. 1967; Tennenhouse et al. 2012; Weladji et al. 2017 for further details and description of the behaviours).

3.3.3 Mating time

The mating season of ungulates starts when male exhibit all behaviors and activities associated with the rutting season (e.g. holding and defending a harem of females; Moyes et al. 2011). In red deer, it has been estimated with roaring dates and sexual aggregation patterns (Loe et al. 2005) and with estrus dates as a cue for the rut period (Moyes et al. 2011). For reindeer, the rutting season of dominant males was shown to follow a specific sequence: first herding, then chasing other males – or any other agonistic interaction as competition behaviours exhibited between males, and finally investigating and courting females (Weladji et al. 2017). Using the mating behaviours that follow this sequence, a first male-based metrics dataset included males' mating behaviours, the year of study, the male's identity, the date when the behaviour was displayed (averaged per year and per male to avoid having data nested across multiple hierarchies), and its related body weight in September and age. From the observed copulations, we kept only the copulation dates that led to the birth of a calf the following calving season and within the gestation length range of 211-229 days (Mysterud et al. 2009) to make sure that females were in estrus those dates. A second dataset thus included female-based metrics with the dates of observed copulations, the year of study, the female's identity together with their body weight in September and age. Because the peak date for males' mating behaviours occurred earlier by on average 2.9 days (95% CI [-4.76, -1.01]) than the peak date for copulation dates and that much more females' copulation dates ($n = 198$) were available in comparison to averaged males' mating behaviours ($n = 78$), we decided to keep the two datasets separate and to run two different models. Males' mating time MMT and females' copulation dates COPD were thus the two variables of interest in this study with MMT the averaged day of the year when males displayed their mating behaviours or the timing of males' rutting activities and COPD the day of the year when copulations were observed. All calendar dates were converted into Julian days starting on 1 January for analysis purposes. In total, 14 years of data from 1996 to 2011 were available for the timing of males' rutting activities (MMT) and 15 years from 1996 to 2013 for copulation dates (COPD).

3.3.4 Population variables

To control for the effect of proportion of males on mating time (Holand et al. 2002; Mysterud et al. 2003; L'Italien et al. 2012), the proportion of males during the mating season was estimated per enclosure as the number of males divided by the number of females over one year

of age present in that specific enclosure. Between 1996 and 2013 (except 1998), the herd was subjected to a number of experiments including manipulation of the proportion of males, leading to the simultaneous use of the two large enclosures, Sinioivi and Lauluvaara. Consequently, the proportion of males was estimated per enclosure for those years. Thanks to the book-keeping of the herd, the identity of the animals involved in any experiment was known, as well as their presence in each enclosure and therefore allowed to relate every mating behavior exhibited by a male and every copulation date to the corresponding, estimated proportion of males in that enclosure. The effect of proportion of males on MMT and COPD was thus accounted for in the analyses. In addition to the proportion of males, we also estimated the population density per enclosure-year as the number total of individuals present in a specific enclosure for a given year in order to account for the effects of population density on MMT and COPD (Langvatn et al. 2004; Burthe et al. 2011). Because male age structure ($\male$ASTR) influence females' estrus date or males' mating time (Holand et al. 2006; L'Italien et al. 2012; Tennenhouse et al. 2012), it was another population parameter taken into consideration in our study. During the rutting periods from 1996 through 2011, the composition of the male segment of the Kutuharju reindeer herd was manipulated. Three male age structures categories were used during the mating season: (1) only adult ($\geq$ 3 years old) males present, (2) only young males (1.5 years old) present, and (3) a mixture of male age classes, including both adult and young males, present (Holand et al. 2006; Tennenhouse et al. 2011). The indirect effect of climatic variability on MMT and COPD was studied through the direct effect of the climatic variables on the pre-rut body weight of individuals. Every year, all animals are gathered in corrals just before the rut period (in September) and different measurements are taken, allowing us to have accurate measurements of pre-rut body weights of males and females ('BW$_{Sept}$'). Given that all factors linked to physical condition in reindeer interact with each other so that older individuals tend to be heavier (Ropstad 2000), the BW$_{Sept}$ was also corrected by the age of the individuals in the models.

3.3.5   Climatic data

From the Finnish Meteorological Institute, three weather stations (Utsjoki, Ivalo airport and Nellim) in northern Finland (68°N, 27°E) were used to obtain local climatic data (daily recorded values for temperature, precipitation and snow cover) from 1996 to 2013. Specifically, to estimate the local climate at our study site with as much reliability as possible, the weighted

mean by the distance from the weather station to our study site was used. The distance between our study site and each of the weather stations was precisely assessed using their respective GPS coordinates and the Great Circle longitude-latitude calculations tool (http://www.cpearson.com/excel/LatLong.aspx). Precipitation can be either rainfall or snowfall depending on the temperature. Temperature daily values included the minimum, maximum and average temperature recorded that day. To better reflect climatic variability and its effects on reindeer's mating time, we preferred to use the minimum and maximum temperature values. A total of four climatic variables were subsequently used in the analyses: minimum temperature (in °C, 'MinTemp'), maximum temperature (in °C, 'MaxTemp'), total precipitation (in mm, 'Prec') and snow cover (in mm, 'Snow').

3.3.6 Statistical analyses

3.3.6.1 Temporal trends

Variation in mating time (timing of males' rutting activities or females' copulation dates), our response variable, was analysed using Linear Mixed-effects Models (LMMs), by running the lmer-function in the R package lme4 (Bates et al. 2015, <www.r-project.org>). Year only was entered as a fixed-effect factor (continuous variable) in the models, and individual identity and year as multilevel random effects to control for repeated measures (Kruuk et al. 1999; Milner et al. 1999). Unstandardized values of the temporal trends were reported and the parameter estimates were derived using the restricted maximum likelihood estimates as recommended for mixed effect models. Linear Models (LMs) with year entered as a covariate were applied to test the temporal trends of the climatic and population variables. The temporal trends were considered statistically significant if 95% confidence intervals (CIs) of the parameter estimates excluded 0.

3.6.1.2 Critical time window of climatic variables

To find the key period of the year having the greatest influence in determining reindeer's mating time, we used a sliding-window approach (Stopher et al. 2014), separately for each climatic variable (temperature, precipitation and snow cover). In this approach, the strength of association between mating time and the mean of a particular climatic variable (or sum for precipitation and snow cover), calculated across a certain time period (window), is tested. The time windows tested were estimated by varying the start date and duration of the window by weekly intervals so that

the minimum interval would be of one week, while the longest interval could be of 52 weeks, and the start date could be anytime from Julian day 1 (January 1st) to Julian day 365 (December 31st). Then, the strength of association between each window and mating time was calculated to identify the critical time window (of each climatic variable) having the greatest influence on mating time (van de Pol and Cockburn 2011). To do so, linear models were used with no other fixed effects included, apart from only one time window at a time. The Akaike Information Criterion values (AIC) of those linear models were then compared and the critical window from the model with the lowest AIC was statistically supported as being the most informative. Once the best critical time period was identified for each climatic variable and each response variable (MMT or COPD), we assessed which combination of the four weather variables had the highest statistical support when included in the same model, separately for males' timing of rutting activities and females' copulation dates. A total of 15 models were therefore tested for all possible combinations of the four climatic variables (minimum and maximum temperature, precipitation and snow cover). Again, the AIC values were used for model comparison, as well as Akaike weights (AIC weights) to compare the relative performance of the tested models (Anderson et al. 2001; Burnham and Anderson 2002). The delta AIC (Δ_i) was calculated to provide a measure of each model (among the 15 models tested) relative to the model with the lowest AIC value, as a way to indicate the relative support of the best model. The best combination given by the model with the lowest AIC value was subsequently used in the path analyses. The AIC values, ΔAIC and AIC weights were obtained from the aictab-function of the AICcmodavg package in R (Bates et al. 2015, <www.r-project.org>).

3.3.6.3 Path analyses

To test the direct or indirect (i.e. through individuals' pre-rut body weight) effects of climatic variability on mating time, we used confirmatory path analysis. Because path analysis can test the structural nature of multiple relationships between different variables (Shipley 2009), we could clearly identify both direct and indirect effects of climate on mating time, while regression analyses only test the dependence of response variables on a set of predictor variables. Confirmatory path analysis also allows to consider a framework accounting for correlations between mating time, population variables and individuals' pre-rut body weight. Because our study design was multilevel, with repeated measurements taken on the same individuals and

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observations nested in different years, the standard methods of testing path models based on maximum likelihood are too difficult to apply (Shipley 2009). Confirmatory path analyses, however, allow intercepts and path coefficients to potentially vary between hierarchical levels (e.g. individual and year). The Shipley's method based on the concept of 'd-separation' was used to test the causal implications of the hypothesized path models (directed separation; Pearl 1988; Shipley 2000). A path model (directed acyclic graph) is formed by a combination of a series of hypothesized causal relationships between pairs of variables (path coefficients), typically represented by a 'box-and-arrow' diagram as in path analysis. The causal relationships in the acyclic graph imply a series of independence relations between pairs of variables that will be determined by the graph-theoretic notion of d-separation (Pearl 1988; Shipley 2000). The concept of d-separation is defined as the necessary and sufficient conditions for two variables in a path model (without feedback loops) to be independent upon conditioning on another set of variables (Shipley 2000). The d-separation therefore represents a topological condition of a directed graph, not a statistical condition of empirical data but this topological condition is directly translated to a predicted independence of variables within the model (i.e. a description of the statistical patterns of conditional dependence and independence that would be true in the observed data if they were generated by the hypothesized causal relationships; Pearl 1988). The causal relationships represented in the causal graph will then be tested by performing a simultaneous test of all independence claims in that causal graph. A 'basis set' is built, implying all of the claims of dependence and independence made by the causal graph. The statistic $C = -2 \sum \ln(p_i)$, calculated on the independence claims of the basis set, follows a chi-square distribution with $2k$ degrees of freedom, where k is the number of independence claims in the basis set and p_i is the null probability of the independence test associated with the ith independence claim generated by the model (Shipley 2000, 2009). The model is supported if the causal relationships hypothesized in the path model are correct, i.e. if a lack of significant ($P > 0.05$) difference between the observed and predicted pattern of independencies in the basis set is reported (Shipley 2009). In our study, the approach is extended using linear mixed-effects models to obtain the null probability (p_i) for each independence claim (known as generalized multilevel path models; Shipley 2009).

The causal relationships tested in the two path models (for MMT and COPD) were hypothesized based on the following aspects:

(1) The identified critical time windows of climatic variables were expected to have indirect effects on reindeer's mating time, through their respective effects on the pre-rut body weight of individuals (females and males).

(2) The critical windows of climatic variables were also expected to have a direct effect on reindeer's mating time.

(3) The documented effect of pre-rut body weight of individuals on mating time was inferred from previous studies, for females (Cameron et al. 1993; Ropstad 2000; Flydal and Reimers 2002) and males (Barboza et al. 2004; Mysterud et al. 2004).

(4) The age of individuals was also pre-supposed to have an effect on the mating time (Flydal and Reimers 2002; Garel et al. 2009) and the known correlation between the body weight of individuals and their age was inferred from previous studies (Ropstad 2000).

(5) Relationships between proportion of males and male age structure on mating time were also hypothesized from previous studies (Komers et al. 1999; Mysterud et al. 2008; Tennenhouse et al. 2012).

(6) The population density was hypothesized to have a direct effect on mating time through promiscuity between individuals causing a higher level of sexual biostimulation (Dauphiné and McClure 1974) and an indirect effect through its influence on individuals' body weight (Langvatn et al. 2004).

(7) Because male ungulates adjust their reproductive effort to the timing of females' estrus (Mysterud et al. 2008), we also included the hypothesized effect of the females' copulation date on males' mating time in the path model of MMT. Given that females' estrus might be stimulated by males' sexual behaviors (Komers et al. 1999) and that females might also control the timing of their ovulation to match the peak reproductive effort of dominant males (Komers et al. 1999; Tennenhouse et al. 2012), the hypothesised effect of males' timing of rutting activities on females' copulation was included in the COPD path model.

(8) The calving date in the precedent spring was also considered to possibly influence the females' copulation dates, directly (Clements et al. 2011) or indirectly through its documented effect on females' body weight the next mating season (Cameron et al. 1993).

The hypothesized structure of the path models was shown in Figure 3.1a for MMT and Figure 3.2a for COPD. The conditional independence of pairs of variables was tested in linear mixed-effects models (LMMs), with individual identity fitted as a random effect to account that

each individual had multiple records. Year was also fitted as a multilevel random effect, to account for stochastic variation between years. Once the appropriate model was identified (i.e. most parsimonious model given the lowest AIC), the same statistical methods were used to test conditional dependence of pairs of variables (i.e. pairs of variables hypothesized to be correlated). The regression coefficients with their standard errors for each path (path coefficients) were reported if dependence associations were found significant. All variables in the path models before calculation of path coefficients were centred and standardized ($\overline{X}$ = 0, SD = 1) to be on a comparable scale. Analyses were performed in R 3.6.0 (R Development Core Team 2019).
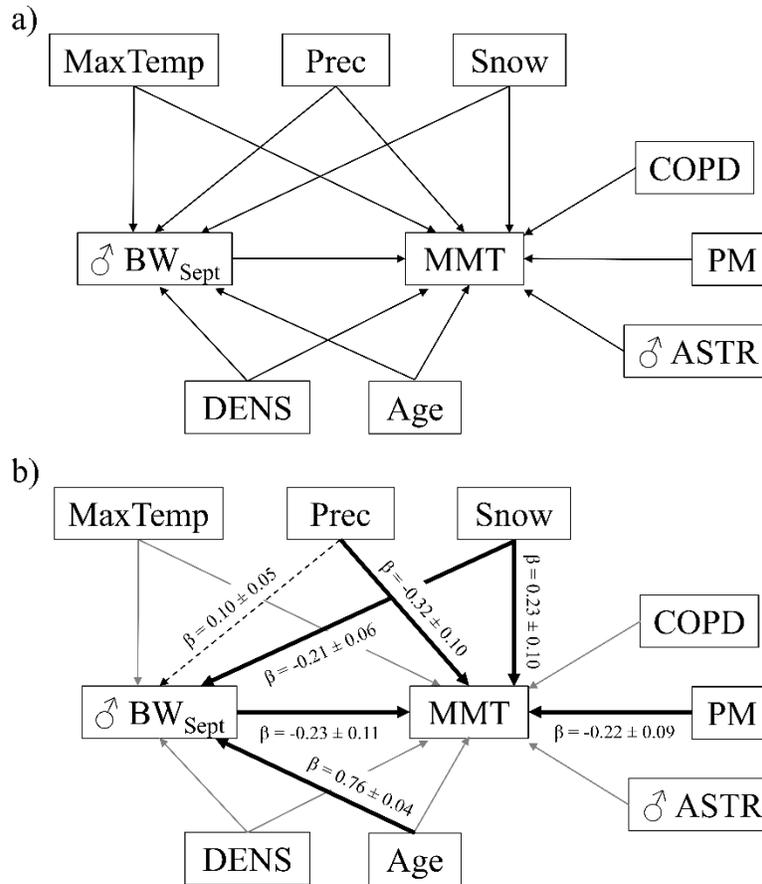
Figure 3.1 Hypothesized path model for how males' timing of rutting activities ('MMT') of reindeer is affected directly and indirectly by climatic variability from 1996 to 2011 in the Kutuharju herd, northern Finland. The definitions and time windows of the climatic variables ('MaxTemp', 'Prec', 'Snow') are provided in the Methods section, as well as the explanation of (a) the hypothesized paths. '♂ BW$_{Sept}$' represents the pre-rut body weight of males (measured in September), 'COPD' the females' copulation date, 'DENS' the population density, 'PM' the proportion of males in the herd and '♂ ASTR' the male age structure (see text for details). All lines in the diagram represent a specific linear mixed-effects model. The path model in (b) shows the standardized coefficients and SEs for paths associated with statistically significant effects. Nonsignificant paths ($P > 0.05$) shown as darker lines in panel (a) have been set as light gray lines in panel (b); significant paths with good evidence ($P < 0.05$) for an effect as thick solid lines (b) and paths with a weak effect ($P \sim 0.05$) as thin dotted line (b).

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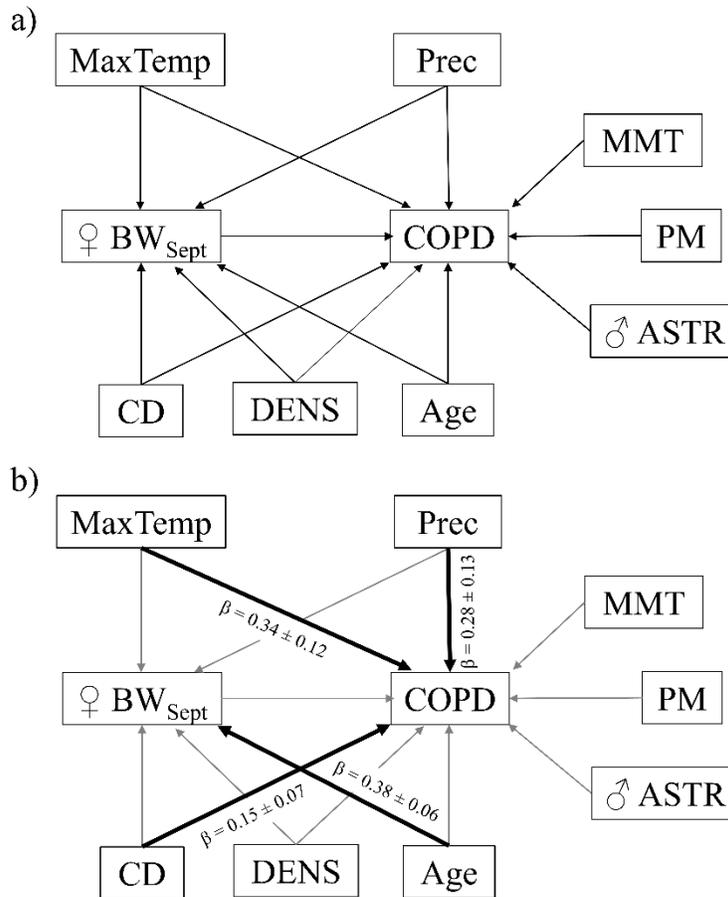
Figure 3.2 Hypothesized path model for how females' copulation date ('COPD') of reindeer is affected directly and indirectly by climatic variability from 1996 to 2013 in the Kutuharju herd, northern Finland. The definitions and time windows of the climatic variables ('MaxTemp', 'Prec') are provided in the Methods section, as well as the explanation of (a) the hypothesized paths. '♀ BW$_{Sept}$' represents the pre-rut body weight of females (measured in September), 'DENS' the population density, 'PM' the proportion of males in the herd, '♂ ASTR' the male age structure, 'MMT' the males' mating time and 'CD' the precedent calving date of females (see text for details). All lines in the diagram represent a specific linear mixed-effects model. The path model in (b) shows the standardized coefficients and SEs for paths associated with statistically significant effects. Nonsignificant paths ($P > 0.05$) shown as darker lines in panel (a) have been set as light gray lines in panel (b); significant paths with good evidence ($P < 0.05$) for an effect as thick solid lines (b) and paths with a weak effect ($P \sim 0.05$) as thin dotted line (b).

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3.4 Results

3.4.1 Temporal trends in mating time

From 1996 to 2011 (except years 1998 and 2002), 78 averaged mating dates were available from 1,441 males' mating behaviours of 57 different males. From 1996 to 2013 (except years 1998, 2008 and 2012), 198 copulation dates were used from 122 different females (Figure 3.6). The years excluded from the analyses were dropped simply because no data were available those years. The peak date for males' mating time was October 7th whereas the mean date for females' copulation dates was October 10th (Figure 3.7). Between 1996 and 2011, the males' mating time (MMT) significantly advanced (95% CI [–0.83, –0.46]; Figure 3.3a), by an estimated 0.64 day per year; leading to an overall shift estimated to about 10 days across 16-years (Figure 3.3a). Between 1996 and 2013, the females' copulation date (COPD) significantly advanced (95% CI [–0.92, –0.52]; Figure 3.3b), by an estimated 0.72 day per year; leading to an overall shift in copulation peak date by 11 days over 18 years (Figure 3.3b). Both the males' mating time and females' copulation dates varied significantly between-years (one-way analysis of variance, $F_{(12, 65)} = 8.49$, $P < 0.001$ for MMT and $F_{(14, 183)} = 10.4$, $P < 0.001$ for COPD, see Figure 3.6).
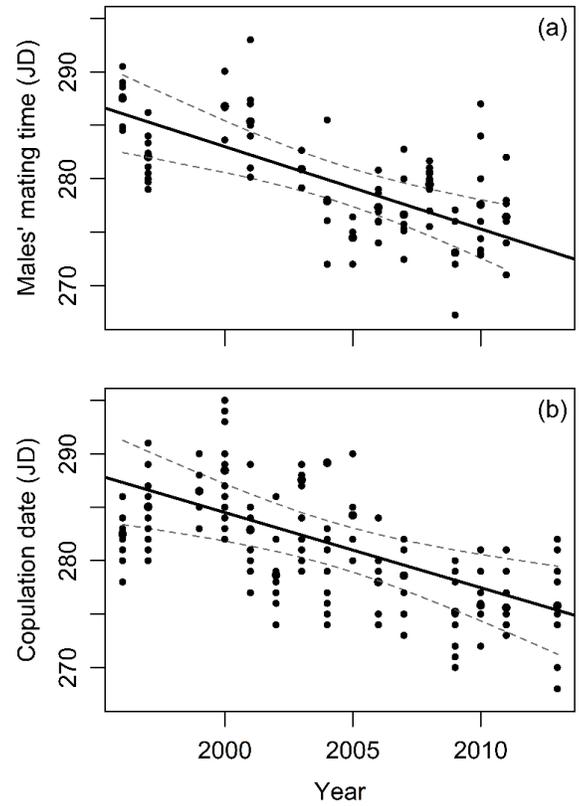
Figure 3.3 Inter-annual variation of (a) males' mating time and (b) females' copulation dates from 1996 to 2013 of a semi-domesticated reindeer population at Kutuharju, northern Finland. Fitted line as well as 95% confidence interval band are provided. The dates are expressed in Julian day (JD) starting January 1st. Data points were weighted by inverse variance (i.e. regression slopes).

3.4.2   Critical time window of climatic variables

After comparison of the AIC values of the models containing various combinations of climatic variables, the critical windows of each climatic variable that best explained variation in males' timing of rutting activities and females' copulation dates separately could be identified. The Table 3.1 provides details of the 15 models of all combinations of the best windows for each climatic variable, separately for MMT and COPD. For males' mating time, the most parsimonious model contained the averaged, maximum temperature for one week between 23 May and 30 May ('MaxTemp$_{MMT}$'), the total amount of precipitation for 8 weeks between 28 April and 23 June ('Prec$_{MMT}$'), and the total snow cover for one week between 21 April and 28 April ('Snow$_{MMT}$'; Table 1). For females' copulation date, the most parsimonious model contained the averaged, maximum temperature for 2 weeks between 13 July and 27 July ('MaxTemp$_{COPD}$') and the total amount of precipitation for one week between 13 January and 20 January ('Prec$_{COPD}$'; Table 3.1).

Table 3.1 Comparison of linear models testing the effect of various combinations of climatic variables on males' mating time and females' copulation date of a semi-domesticated reindeer population in the Kutuharju field reindeer research station in Kaamanen, northern Finland (69°N, 27°E) from 1996 to 2013.

Variables	K	AIC	ΔAIC	AIC$_{wt}$
Males' mating time				
MaxTemp + Prec + Snow	3	436.39	0.00	0.37
Prec + Snow	2	437.87	1.48	0.18
MaxTemp + MinTemp + Prec + Snow	4	438.26	1.87	0.15
MaxTemp + MinTemp + Prec	3	439.37	2.97	0.08
MinTemp + Prec + Snow	2	439.74	3.35	0.07
MinTemp + Prec	3	439.83	3.43	0.07
MaxTemp + Prec	2	441.32	4.93	0.03
MaxTemp + Snow	2	441.75	5.36	0.03
MaxTemp + MinTemp + Snow	3	443.75	7.35	0.01
MaxTemp + MinTemp	2	444.57	8.18	0.01
Prec	1	446.15	9.76	0.00
MaxTemp	1	449.80	13.41	0.00
MinTemp	1	452.11	15.71	0.00
MinTemp + Snow	2	453.15	16.76	0.00
Snow	1	455.13	18.73	0.00
Females' copulation date				
MaxTemp + Prec	2	1291.65	0.00	0.42
MaxTemp + Prec + Snow	3	1292.77	1.12	0.24
MaxTemp + MinTemp + Prec	3	1293.65	2.00	0.16
MaxTemp + MinTemp + Prec + Snow	4	1294.52	2.86	0.10
MinTemp + Prec	2	1296.56	4.91	0.04
MinTemp + Prec + Snow	3	1297.09	5.44	0.03
Prec	1	1298.77	7.12	0.01
Prec + Snow	2	1300.75	9.10	0.00
MaxTemp + MinTemp	2	1305.94	14.28	0.00
MaxTemp + MinTemp + Snow	3	1306.02	14.37	0.00
MinTemp + Snow	2	1309.12	17.47	0.00
MinTemp	1	1309.51	17.85	0.00
MaxTemp	1	1310.08	18.43	0.00
MaxTemp + Snow	2	1312.08	20.43	0.00
Snow	1	1355.99	64.33	0.00

The linear models had no other fixed effects than climatic variables. A total of 15 models were fitted per response variable (males' mating time and females' copulation date). The models were compared and ordered by AIC values. K represents the number of climatic variables fitted in the model. The ΔAIC (difference with the AIC of the best model) and AIC weights (AIC$_{wt}$, weight of the model relative to all 15 models fitted for that response variables) were also provided (see text for details). The dates defining the critical time window for each climatic variable were given in Results.

3.4.3 Path analyses

The design of the hypothesized path model for males' mating time is depicted in Figure 3.1a, while the design of the hypothesized path models for females' copulation date is depicted in Figure 3.2a. The same path models but showing the significant paths (i.e. statistically significant path coefficients), with nonsignificant paths removed are shown in Figure 3.1b and Figure 3.2b for MMT and COPD respectively. The models were both supported as providing a good fit to the observed data, indicated by a non-significant P-value of the goodness-of-fit (MMT: $\chi^2 = 0.68$, df $= 4$, $P = 0.95$; COPD: $\chi^2 = 6.7$, df $= 8$, $P = 0.57$).

From the males' timing of rutting activities path model, several results can be drawn (Figure 3.1b). First, the males' mating time was directly affected by the snow cover between 21 April and 28 April, the amount of precipitation between 28 April and 23 June, the pre-rut body weight of males and the proportion of males in the herd (Figure 3.1b). A delay in MMT was observed when the snow cover increased in late April (Snow$_{MMT}$, $P < 0.05$, Figure 3.4a). On the other hand, a higher amount of precipitation between late April and late June (Prec$_{MMT}$) contributed to an advancement in males' mating time ($P = 0.002$, Figure 3.4b). The MMT was also advanced when the males' body weight in September (BW$_{Sept}$) was higher ($P < 0.05$, Figure 3.4c) and when a higher number of males (PM) was present in the herd around the time of the rut ($P < 0.05$, Figure 3.1b). The males' mating time was also indirectly affected by the snow cover in late April through the direct effect of the snow cover on the males' pre-rut body weight ($P < 0.001$, Figure 3.1b). To a lesser extent, an indirect effect of Prec$_{MMT}$ could also be reported on MMT through the pre-rut body weight of males but the effect of Prec$_{MMT}$ on males' BW$_{Sept}$ was non statistically significant ($P = 0.06$).

The females' copulation date was directly affected by three identified variables: the maximum temperature between 13 July and 27 July, the amount of precipitation between 13 January and 20 January and the females' previous calving date (Figure 3.2b). A delay in COPD was observed after an increasing amount of precipitation in the third week of January (Prec$_{COPD}$, $P < 0.001$, Figure 3.5a), an increasing maximum temperature between mid- and end of July (MaxTemp$_{COPD}$, $P = 0.07$, Figure 3.5b) and a later calving date the previous calving season (CD, $P < 0.05$, Figure 3.5c). There was no indirect effects reported to have an influence on COPD and surprisingly, the females' pre-rut body weight did not affect their copulation date (Figure 3.2b).

For both males and females, the age of the individuals had a strong, statistically significant positive effect on their body weight in September (all $P < 0.001$) but the age did not influence directly the MMT or COPD (Figure 3.1b and Figure 3.2b respectively).

3.4.4   *Temporal trends in climatic and population variables*

The phenological change of an earlier males' mating time overtime followed the statistically significant temporal trends of a decreasing snow cover between 21 April and 28 April ($b = -24.4$, 95% CI [-28.6, -20.2], Figure 3.4d), more precipitation between 28 April and 23 June ($b = 2.15$, 95% CI [1.61, 2.69], Figure 3.4e), an improvement in the pre-rut body weight of males ($b = 3.70$, 95% CI [2.63, 4.77], Figure 3.4f) and more males present in the herd around the time of the rut ($b = 0.009$, 95% CI [0.005, 0.01]) from 1996 to 2011. The reported advancement in females' copulation date overtime followed the statistically significant temporal trends of less precipitation (snowfalls at this time of the year) between 13 January to 20 January ($b = -0.46$, 95% CI [-0.56, -0.35], Figure 3.5d), a decreasing maximum temperature between 13 July and 27 July ($b = -0.24$, 95% CI [-0.30, -0.17], Figure 3.5e) and earlier calving dates in the previous calving season ($b = -0.80$, 95% CI [-1.05, -0.55], Figure 3.5f) from 1996 to 2013.
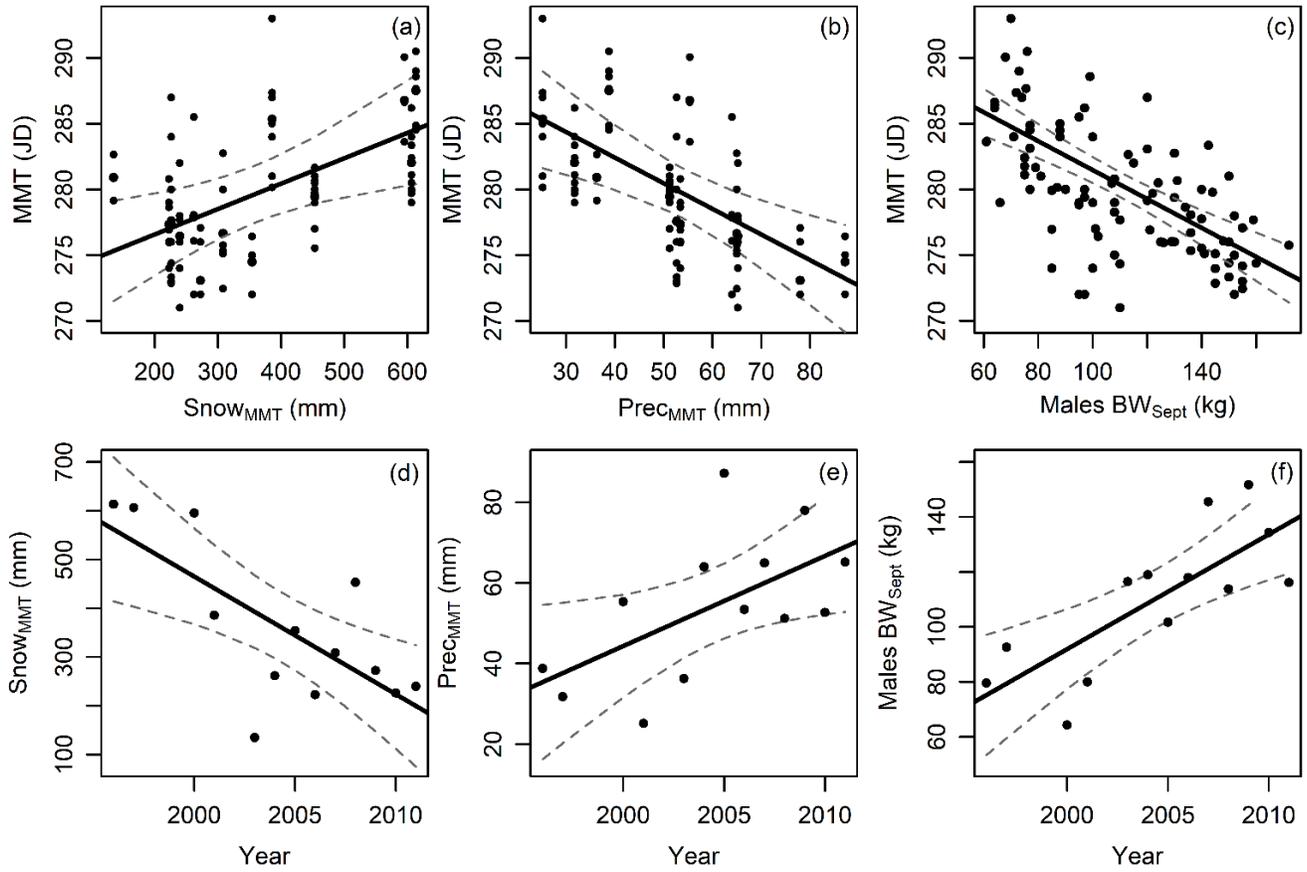
Figure 3.4 Response of males' mating time ('MMT') of a semi-domesticated reindeer population in northern Finland between 1996 and 2011 to (a) the total snow cover between 21 April and 28 April ('Snow$_{MMT}$'), (b) the amount of precipitation between 28 April and 23 June ('Prec$_{MMT}$'), and (c) the males' body weight in September ('BW$_{Sept}$'). The reported temporal trends of those variables were (d) a decreasing snow cover in late April, (e) more precipitation in May-June and (f) an increasing pre-rut body weight of males. All dates are expressed in Julian day (JD). Graphs are presented with the 95% confidence interval band around the fitted line.
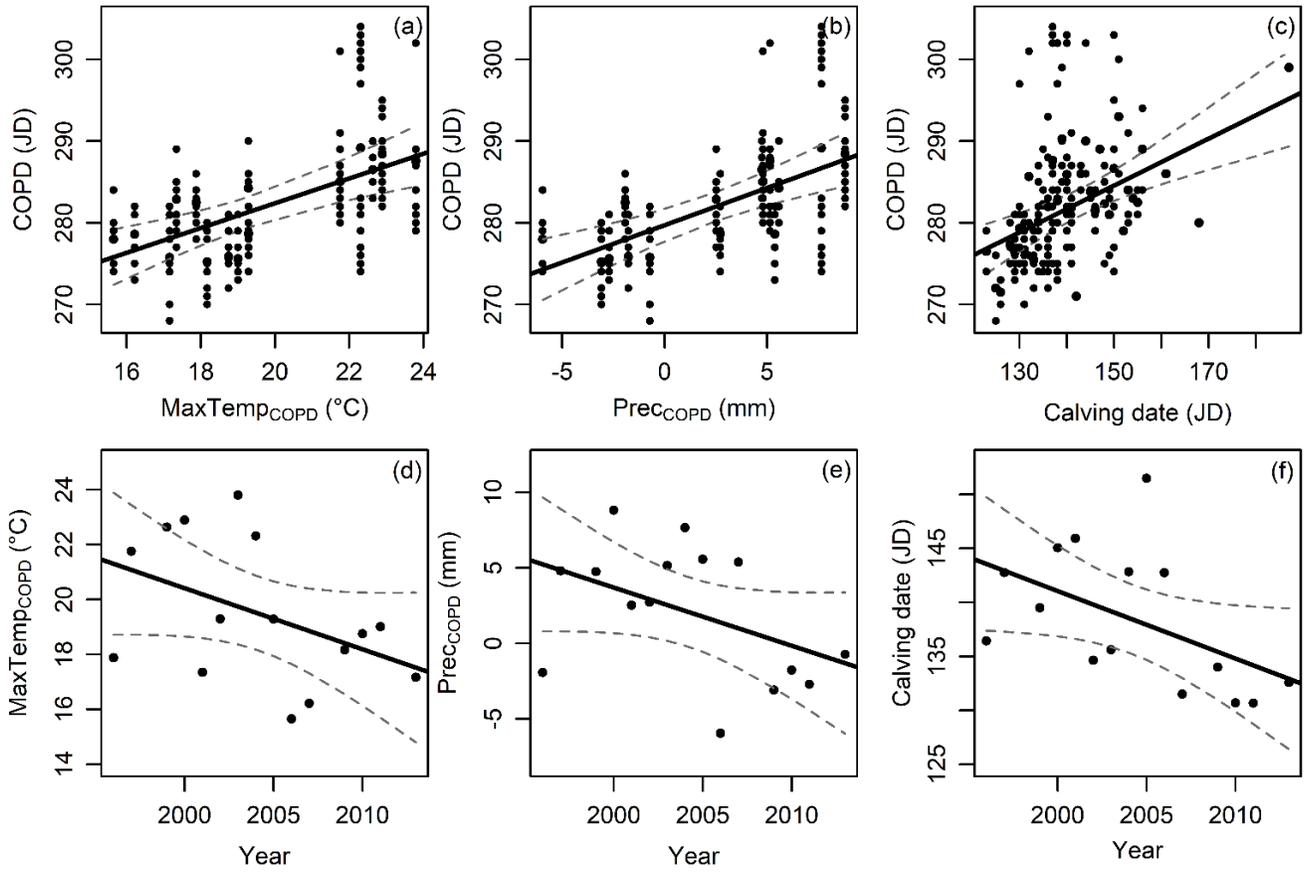
Figure 3.5 Response of females' copulation dates ('COPD') of a semi-domesticated reindeer population in northern Finland between 1996 and 2013 to (a) the maximum temperature between 13 July and 27 July ('MaxTemp$_{COPD}$'), (b) the amount of precipitation (snowfalls) between 13 January and 20 January ('Prec$_{COPD}$') and (c) the previous calving date. (d) MaxTemp$_{COPD}$ and (e) Prec$_{COPD}$ were reported to have decreased over time in the study area, and (f) the calving dates to have occurred earlier. All dates are expressed in Julian day (JD). The 95% confidence interval band around the fitted line is provided.

3.5 Discussion

Confirming our hypothesis, the males' timing of rutting activities and females' copulation dates varied in response to climatic variables at different key periods in the annual breeding cycle of reindeer: winter, early spring and summer. The phenological advancement in reindeer's mating time also followed the climatic changes recorded in the study area. Both direct (i.e. thermoregulation) and indirect (i.e. plant growth and food availability) effects of climatic conditions may have important influence on herbivore phenology and demography (Post and Stenseth 1999). Therefore, the observed relationships between phenology and climatic variables in our study population were interpreted by dissociating the direct and indirect (i.e. through body weight) effect of climate on reindeer mating time.

3.5.1 *Temporal trend of the mating season*

The mating season of the semi-domesticated reindeer population of the Kutuharju field reindeer research station in Kaamanen, northern Finland has advanced significantly by 10 days over 16 years for the timing of males' rutting activities and 11 days over 18 years for females' copulation dates (Figure 3.3). The reproductive season of *Rangifer* occurs in a highly synchronous, brief period among individuals, with 90% of females impregnated during a period lasting 10 to 21 days in the end of September or early October in reindeer (Eloranta and Nieminen 1986) and 80% of 64 conceptions that occurred the first 11 days of a 4–5 week mating period in caribou (Dauphiné and McClure 1974). An advancement of 10 days in just 16 years for MMT and of 11 days in 18 years for COPD thus represents an important change in the mating season of reindeer even if most of the reindeer mating would remain (to date) in its historical time window. A phenological rate of change of -6.4 days.decade^{-1} for MMT and -7.2 days.decade^{-1} for COPD reported in our study population fell in the range of the reported rates of shift in spring phenology of -9.6 days.decade^{-1} for mammal species (Parmesan 2007) and of -5.1 days.decade^{-1} for temperate-zone species (Root et al. 2003). The breeding phenology of a red deer population was reported to have advanced by between 5 and 12 days across a 28-year study period, with a rate of advancement of 0.26 days.year^{-1} for females' estrus date and 0.21 days.year^{-1} for males' rut start date (Moyes et al. 2011). Similarly, Post and Forchhammer (2008) reported that the onset of calving season in a caribou population in West Greenland has advanced by 0.29 days.year^{-1} between 1993 and 2006. Therefore, the rates of phenological change reported in our reindeer population matched with the

rates recorded broadly for mammals but were much higher than in other species of the same family. This would suggest that either our population is more plastic to environmental change, with a greater ability to track environmental cues and can thus adjust mating time at a faster rate. The underlying explanation would be that supplemental feeding given to the animals in late winter by contributing to improve their body condition might render them physiologically able to be more plastic to environmental change than natural populations (Nussey et al. 2005a; Williams et al. 2017). Unfortunately, we were unable to test this assumption with certainty due to the lack of detailed information on the duration or the amount of supplemental feeding given every year to the animals. Alternatively, the abiotic changes in the Arctic exceeding those in temperate, tropical and montane biomes (Weladji et al. 2002a; Post et al. 2009; Vors and Boyce 2009), would cause animals' phenology of reproduction to advance at a faster rate to keep up with their respective changing climate (Caro et al. 2013). Either way, it points out the need of proper consideration of site/species specific differences when discussing climate-phenology relationships. Our study can, however, be added to the growing body of literature showing the significant impact of recent climatic warming on the alterations of animal and plant populations' phenology (Root et al. 2003).

3.5.2   *Effects of January snowfalls on females' copulation date*

The first key-period having a significant influence on females' mating phenology appeared to be winter with reported earlier copulation dates occurring after a decreasing amount of precipitation in the third week of January (Figure 3.5a). Winter climatic conditions for northern ungulates are responsible for poorer condition, increased mortality of young and reduced reproduction, through mediated effects on food availability and particularly lichens (Kumpula and Nieminen 1992; Reimers 1997; Tyler 2010). For example, the calf production in Finnish Lapland was negatively correlated with temperature and precipitation in winter (Lee et al. 2000). Winter consumption of low-N food such as lichens and senescent browse may result in the depletion of body fat reserves by animals (Barboza and Parker 2008) and daily food intakes were shown to be modulated by changes in energy demands for thermoregulation and activity during winter (Parker and Robbins 1985). Females in particular have to live on such a low-N winter food diet when reproductive demands for N for fetal growth and development add to costs of thermoregulation and mobility in deep snow (Parker et al. 1990). The accessibility of winter forage also depends mainly on snow depth and hardness (Post and Stenseth 1999; Hansen et al. 2011); ice crusts or

exceptionally deep snow may result in many consequences such as starvation and increased animal mortality, low calf recruitment and delayed timing of births (Tyler 2010; Aikio and Kojola 2014). A compensatory mechanism was thus highlighted in several deer species where females compensate for winter nutritional deprivation by extending gestation length (elk: Cook et al. 2004, red deer: Asher 2007) and that some flexibility in gestation length as a reproductive tactic exists in response to environmental conditions for large mammals living in seasonal environments (Mysterud et al. 2009; Clements et al. 2011; Williams et al. 2017). In reindeer females of the Kaamanen population, Finland, the estrus and subsequently conception date were delayed or gestation length prolonged when the body condition of females was reduced (Flydal and Reimers 2002). Females in our study population delayed timing of births in response to an increasing amount of snowfalls in January ($b = 0.40 \pm 0.07$ SE, $P < 0.001$) that would lead to a delay in copulation date the following mating season as conception was found to be positively correlated with the previous calving date (Figure 3.5c). On the other hand, decreasing snowfalls in January as reported in the study area (Figure 3.5e), might have allowed females to shorten their gestation length and calf earlier overtime (Figure 3.5f), giving the opportunity to breed earlier the next mating season. Surprisingly, however, the effect of snowfalls in the third week of January on females' copulation date was not mediated through the females' pre-rut body weight (Figure 3.2b). *Rangifer* species usually draw on body fat reserves during winter to sustain maintenance costs when snow reduces forage availability and movements and digging for forage are energetically costly (Hansen et al. 2011). The females' fat reserves would therefore act as a buffer against winter energetic expenditures but an unresolved physiological mechanism would induce females to still lengthen their gestation length and delay their birth timing to optimize the fetus development when the winter climatic conditions deteriorate.

3.5.3   *Effect of maximum temperature in July on females' copulation date*

Interestingly, females' copulation dates were also directly affected by maximum temperature in the last two weeks of July (Figure 3.5a). A decreasing maximum temperature in July overtime (Figure 3.5d) induced earlier copulation dates in females (Figure 3.5a). Contrary to males, females in summer have to face high energetic costs due to the lactation period (Clutton-Brock et al. 1989) that irremediably increases nutritional demands in summer (Parker et al. 1990, 2009; Barboza and Parker 2008). Therefore, an inadequate summer forage quality and nutrition

could adversely impact females' reproduction (particularly of lactating females), that in turn affects pregnancy rates, overwinter adult survival rates, litter size as well as calf birth mass, milk production, calf growth rate and early juvenile survival (Cameron et al. 1993; Reimers 1997; Cook et al. 2001). Several studies have already reported summer grazing conditions to be the main factor affecting growth rate and body size in reindeer/caribou (review in Reimers 1997). However, beginning in July, forage quality declines as plants mature and fiber accumulates, while insect harassment from primarily skin warble flies *Hypoderma tarandi* (Oestridae) and nasal bot flies *Cephenemyia trompe* (Oestridae) increases. The coincidence of a higher level of insect harassment caused by warmer temperatures in July might therefore degrade reindeer's foraging conditions. Harassing insects were shown to be detrimental to autumn body weight (carcass weight) of ungulate species (Weladji et al. 2003a), by preventing them from feeding effectively (Reimers 1997). The blood-sucking insects induce in reindeer a behavioral change of a reduced grazing time and an increased energy expenditure caused by their disturbance (Reimers 1997; Weladji et al. 2003a, review in Mallory and Boyce 2017). Although the females' body weight in September was not directly affected by the maximum temperature in July (Figure 3.2b), harassing insects by reducing the ability of females to feed optimally during the critical lactation period would slow down females' summer growth rate, with related consequence on future reproductive performance (Vors and Boyce 2009; Mallory and Boyce 2017). In this population, a delay in females' estrus dates the next breeding season was thus reported (Figure 3.5d). It has already been hypothesized that summer climatic variables might be affecting more the pre-rut body condition of females, while winter climate might be acting during pregnancy through fetal mortality (Weladji and Holand 2003a), explaining why females better have to lengthen their gestation period when winter climatic conditions deteriorate.

3.5.4 *Effects of late winter snow cover and summer precipitation on males' mating time*

Snow cover in late winter had a direct and indirect effect in males' mating time (Figure 3.1b), with an earlier males' timing of rutting activities (Figure 3.4a) following the temporal trend of a decreasing snow cover in late April (Figure 3.4d). Late winter is a key period for reindeer in Arctic since the individuals' body mass is at its lowest point at that time (Tveraa et al. 2003; Albon et al. 2017) and they have to recover from winter harshness while availability of food is reduced

due to hard and thick snow cover (Pettorelli et al. 2005; Tveraa et al. 2007). Availability of food will therefore depend on the emergence of snow free patches allowing reindeer to have access to lichens and dwarf shrubs (Kumpula and Nieminen 1992; Helle and Kojola 2008). Recent climatic changes in the Arctic, resulting in warmer temperatures in spring and summer, an earlier timing of snowmelt and changes to hydrologic regimes have in turn advanced the onset and extended the vegetative growing season (review in Serreze et al. 2000). Spring climatic conditions strongly determine plant growth season pattern in spring and food availability during summer (Pettorelli et al. 2005) so such changes have also contributed to an increase in total forage biomass and nutritional content in the Arctic (Pearson et al. 2013). Therefore, a decreasing snow cover in late April (Figure 3.4d) and more precipitation from late June to late April as recorded in the study area (Figure 3.4e), by helping males to recover their body weight and replenish their fat reserves faster in spring and summer (Cook et al. 2004; Parker et al. 2009) allowed the males' body weight in September to increase (Figure 3.1b), advancing the time of their rutting activities the following mating season (Figure 3.4a, b, c). October body mass in Svalbard reindeer was also shown to increase as a result of greater plant productivity (Albon et al. 2017). Therefore, the decreasing snow cover in late winter, combined with an increasing amount of precipitation in May-June might have influenced males' mating time through effects on spring forage phenology and thereafter on summer forage quality and quantity (Weladji et al. 2002b; Pettorelli et al. 2005; Helle and Kojola 2008). A better spring and summer nutrition, in complementarity with supplemental feeding given in late April, could have in turn helped improving the pre-rut body weight of males. A delay in mating season due to poor body condition has already been highlighted in other ungulate species (bighorn sheep: Festa-Bianchet 1988; red deer: Clutton-Brock et al. 1989; elk: Cook et al. 2001; moose (*Alces alces*): Garel et al. 2009). However, our study appears to be the first to reveal the key role that climatic conditions may be having on this pattern.

3.5.5   *Limitations*

Supplementary winter feeding in semi-domesticated reindeer populations is used as a common management practice to buffer the effects of environmental stochasticity on the body condition by protecting individuals from late winter starvation (Helle and Kojola 1993) and has started to become a management practice only since the 1980s in the northern part of Finland (Helle and Kojola 1993; Helle and Jaakkola 2008). Therefore, whether the improvement in both

males' (Figure 3.4f) and females' ($b = 0.49 \pm 0.12$, $P < 0.001$) body weight in September is attributable to supplemental feeding only or to a combination with a better food availability in the natural environment is impossible to disentangle in this study. Despite supplemental feeding, that occurs regularly in late April, we still found a direct effect of certain climatic variables on reindeer's mating time. This suggests that animals would still be sensitive to climatic conditions as environmental cues to adjust their reproductive phenology. In a recent study, environmental factors were shown to affect Julian birth date and birth mass of white-tailed deer (*Odocoileus virginianus*) even though mothers were continuously allowed access to a high-quality diet (Wolcott et al. 2015). The study on white-tailed deer therefore demonstrated first that environmental factors may have a greater influence on reproductive outputs than previously supposed in ungulates and that constant supplemental feeding was not enough to curtail the environmental effects on reproductive traits. However, the direct effects of climatic variables on either males' mating time or females' copulation date suggest that other mechanisms (other than just the body weight) might be responsible for the plastic response of reindeer's mating time to environmental change. The causal effect of climatic conditions on seasonal timing of animals is still an unsolved mystery that we have just started to explore. For instance, Caro et al. (Caro et al. 2013) have proposed that the thermoregulation might be the starting point explaining the link between ambient temperature and seasonal timing of endotherms, through several effector pathways: thyroid hormones, prolactin, melatonin and the preoptic area. Understanding how the body perceives other environmental cues (e.g. precipitation), integrates it into the neuroendocrine system, and translates it into effector mechanisms that shape seasonal timing is still a major challenge (Caro et al. 2013).

3.6 Conclusions

The males' timing of rutting activities has advanced in response to a decreasing snow cover in late April and more precipitation in May-June in a semi-domesticated reindeer population in Finnish Lapland. An improvement in males' pre-rut body weight following those climatic changes and mediated by a better vegetation productivity in spring and summer has certainly contributed to such observed phenological change. Females' copulation dates have advanced in response to decreasing snowfalls in the third week of January and a decreasing maximum temperature in the last two weeks of July. A compensatory mechanism by which females extend their gestation length

in response to winter nutritional deprivation (Asher 2007) might explain the delay in timing of births and then copulation dates when the snowfalls in January increase. The decrease in forage quality, along with a higher level of insect harassment in July might have degraded females' foraging conditions, after which they have conceived later in fall.

Despite supplemental feeding in the semi-domesticated populations, reindeer populations may therefore be more responsive to climate change than previously acknowledged (Tveraa et al. 2007; Mallory and Boyce 2017). Birth dates of a given female did not respond to increasingly earlier onset of spring across years in roe deer (Gaillard et al. 1993; Plard et al. 2013b), and the explanation proposed was that the ovulation and conception dates of roe deer appear to be under the control of photoperiod (Sempéré et al. 1993). On the other hand, reindeer's birth dates were advanced following better climatic conditions in early spring (Paoli et al. 2018) and red deer's calving dates were delayed following higher autumn rainfall (Nussey et al. 2005a). That both reindeer and red deer showed a plastic response of calving dates to climatic variables suggest that capital breeders as a whole could use photic periodicity, in interaction with climatic variables as environmental cues to time seasonal reproduction. The mechanism being invoked is that the plasticity in the allocation of their endogenous stores towards reproduction would allow animals to adjust their timing so that the peaks in resource availability and energy demands are appropriately synchronized (Williams et al. 2017). If animal species are able to reliably follow environmental cues (i.e. other than just photoperiod) to time their reproductive efforts, then their viability and survival should be ensured even in case of unusual climatic variability. As pointed out before, the changes in winter climate, with related effects on winter food availability, along with the changes in vegetation spring green-up and its consequences for summer food availability are certainly key factors in forecasting the future of *Rangifer* in tundra ecosystems (Tveraa et al. 2003; Mallory and Boyce 2017).

3.7 Appendices
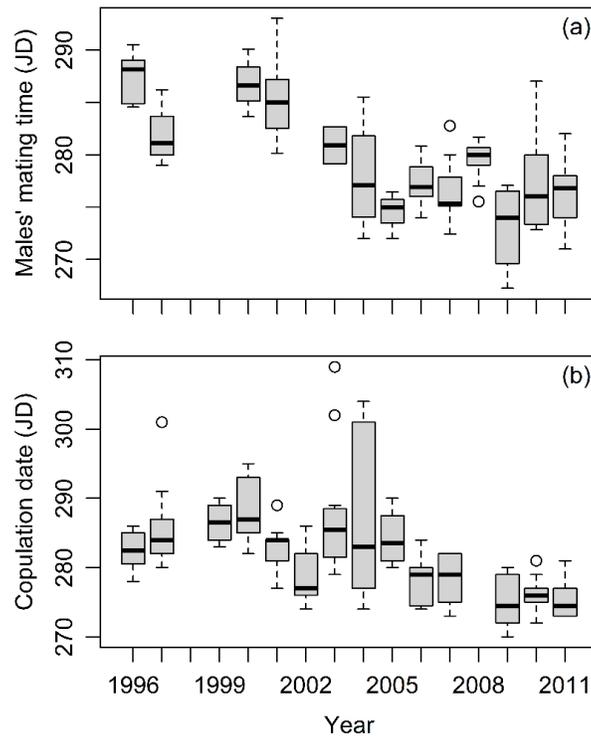
Figure 3.6 Annual distribution of (a) male's mating time and (b) females' copulation date from the Kutuharju reindeer herd in Kaamanen, northern Finland in the period from 1996 to 2011. The dates are expressed in Julian day (JD), starting January 1st. The thick, solid lines represent the median and the dashed lines represent the 25th percentile for the lower part and the 75th percentile for the upper part. The empty circles represent the extreme values. Data were missing for some years.
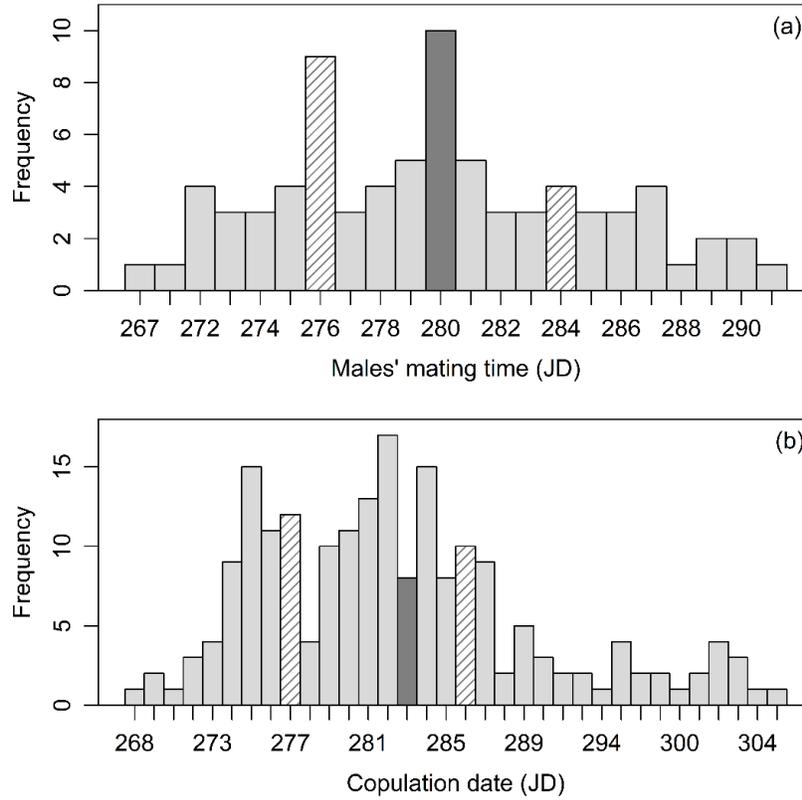
Figure 3.7 Distribution of (a) males' timing of rutting activities and (b) females' copulation dates, expressed in Julian day (JD) starting January 1st, from a semi-domesticated reindeer herd in Kaamanen, northern Finland from 1996 to 2011. The darker bar represents the mean of the distribution, while the two striped bars represent respectively the 25th and 75th percentile of the distribution.
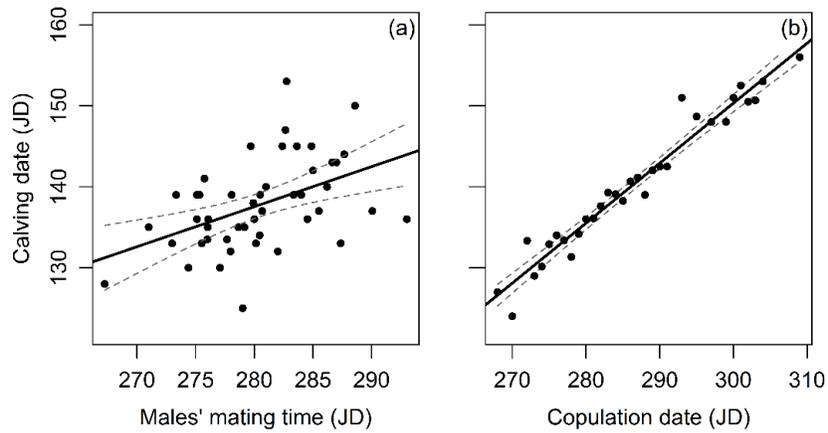
Figure 3.8 Positive relationships between (a) the male's timing of rutting activities and the subsequent calving date of the female that the male has impregnated and (b) females' copulation date at the mating season and the consecutive calving dates of a semi-domesticated reindeer population in Finnish Lapland from 1996 to 2011. The dates are expressed in Julian day (JD), starting January 1st. The 95% CI band around the fitted line and the fitted line are also presented.

Chapter 4 Early-life conditions determine the between-individual heterogeneity in plasticity of calving date in reindeer

The following chapter is based on the manuscript: Paoli A, Weladji RB, Holand Ø and Kumpula, J Early-life conditions determine the between-individual heterogeneity in plasticity of calving date in reindeer. Accepted for publication in *Journal of Animal Ecology* on 07/07/2019.

4.1 Abstract

Phenotypic plasticity has become a key-concept to enhance our ability to understand the adaptive potential of species to track the pace of climate change by allowing a relatively rapid adjustment of life history traits. Recently, population-level trends of an earlier timing of reproduction to climate change have been highlighted in many taxa but only few studies have explicitly taken into consideration between-individual heterogeneity in phenotypic plasticity. Using a long-term data of a semi-domesticated reindeer population, we demonstrated that females differed greatly in their mean calving date but only slightly in the magnitude of their plastic response to the amount of precipitation in April. We also showed that despite the absence of a population trend, females individually responded to the amount of precipitation in April by delaying their calving dates. Females' calving date under average climatic conditions was best predicted by their birthdate, their physical condition in March-April-May before their first calving season and by their first calving date. The degree of their phenotypic plasticity was not dependent on any of the females' attributes early in life tested in this study. However, females who delayed their calving dates in response to a higher amount of precipitation in April slightly produced less calves over their reproductive life. These findings confirmed that early life conditions of female reindeer can shape their phenotypic value during reproductive life, supporting the importance of maternal effects in shaping individuals' lifetime reproductive success. Whether females differed in the magnitude of their plastic response to climatic changes has received contrasted responses for various ungulate species. This calls for more research to enhance our understanding of the underlying mechanisms leading to the complexity of plastic responses among populations to cope with current climate change.

4.2   Introduction

Phenotypic plasticity, defined as the expression of several phenotypes by a single genotype when facing heterogeneous climatic conditions, has become a key-concept in understanding how animal species will be able to track large-scale environmental processes, such as climate change (Boutin and Lane 2014). Phenotypic plasticity allows species a relatively rapid adjustment of morphological and life history traits to climatic changes (Boutin and Lane 2014). Under the current context of climate change, the timing of reproduction is one key life history trait that species would need to adjust to ensure their viability. Indeed, an advantageous timing of reproduction will generally ensure that young are born at the time of the year best suited for their survival (Festa-Bianchet 1988; Gaillard et al. 1993), which determine the population's recruitment rate (Berger 1992; Post and Klein 1999) and thereafter the population dynamics. Recently, such timing of reproduction was broadly shown to vary at the population level with climatic changes observed the last decades between different groups of species (bird: Visser et al. 1998; Bourret et al. 2015; amphibian: Blaustein et al. 2001; fish: Asch 2015; mammal: Réale et al. 2003; Post and Forchhammer 2008; Moyes et al. 2011; marine species: review in Poloczanska et al. 2013). However, on top of those population-level trends, knowing how changing timing of reproduction vary between individuals in response to climate change has not received enough attention, yet very much needed for a better understanding of the evolutionary consequences of the changes.

At the population level, observed correlations between climate and phenotype are thought to be induced by phenotypic plasticity at the individual-level. For example, Przybylo et al. (2000) reported laying date between and within females collared flycatchers (*Ficedula albicollis*) to vary in response to the NAO index, while Réale et al. (2003) found that the advance in parturition date to increased food availability of female North American red squirrels (*Tamiasciurus hudsonicus*) was a result of phenotypic changes within generations. According to these studies, such a population-level change in breeding time to the environment could be explained largely by maternal plasticity as the responses across and within individuals were similar. However, the degree to which females varied in their plastic response was not explicitly quantified. To date, only few studies have explicitly examined between-individual heterogeneity in phenotypic plasticity, and most found that females differed in the way they adjusted breeding time in response to climate change (bird: Brommer et al. 2005; Nussey et al. 2005b; ungulate: Nussey et al. 2005a). To clarify

this issue, Nussey et al. (2005b) applied the linear reaction norm approach (Brommer et al. 2005; Nussey et al. 2005b) on a red deer population, stating that an individual's phenotypic response to climatic changes can be estimated using regression coefficients of models describing the variation in the value of a certain phenotypic trait along a climatic gradient. We can then differentiate an individual's intercept (reflecting the expected trait value in the average climate) and slope (the plastic response to the climatic gradient). Two main population-level phenotypic plastic responses to climatic variability have been described by Pigliucci (2001; see Figure 1.2d, e in Pigliucci 2001). In the first one, all individuals of a population respond in the same way and vary in their intercept but not in their slope (scenario 1; Figure 4.6a adapted from Figure 1.2d in Pigliucci 2001). In the second one, all individuals will show different plastic responses to climate change and will therefore vary in their slope (scenario 2; Figure 4.6b adapted from Figure 1.2e in Pigliucci 2001). Where individual intercepts show no variation but slopes do vary or where intercepts and slopes both vary and also co-vary, levels of phenotypic variance in the trait measured is predicted to change across the climatic gradient (Postma and van Noordwijk 2005). The presence of an individual by environment interaction (I×E) might also determine the adaptive potential for change in the average plastic response of the population (Nussey et al. 2007). Distinguishing which of those patterns is occurring in an animal population is therefore determinant for our understanding to any population's ability to cope with climate change and has important implications for population dynamics (Przybylo et al. 2000; Réale et al. 2003; Nussey et al. 2005a).

In a theoretical framework, an individual is expected to follow its optimal trait-climate trajectory by responding to the climate depending on its physical condition (Roff 1992). However, understanding how the between-individual differences in phenotypic plasticity are explained by climatic conditions or physiological state is largely unknown. If a large intraspecific difference in body mass exists, then the second pattern of phenotypic plasticity (scenario 2; Figure 4.6b) is usually expected in those species (Skogland 1983). The social hierarchy in reindeer causes large differences in resource access (e.g. food), with high-ranked females having access to the best food patches (Skogland 1983). As a consequence, reindeer present large intraspecific differences in size and body mass (Skogland 1983, 1984). In addition, maternal characteristics were shown to exert a great influence on calving date (Cameron et al. 1993; Adams and Dale 1998; Flydal and Reimers 2002; Mysterud et al. 2009; Rowell and Shipka 2009). As such, a plastic response of

birthdate to climatic variability is expected following a pattern where females will differ both in their intercept and in their slope values (scenario 2; Figure 4.6b).

To further dissect the average plastic response of the population from the individual's plastic responses to climatic changes, the within-subject centering method for climatic variables can be employed (van de Pol and Wright 2009). This technique was developed to separate individual heterogeneity from population trend, while considering that each female might experience a different set of climatic conditions. The between-individual effect for a certain climatic variable would indicate a population-level, evolutionarily fixed plasticity of calving date to this climatic variable (i.e. certain phenotypes are consistently found more frequently in certain climatic conditions). If, in addition, a within-individual effect of the same climatic variable was found, it would indicate that females alter their calving date in response to that variable within their reproductive lifetimes. Van de Pol and Wright (2009) also proposed a method to test if the direction of the individual- and population-level trends was the same or not. Accordingly, four different scenarios have been described (Figure 4.1 and Table 4.4), that are important in understanding how species will be able to cope with their changing climate. The within- and between-individual effects of a particular trait in response to a climatic gradient highlight its flexibility in a population, and therefore represents alternative adaptive outcomes of selection (van de Pol and Wright 2009). In three of the four scenarios (Figure 4.1a, b, d), a population-level response to the climatic gradient is observed but do not necessarily mean that individuals are responding plastically to climate change (Figure 4.1b). In such case, plasticity in calving date is observed at the population-level but the absence of phenotypic plasticity at the individual level would cause females to be maladapted in the future regarding the ongoing climate change. Conversely, individuals might be responding to climate change, while a population-level trend might be null due to a low plasticity in the phenotypic trait along a climatic gradient (Figure 4.1c). Population-level analyses therefore appear insufficient in inferring the ability of individuals to alter the expression of a phenotypic trait in response to climatic conditions and thus the potential for individuals to track their changing climate. Furthermore, an individual-level response might also mask the fact that slopes between females can differ (e.g. female 1 might have a negative slope, while female 3 might have a positive slope, see Figure 4.1a, c, d). The population- and individual-level trends therefore demand to be studied while accounting for a potential between-individual heterogeneity in plasticity. In our study, we predict that if females are all in a good enough

physiological state to respond to climatic variability (Nussey et al. 2005a), an individual-level response to climate change would be observed (Figure 4.1a, c, d), in addition to an individual heterogeneity in plasticity as stated above.

Using records from a long-term intensive study of a semi-domesticated reindeer population situated in Kaamanen, northern Finland, the aims of this study were the following. (1) To investigate if there is a between-individual heterogeneity in plasticity of calving dates in response to climatic variability and to assess which pattern of phenotypic plasticity among the two scenarios adapted from Pigliucci (2001) is occurring in this reindeer population. (2) To assess whether the within- and between-individual responses of calving date to climatic variables go in the same direction (van de Pol and Wright 2009). (3) To determine the females' attributes shaping or explaining the pattern of phenotypic plasticity observed; and (4) to determine if the among-individual heterogeneity in phenotypic plasticity can lead to fitness consequences. Climatic conditions while *in utero* and early in life usually shape the total lifetime reproductive success (Kruuk et al. 1999; Post and Stenseth 1999; Forchhammer et al. 2001). Therefore, we separately assessed if mothers' physical condition during pregnancy and/or females' own physical condition at birth and/or at age of first calving would shape the between-individual heterogeneity in phenotypic plasticity, and if further consequences on the reproductive success of females were observed.
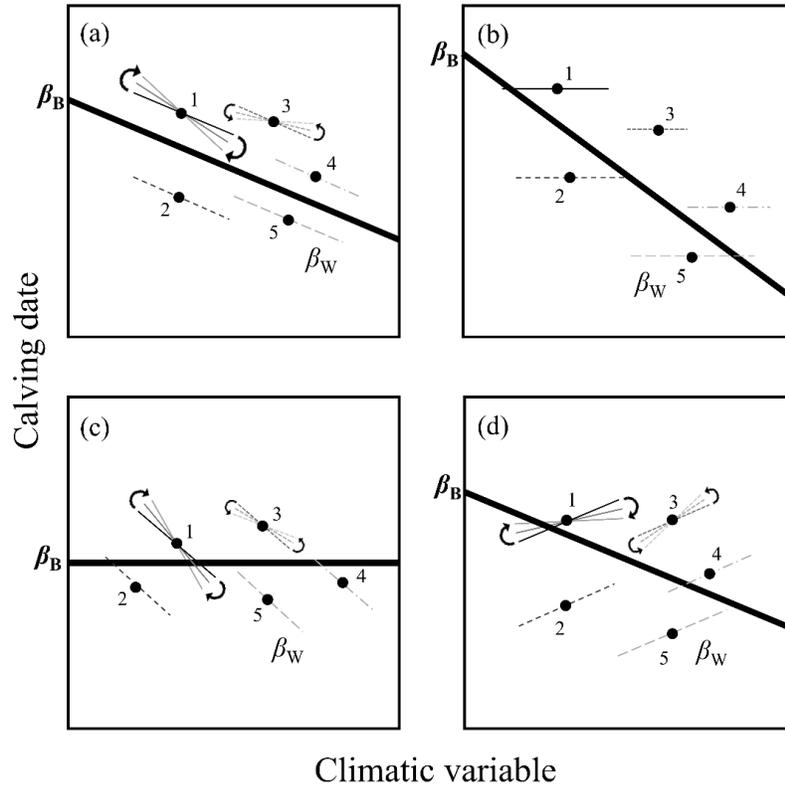
Figure 4.1 Four different scenarios for how within- and between-individual plastic responses of calving date to a climatic variable can differ (or not) in a population. The between-individual slope was schematically represented with a thick solid line (β_B), depicting the population trend. The within-individual slopes were represented for five different females (1 to 5) with thin lines (β_W). Each black dot (●) was the mean calving date of a female on the y-axis and the average climatic conditions that she has experienced over her lifetime on the x-axis, while the line represented her plastic response of calving date to climatic variability. The slopes between females could differ such that female 1 could have a negative slope, while female 3 could have a positive slope, as represented by the lighter slopes and the arrow showing the direction of the change.

4.3 Material and Methods

4.3.1 Study area and reindeer population

The herd studied consists of about 100 animals every year (including males, females and calves) from a semi-domesticated reindeer population at the Kutuharju field reindeer research station in Kaamanen, northern Finland (69°N, 27°E). The herd is free ranging most of the year in two large fenced enclosures, the north-west section (Lauluvaara ~ 13.8 km²) and the south-east section (Sinioivi ~ 15 km²). After the mating season in late October the animals are gathered and taken to a winter grazing area (15 km²) where they can graze freely on natural pastures. Supplemental feed (pellets and hay) was given to the animals in late winter, in addition to natural pastures. After harsh winters, the amount of supplemental feed was higher than this average level of feeding. We therefore excluded the calving dates from females that have been subject to experimental manipulations requiring extra-feeding, as this may affect between-individual heterogeneity in phenotypic plasticity of calving date to climatic conditions. By the end of winter, females are transferred into a calving enclosure (approximately 0.5 km²) where newborn calves are captured, weighed, sexed and marked with ear tags. The enclosure is surveyed daily during the calving season that occurs mainly from mid-May to end of May (Eloranta and Nieminen 1986), so that calving date is known for all individuals and has been recorded since 1970.

4.3.2 Climatic variables

The daily recorded values of temperature, precipitation and snow depth from 1970 to 2016 were obtained from three weather stations (Utsjoki, Ivalo airport and Nellim) in northern Finland (68°N, 27°E) from the Finnish Meteorological Institute. The weighted mean by the distance from the weather station to our study site was then used to estimate the daily values of local climate at our study site with as much reliability as possible. The temperature was used as a monthly average, while the amount of precipitation was summed over a month. Precipitation can be either rainfall or snowfall depending on the temperature. From the daily snow depths, a snow depth index (SDI) was calculated as the cumulative sum of daily snow depths on the 15th day in each month.

4.3.3 Females' attributes early in life

Eleven female's attributes were used in the analyses, six of which were estimated at birth and five at first calving. (1) The attributes of a female at birth included: the birth weight, year of

birth, birth date, and the mother's physical condition estimated in autumn, winter and early spring. (2) The attributes at first calving included: the female's age, physical condition in autumn, winter and early spring, and the calving date of her first calf. Thanks to the long-term records of the herd demography and the use of ear tags on females (affixed at birth) allowing unique identification and colored collars fitted on their mother, we could track down their conditions at birth and at first calving. Factors linked to maternal physical condition in reindeer interact with each other so that older individuals tend to be heavier (Mysterud et al. 2009). Therefore, we used a female body condition index (BCI) to consider effects of both female body weight and female age on calving date at once in the models while avoiding multicollinearity between these two highly correlated variables, as an age-specific residual body mass (see Weladji et al. 2003b). To also account for the reported senescence in female reindeer from this population (Weladji et al. 2010), we extracted the residuals from the quadratic forms of the relationship between females' body weight and females' age. The females' physical condition variable included in the base models (described below) to test H1 and H2 was calculated as the average of the 12 body condition indexes of a specific female over the year preceding the calving season (year t from January to May and year t – 1 from June to December). For the analyses testing H3, the mothers' and females' BCI was averaged for three periods: autumn before the rut period the previous year (September-October), winter (December-January-February) and early spring before the calving season (March-April-May). This allowed us to specifically assess which period's BCI of the mother or of the female (preceding her first calving season) had the greatest influence in shaping among-individual heterogeneity in plastic responses.

4.3.4 Fitness attributes

To estimate the females' reproductive success as an index of her fitness, we used three different attributes, such as the body weight of her calves, the first-summer survival of her calves and the cumulative number of calves that the female produced over her reproductive life. The causes of death of a calf excluded from the analyses were those with 'no information' or 'slaughtered'. The values for the survival of a calf ranged from 0: dead during calving season to 1: survived to autumn.

4.3.5   Statistical analyses

From the original dataset of reindeer calving dates of the Kutuharju herd used by Paoli et al. (2018), only data from females with available records for at least four calving events (1,770 calving dates from 272 females, on average 6.51 ± 1.90 calving dates per female) were kept in the analyses. Four calving events allowed us to obtain an individual slope estimate reliable enough to reflect a possible individual plastic response to its changing climate. Moreover, the analysis restricting the data to females with 2 calving records or more (≥ 2 calving dates), 3 or more (≥ 3 calving dates), 4 or more (≥ 4 calving dates) yielded similar results (See Table 4.5). Among the 272 females, 17.3% had 4 calving records, 17.6% had 5 calving records, 18.8% had 6 calving records, 17.3% had 7 calving records, 21.3% had between 8 to 9 calving events and 7.7% had 10 or more calving dates. All calendar dates were converted into Julian days since 1 January for analysis (data available from 1970 to 2016). All continuous explanatory variables were standardized ($\overline{X} = 0$, SD = 1) prior to inclusion in the models (Pinheiro and Bates 2000). We also examined whether or not there were consistent among-individual differences in calving date by computing the repeatability in calving date (also known as the intraclass correlation coefficient, ICC, Wolak et al. 2012). The repeatability was calculated by dividing the variance in calving date due to differences among individuals by the total phenotypic variance using the R package 'ICC' (Wolak et al. 2012). Analyses were performed in R 3.4.1 (R Development Core Team 2019).

4.3.5.1   Individual differences in mean calving date (intercept) and between-individual heterogeneity in phenotypic plasticity (slope)

Given the previous results from Paoli et al. (2018), we constructed three base models to explain variation in calving date. Here, (1) individual identity (ID) and year of study were included as multi-level random effects to control for repeated measures and to account for between-year variations (Kruuk et al. 1999) and; (2) the proportion of males present in the herd the preceding mating season (PM) and the yearly body condition index of females (BCI) were included as fixed-effect factors to control for their respective effects on calving date (Cameron et al. 1993; Flydal and Reimers 2002; Holand et al. 2002; Cook et al. 2004; Mysterud et al. 2009). Then, the same climatic variables reported to be important in explaining calving date in (Paoli et al. 2018) were included in three separate models: mean temperature in May (T°May) and precipitation in April (PrecApril) for model 1, mean temperature in April-May (T°April-May) and PrecApril for model

2 and T°May and snow depth index (SDI) in April (SDIApril) for model 3. As an addition to Paoli et al. (2018) and Nussey et al. (2005b), we applied a within-subject centering method by subdividing the climatic variables into a within-individual (β_W) and a between-individual (β_B) component (see the detailed method in the next paragraph) to consider that not all females have experienced the same set of climatic variables. We further tested our models for multicollinearity by calculating the variance inflation factor (VIF) of the predictor variables used in each model. Multicollinearity was not an issue since all VIF were < 3 (Zuur et al. 2010).

To test our first hypothesis, we then investigated the presence of between-individual heterogeneity in plasticity (i.e. differences in slopes across individuals), as an individual by environment interaction (IxE) with a random regression analysis (Nussey et al. 2007). For each of the base models, the fixed effects were kept unchanged in the model while the mixed model structure described above was modified to test patterns of heterogeneity in individual plasticity of calving date (scenario 1 versus scenario 2, Figure 4.4). More precisely, a random effect on females' slopes of calving date to the β_W component of climatic variables considered can be fitted in a mixed model (Nussey et al. 2005a; Bourret et al. 2015). In this case, ID estimates the variance component due to between-individual differences in their mean calving date in the average climate (intercept), while the random interaction term estimates the variance component resulting from differences between females in their calving date - climate relationship (slopes). A statistically significant difference in deviance between LMMs with and without a random slope term for β_W component of climatic variables would indicate that females differ in their plastic response of calving date to climatic variables, allowing discrimination between scenario 1 (Figure 4.6a) and scenario 2 (Figure 4.6b). Such difference in deviances and increase in structure complexity of random effects was statistically tested by performing likelihood ratio tests (LRT, Pinheiro and Bates 2000), including random slopes with climatic variables (IxE). The analyses performed used Linear Mixed-effects Models (LMMs), by running the lmer-function in the R package lme4 (Bates et al. 2015, <www.r-project.org>).

4.3.5.2 Within- and between-individual response of calving date to climatic variability

To test our second hypothesis, we applied the within-subject centering method on our climatic variables, obtained by the following equation (van de Pol and Wright 2009):

Equation 4.1 Within-subject centering method $= y_{ij} = \beta_0 + \beta_W(x_{ij} - \bar{x}_j) + \beta_B\bar{x}_j + u_{0j} + e_{oij}$

where β_0 represents the constant intercept of the equation; u_{0j} the random individual intercept and e_{oij} the residual error term. The between-individual effect β_B for each female was calculated as the mean of all observation values of a specific climatic variable she has experienced over her lifetime $\bar{x}_j$ (reflecting the population trend). The within-individual component β_W was calculated by subtracting the female's mean value $\bar{x}_j$ from each observation value x_{ij} for that climatic variable (reflecting individual plasticity). The slope for the effect of a specific climatic variable on calving date at the population-level was therefore given by β_B, while it was given by β_W at the individual-level. We ran the base models by including as fixed effects the within-individual (β_W) and between-individual (β_B) components of the climatic variables present in each model (see Table 4.1). As random effects, the random intercept on Year was included, along with the random intercept and/or the random slope on ID. If a between-individual heterogeneity in the slope was previously found when testing H1, the random intercept and random slope on ID would be included. If individual differences in the intercept only were reported when testing H1, then the random intercept on ID would be included (and not the random slope). Finally, whether the within- and between-individual components of the climatic variables differed from each other was assessed by looking if the estimate (β_B - β_W) is close to zero and statistically non-significant (see the method in van de Pol and Wright 2009). Following the procedure that we recently presented (Paoli et al. 2018), we reported the averaged estimates of the coefficients of parameters in the base models, following the model averaging approach (Schielzeth 2010; Symonds and Moussalli 2011) and using the model.avg function in the R package AICcmodavg (Mazerolle 2019, <www.r-project.org>). The variables included in the models were considered important if their 95% CIs excluded 0.

4.3.5.3 Females attributes early in life and between-individual heterogeneity in mean calving date and in phenotypic plasticity

To evaluate the hypothesis that conditions early in life would shape female lifetime phenotypic value (i.e. calving date) or females' plastic response to climatic changes (i.e. individual slopes), we tested the interaction term between each of the female attribute and the within-individual component (β_W) of the climatic variables in independent models, similar to the following as an example: $Calving\ date \sim \text{T°May}_{within} + \text{T°May}_{between} + \text{PrecApril}_{between} + \text{BD} * \text{PrecApril}_{within} + (1|\text{Year})$

The interaction term was tested in each of the base models and then model-averaged. If a statistically significant between-individual heterogeneity in slopes was precedently found, then we would focus on the interaction term with the climatic variable for which the plastic response differ between individuals (e.g. PrecApril$_{within}$). This method applied on the base models would allow to simply test if a certain female attribute (e.g. BD) would cause consistent differences in intercept and eventually slopes among females in regard to their plastic response to climatic variables. Given that the females' attributes had only one value per female and to avoid the random intercept on ID to capture too much variability that we tried to explain by females' attributes, we decided to remove the random intercept on ID from the models. Moreover, as our hypothesis was focusing on the females' attributes trying to explain the inter-individual differences in intercept and slope regarding climatic variability; we also removed the fixed-effects of females' BCI and proportion of males from the models.

<p style="text-align:center">4.3.5.4   Fitness consequences of between-individual heterogeneity in mean calving date and in phenotypic plasticity</p>

We used the same method as above to test our fourth hypothesis that individual differences in mean calving date or between-individual heterogeneity in phenotypic plasticity could lead to fitness consequences later on. As such, we tested the interaction term between attributes of fitness and the within-individual component (β_W) of the climatic variables, similar to the following as an example:

$$Calving\ date \sim \text{T°May}_{within} + \text{T°May}_{between} + \text{PrecApril}_{between} + \text{Calf birth weight} * \text{PrecApril}_{within} + (\text{PrecApril}_{within}|\text{ID}) + (1|\text{Year})\ .$$ The interaction term was tested in each of the two base models and then model-averaged. To focus on the inter-individual differences in intercept and slope regarding climatic variability having potential fitness consequences, we also removed the fixed-effects of females' BCI and proportion of males from the models. However, and given that one different fitness attribute value was available per calving date, we kept the random intercepts on ID and year.

4.4   Results

Applying the within-subject centering method on the three best-fitted models from Paoli et al. (2018), and with a reduced dataset of females who calved at least four times over their reproductive life, made the fit of the third base model to drop substantially, with a ΔAIC > 4 (Table 4.1). Only the two first base models were therefore kept in the subsequent analyses. A statistically

significant repeatability was found for calving date (ICC = 0.19, 95% CI [0.15, 0.24]), with the within-female variation being higher than the among-female variation.

Table 4.1 Competing linear mixed-effects models for calving date of a reindeer population in Kaamanen, northern Finland in relation to climatic variability.

Rank	Models	AICc	df	AICc weights	ΔAICc
1	BCI + PM + T°May$_{within}$ + T°May$_{between}$ + PrecApril$_{within}$ + PrecApril$_{between}$	11533.8	10	0.61	0.0
2	BCI + PM + T°April-May$_{within}$ + T°April-May$_{between}$ + PrecApril$_{within}$ + PrecApril$_{between}$	11535.1	10	0.32	1.3
3	BCI + PM + T°May$_{within}$ + T°May$_{between}$ + SDIApril$_{within}$ + SDIApril$_{between}$	11538.0	10	0.07	4.2

From Paoli et al. (2018), the same climatic variables were used (mean temperature in May 'T°May'; mean temperature in April-May 'T°April-May'; the amount of precipitation in April 'PrecApril' and the snow depth index in April 'SDIApril') but with a reduced dataset of females who calved at least four times over their lifetime ($n = 1{,}770$ calving dates from 272 different females). All models included female identity and year as random factors, as well as females' body condition index (BCI) and proportion of males in the herd (PM) as fixed effects. A within-individual centering technique was applied as suggested by van de Pol and Wright (2009) to distinguish between population- ($\beta_{B,\ 'between'}$) and individual-level ($\beta_{W,\ 'within'}$) trends (see text for details).

4.4.1 Individual differences in mean calving date and between-individual heterogeneity in phenotypic plasticity

The comparison of different random structures of our two base models revealed an increase of all models' fit when female ID was entered as a random factor (Table 4.2), indicating that females varied in their average calving date (i.e. intercept). The inclusion of a random effect of female identity on slopes for precipitation in April also significantly decreased the deviance of the models (Table 4.2). A negative correlation was found between intercepts and slopes (r = -0.24 in model 1 and r = -0.25 in model 2) such that females with earlier calving dates in the average climate were more likely to delay their calving dates in response to the amount of precipitation in April. On the contrary, females with later calving dates advanced their calving dates with an increasing *PrecApril*. The best random structure of all models therefore appeared to be with a random intercept on female ID and with a random slope for *PrecApril* (Table 4.2), confirming scenario 2 of phenotypic plasticity described in the introduction (Figure 4.6b). Both the fixed and random effects of those models explained between 44% and 45% of the variation in calving date, with 65% of the total variance explained by the residuals. For the random effects, 15% of the total variance was explained by the random intercept on year, 18% by the random intercept on ID and only 2% by the random slope of ID on PrecApril$_{within}$.

Table 4.2 Comparison of linear mixed-effects models of calving date to climatic variables in the Kutuharju area, northern Finland with different random structures and showing deviance estimates and log-likelihood ratio test (LRT) statistics.

Set of models	Models	Log-L	Deviance	df	Test	LRT	P-value
1	0. Year	-5822.3	11645				
	1. Year + ID	-5756.8	11514	1	0 vs. 1	131	< 0.001
	2. Year + ID × T°May$_{within}$	-5755.2	11510	2	1 vs. 2	3.23	0.20
	3. Year + ID × PrecApril$_{within}$	**-5753.4**	**11507**	**2**	**1 vs. 3**	**6.78**	**0.03**
2	0. Year	-5823.6	11647				
	1. Year + ID	-5757.5	11515	1	0 vs. 1	132	< 0.001
	2. Year + ID × T°April-May$_{within}$	-5757.5	11515	2	1 vs. 2	0.07	0.96
	3. Year + ID × PrecApril$_{within}$	**-5754.0**	**11508**	**2**	**1 vs. 3**	**6.96**	**0.03**

The number for the set of models indicates which one of the base models was used (see Table 4.1). Random slopes were regressed with the within-individual component (β_W, 'within') of climatic variables. The models in bold text appeared to be the models with the best random structure in explaining variation in calving date.

4.4.2 Within- and between-individual response of calving date to climatic variability

The averaged fixed-effect estimates of our two models with their respective best random structure (see Table 4.2) showed a population-, as well as an individual-level trend of earlier calving dates following warmer temperatures in May (Table 4.3; Figure 4.2a). An individual-level trend of earlier calving dates with warmer temperatures in April-May was also found but with non-statistically significant population trend (Table 4.3; Figure 4.2b). Based on the method described by van de Pol and Wright (2009), the individual- and population-level trends were statistically similar and going in the same direction for both T°May and T°April-May (respectively β_B - β_W = -0.58, 95% CI [-1.96, 0.72] and β_B - β_W = -0.20, 95% CI [-1.44, 0.95]). As such, the phenotypic plasticity of calving date to T°May corresponded to scenario 1 in Figure 4.1a, while the plastic response to T°April-May corresponded to scenario 3 (Figure 4.1c). An individual-trend of earlier calving dates following a decreasing amount of precipitation in April was also found (Table 4.3, Figure 4.2c). However, the individual plastic responses were not reflected at the population level since the individual- and population-level trends for PrecApril were statistically different and going in the opposite direction (respectively β_B - β_W = -1.80, 95% CI [-3.37, -0.24] in model 1 and β_B - β_W = -1.56, 95% CI [-3.07, -0.04] in model 2). At the population-level, delayed calving dates were observed with less precipitation in April but the trend was not statistically significant (β_B component in Table 3). The plastic response of calving date to PrecApril clearly corresponded to scenario 3 in Figure 4.1c. We also consistently found earlier calving dates with females in better physical condition the year preceding calving (Table 4.3) and in years with a higher proportion of males present in the herd the preceding mating season (Table 4.3).

Table 4.3 Model-averaged estimates of fixed effects from the linear mixed-effects models of calving date of a reindeer population in relation to climatic variables in Kaamanen, northern Finland, produced from a dataset of females who calved more than four times (272 mothers), between 1970 and 2016.

Variable	Estimate	Unconditional SE	Nbr models	Relative importance	95% CI
Females' BCI	**-1.24**	0.22	2	1.00	**-1.68, -0.80**
Proportion of males	**-1.50**	0.32	2	1.00	**-2.12, -0.87**
PrecApril$_{within}$	**1.00**	0.44	2	1.00	**0.14, 1.86**
PrecApril$_{between}$	-0.71	0.85			-2.38, 0.95
T°May$_{within}$	**-0.98**	0.45	1	0.63	**-1.85, -0.10**
T°May$_{between}$	**-1.55**	0.72			**-2.96, -0.15**
T°April-May$_{within}$	**-1.06**	0.50	1	0.37	**-2.05, -0.08**
T°April-May$_{between}$	-1.27	0.66			-2.57, 0.03

The estimates were subdivided into a within-individual component ($\beta_{W,\ 'within'}$) and a between-individual component ($\beta_{B,\ 'between'}$) as suggested by van de Pol and Wright (2009) (see text for details) and those in bold type were deemed important (whose 95% CI excluded 0) in explaining calving date. "Nbr models" is the number of models (out of the two best models in Table 4.1) including that variable.
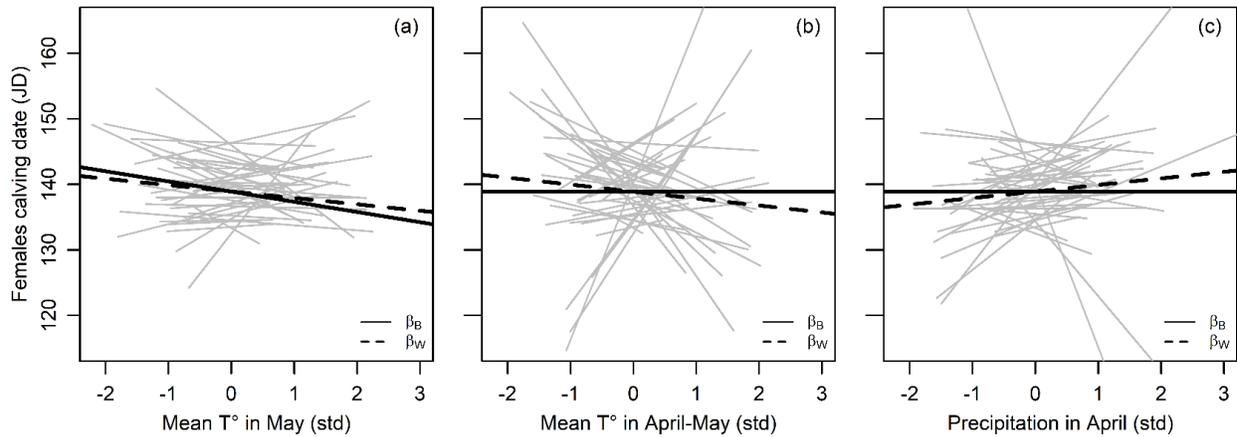
Figure 4.2 Individual-specific plasticity of calving date (in Julian days) for 50 randomly chosen reindeer females (from a total of 272 females) of the Kutuharju herd to (a) mean temperature in May, (b) mean temperature in April-May and (c) amount of precipitation in April. The grey lines represent the model-averaged individual estimates for intercept and slope, obtained by running linear regression models of calving date against (1) mean temperature in May and the amount of precipitation in April for model 1 and (2) mean temperature in April-May and the amount of precipitation in April for model 2, separately for each female. Following the subject-centering method, the climatic variables were subdivided into a within- (β_W) and a between-individual component (β_B). The bold, straight black lines represent the average population-level plastic response (β_B) of calving date to the climatic variable of interest, while the bold, dotted black lines represent the individual-level trend (β_W). The population- and individual-level trends were obtained from the model-averaged estimates in Table 4.3.

4.4.3 Females attributes early in life and between-individual heterogeneity in mean calving date and in phenotypic plasticity

A total of 22 models were performed, 11 models for each of the base model, with 2 base models kept, and corresponding to the 11 females attributes early in life. Among the 11 females' attributes used to test our last hypothesis, three were found to influence the females' intercept but none influenced their plastic response to precipitation in April. Females will have consistently earlier calving dates in the average climate throughout their reproductive life (i.e. lower intercepts) when (1) their birthdate ('BD') was earlier ($b = 0.98$, 95% CI [0.65, 1.32], $n = 1,611$, Figure 4.3b), (2) their averaged physical condition from March to May before their first calving season ('COND_FST_CALF') was higher ($b = -0.48$, 95% CI [-0.84, -0.11], $n = 1,333$, Figure 4.3b) and (3) their first calving date ('BD_FST_CALF') was earlier ($b = 1.51$, 95% CI [1.19, 1.82], $n = 1,688$, Figure 4.3c). Females with a higher physical condition in March-April-May before their first calving season will also have an earlier BD_FST_CALF ($b = -0.38$, 95% CI [-0.37, -0.29]).
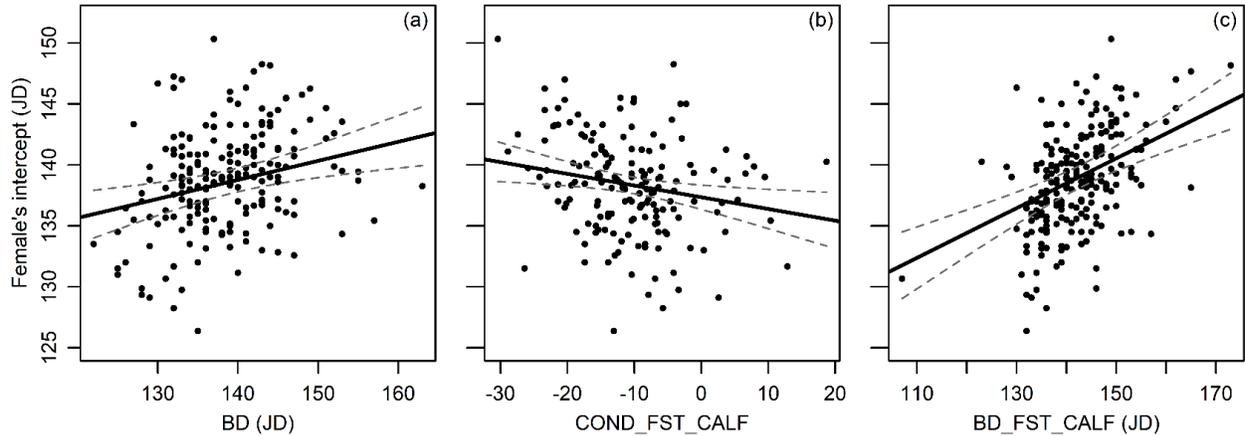
Figure 4.3 The between-individual heterogeneity in intercept of calving date in response to climatic variability from a semi-domesticated reindeer population in Kaamanen, northern Finland was influenced by (a) the birthdate of the female of interest ('BD'), (b) the average physical condition of the female in March-April-May before her first calving season ('COND_FST_CALF') and (c) her first calving date ('BD_FST_CALF'). BD and BD_FST_CALF were expressed in Julian days. Each dot (●) represented the model-averaged female's intercept from individually independent regression fits of calving date against (1) mean temperature in May and the amount of precipitation in April for model 1 and (2) mean temperature in April-May and the amount of precipitation in April for model 2. Following the subject-centering method, the climatic variables were subdivided into a within- (β_W) and a between-individual component (β_B).

4.4.4 Fitness consequences of between-individual heterogeneity in mean calving date and in phenotypic plasticity

A total of 6 models were performed, 3 models for each of the base model, with 2 base models kept, and corresponding to the 3 fitness attributes of females. In terms of fitness consequences, females with earlier calving dates throughout their reproductive life (i.e. lower intercepts) had heavier calves (b = -0.94, 95% CI [-1.26, -0.62], n = 1,750, Figure 4.4a), calves with a higher first-summer survival (b = -0.80, 95% CI [-1.11, -0.50], n = 1,733, Figure 4.4b) and an overall higher number of calves (b = -0.70, 95% CI [-1.02, -0.37], n = 1,764, Figure 4.4c). Females with a negative plastic response to *PrecApril* (i.e. I×E < 0) also had an overall higher number of calves over their reproductive life (b = -0.48, 95% CI [-0.79, -0.16], n = 1,764, Figure 4.5).
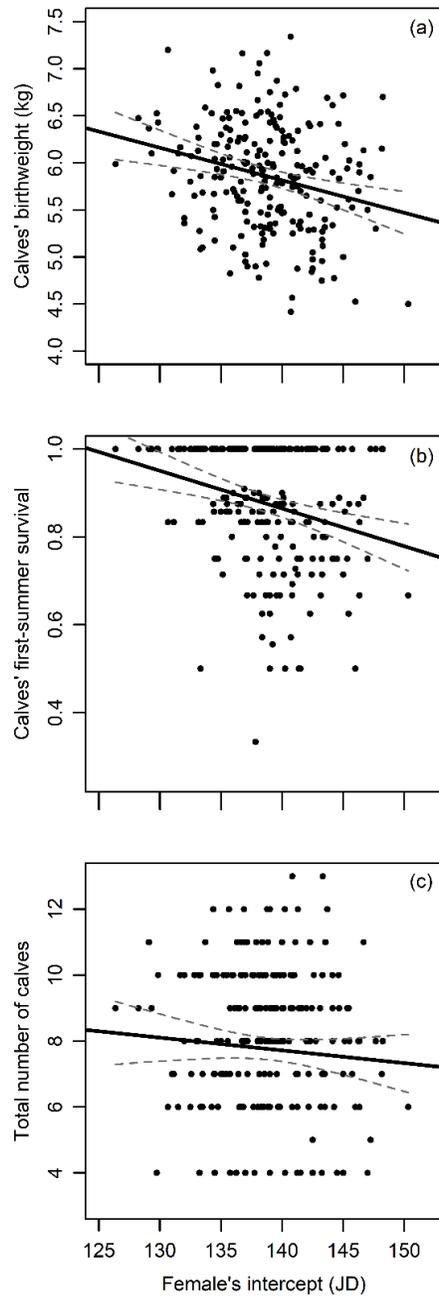
Figure 4.4 The between-individual heterogeneity in intercept of calving date in response to climatic variability from a reindeer population in Kaamanen, northern Finland and its consequences on (a) the calves' birth weight, (b) the calves' first-summer survival and (c) the total number of calves of a female. Each dot (●) represented the model-averaged female's intercept from individually independent regression fits of calving date against (1) mean temperature in May and the amount of precipitation in April for model 1 and (2) mean temperature in April-May and the amount of precipitation in April for model 2. Following the subject-centering method, the climatic variables were subdivided into a within- (β_W) and a between-individual component (β_B).
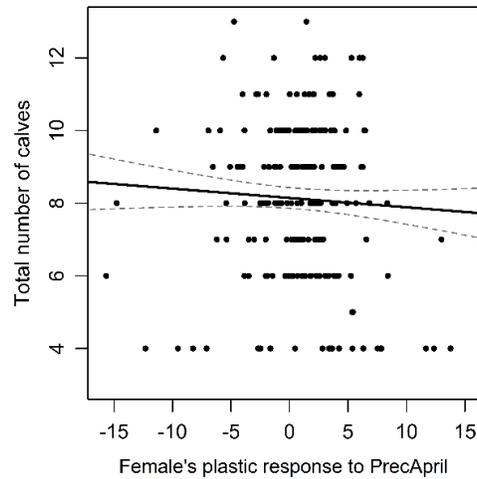
Figure 4.5 The between-individual heterogeneity in the plastic response of calving date to the amount of precipitation in April ('PrecApril') of the females in the Kutuharju herd, northern Finland and its consequences on the total number of calves of a female. Each dot (●) represented the model-averaged female's slope to the amount of precipitation in April from individually independent regression fits of calving date against (1) mean temperature in May and the amount of precipitation in April for model 1 and (2) mean temperature in April-May and the amount of precipitation in April for model 2. Following the subject-centering method, the climatic variables were subdivided into a within- (β_W) and a between-individual component (β_B).

4.5 Discussion

4.5.1 *Individual differences in mean calving date and between-individual heterogeneity in phenotypic plasticity*

Our 45 years-long dataset of calving season allowed to demonstrate that the magnitude of the plastic response of calving date to a reduced amount of precipitation in April (mainly snowfalls at this time of the year) did vary among females (Table 4.2). Females also differed markedly in their mean calving date, confirming a between-individual heterogeneity in plasticity (as in Figure 4.6b). The between-individual heterogeneity in maternal plasticity of birth timing has already been investigated in a number of animal species [collared flycatchers: Przybylo et al. 2000; common gull (*Larus canus*): Brommer et al. 2008; Ural owl (*Strix uralensis*): Brommer et al. 2003; Columbian ground squirrels: Lane et al. 2012; North American red squirrels: Réale et al. 2003; red deer: Nussey et al. 2005a; tree swallow (*Tachycineta bicolor*): Bourret et al. 2015; review in Boutin and Lane 2014], but so far this is the first study to demonstrate that in *Rangifer*. In addition, repeatability in calving date appeared to be quite low compared to birds, where the repeatability of laying date range between 0.10 and 0.61 (Wiggins 1991; Potti 1999). In mammals, a repeatability ranging from 0.54 to 0.93 was found in roe deer (Plard et al. 2013b) and a repeatability of 0.10 in red deer (Nussey et al. 2006). A repeatability of 0.19 thus suggests a high level of plasticity for calving date in this population. As expected, the large intraspecific differences in body mass of females reported in this herd (see Figure 1 in Paoli et al. 2018), resulted in a between-individual heterogeneity in plasticity. In reindeer, large between-individual heterogeneity in females' body weight is mainly due to variations in food acquisition resulting from social dominance such that high-ranked females have access to the best food patches (Skogland 1983, 1989). Given that calving date is highly determined by a female's physical condition (Cameron et al. 1993; Flydal and Reimers 2002; Cook et al. 2004; Barboza and Parker 2008), it resulted in females with a better overall physical condition being the ones calving earlier (Table 4.3). The high plasticity reported in calving date would thus be accounted for by the among-females large variability in body weight.

That Nussey et al. (2006) found a similarly low repeatability and that the magnitude of phenotypic plasticity between calving date and autumn rainfall did vary among hinds in their wild red deer population study (Nussey et al. 2005a) points out that wild and domesticated populations

of ungulate species may respond to climate change in an individual-specific manner. However, the variation in individual slope (IxE) in our study accounted for 2% of the total variance, while it accounted for 5.1% in the study of Nussey et al. (2005a) and the between-individual heterogeneity in intercept was much higher in our study (18% versus 9.6% in Nussey et al. 2005a). It suggests that management practices could act to reduce the between-individual heterogeneity in slopes (i.e. reduce IxE), although the individual, genetic variation in calving date is present (Nussey et al. 2007) and higher than in red deer. Management practices are directed towards optimizing meat production through the slaughtering of calves (Kumpula et al. 1998). Given the economic aspect of reindeer husbandry, reindeer herders are less likely to keep females with a physical condition below the threshold to be able to reproduce in the herd. The supplemental feeding given to the animals in late winter would cause females with a very low physical condition to not be represented in this population, which may not be the case for wild populations. Therefore, while supplemental feeding was unable to buffer completely the effects of climatic variability on calving season (see Paoli et al. 2018) and to counteract the high among-females heterogeneity of plasticity in calving date, it could have contributed to homogenize the plastic responses of females to the amount of precipitation in April.

4.5.2 *Within- and between-individual response of calving date to climatic variability*

An individual-level trend of earlier calving dates following warmer temperatures in May and in April-May was found using this reduced dataset of multiparous females (Figure 4.2a, b and Table 4.3). Combined with the absence of a statistically significant variation in individual slope (Table 4.2), it suggests that all females were able to respond to warmer temperatures in May and in April-May by adjusting their calving date in the same way. However, a slight difference among individual slopes was found for the amount of precipitation in April (Figure 4.2c and Table 4.2), with a statistically significant individual response as well (Table 4.3). Those findings confirmed that the precedent observed population-level correlations between calving date and climatic variability (in Paoli et al. 2018) were driven by phenotypically plastic responses at the individual-level. The supplemental feeding by sustaining the females' body weight above a certain threshold might have helped females to be physiologically able to respond in a similar manner to climatic conditions in spring. The mediated effect of the amount of precipitation in April on females' physiological condition would, however, result in more heterogeneity in their plastic responses.

The explanation as to why the amount of precipitation creates a higher among-females heterogeneity in phenotypic plasticity than the temperature is uncertain. Perhaps a higher amount of precipitation in April leads to a greater climatic deterioration in comparison to the mean temperature in May or in April-May, resulting in reduced food availability for individual females. The social dominance in reindeer with high-ranked females having access to the best food patches by digging under the snow (Skogland 1983, 1989) would then slightly accentuates the among-females differences in physical condition when the climate deteriorates (i.e. more snowfalls).

At the population-level, earlier calving dates were reported in environments with warmer temperatures in May (Figure 4.2a and Table 4.3), while the between-individual effect in response to precipitation in April was not statistically significant (Figure 4.2c and Table 4.3). This might arise because the absence of a statistically significant temporal trend for the amount of precipitation in April (95% CI [-0.05, 0.08]) would lead the average climate between females to be quite similar. On the contrary, significantly warmer temperatures in May ($b = 0.03$, 95% CI [0.03, 0.04]) over the past 45 years have contributed to produce more heterogeneous climatic conditions between females, that have in turn influenced the between-female effect. This result therefore demonstrates that a non-statistically significant population trend (scenario 3 in Table 4.4 and Figure 4.1c) does not necessarily mean that individuals will not be able to track their changing climate by altering the expression of a phenotypic trait such as calving date. On the contrary, an absence of an individual-level trend does not mean that the population lacks plasticity of a particular trait to be able to respond to climatic variability and a population-level trend might still be reported because certain phenotypes occur more frequently with certain climatic conditions (scenario 2 in Table 4.4 and Figure 4.1b). More emphasis should be put into differentiating individual- from population-level analyses of phenotypic plasticity for such reason. If the amount of precipitation in April was to change more in the future, however, more heterogeneous climatic conditions between females, along with the inter-individual differences in phenotypic plasticity could cause some females to be maladapted. As such, variability in plasticity if genetically-based would then be under selective pressures (Coulson et al. 2003; Réale et al. 2003; Brommer et al. 2005; Nussey et al. 2005b) to favor females better adapted to ongoing climatic changes in Finnish Lapland, favoring the resilience of reindeer populations to climate change.

4.5.3 Females attributes early in life and between-individual heterogeneity in mean calving date and in phenotypic plasticity

The majority of studies on phenotypic plasticity investigated whether or not being plastic conferred a selective advantage (Brommer et al. 2003; Nussey et al. 2005a; Lane et al. 2012) or even if such plasticity was under selection pressure (Coulson et al. 2003; Réale et al. 2003; Brommer et al. 2005; Nussey et al. 2005b). However, most of these studies have not assessed how conditions experienced early in life could explain a between-individual heterogeneity in the average phenotype or in phenotypic plasticity (except Nussey et al. 2005a). Unexpectedly, the different plastic responses to the amount of precipitation in April were not shaped by a female's physiological condition (95% CI [-0.32, 0.44]; contrary to Nussey et al. 2005a; Bårdsen et al. 2008; Stopher et al. 2008) or by any of the females attributes early in life tested in this study. However, and as commonly observed in ungulate species, we found a variation in mean calving date among females. Females born later than the population average and that also conceived later at their first calving event will begin their reproductive life at a disadvantage since giving birth consistently later throughout their reproductive life (Figure 4.3b, d). As previously shown in ungulate species, late-born calves are disadvantaged, as summer forage quality becomes increasingly low and they are also provided with less time to grow before their first winter (Festa-Bianchet 1988; Côté and Festa-Bianchet 2001; Cook et al. 2004). On the contrary, their early-born counterparts have a "head-start" benefit via an accelerated growth, and this "head-start" advantage is maintained throughout lifetime (Cook et al. 2004; Feder et al. 2008).

As previously reported (see Kumpula and Colpaert 2003; Aikio and Kojola 2014; Paoli et al. 2018), the early spring period appeared a key period for the reproductive success of reindeer as females with a higher physical condition in spring before their first calving season will have an earlier first calving date and thereafter earlier calving dates throughout their lifetime (Figure 4.3c). A better physical condition during the last trimester of pregnancy certainly contributed to advance the date at which the foetus is mature, resulting in an earlier birth (Rowell and Shipka 2009). Based on our previous results (Paoli et al. 2018), we believe that phenotypic plasticity in gestation length (Mysterud et al. 2009; Clements et al. 2011) allowed calving date to be fine-tuned by proximate cues such as climatic conditions in late pregnancy through a mediated effect on the maternal nutrition and physiological state (Ropstad 2000; Barboza and Parker 2008; Rowell and Shipka 2009). These findings thus indicate that a female's starting point when facing climatic changes is

best predicted by her own phenotypic quality at birth and all the way up to her first calving event, supporting the importance of maternal-offspring inheritance of genetic and phenotypic components (Weladji et al. 2006; Muuttoranta et al. 2013). It also supports the assumption that differences among individuals early in life may contribute to consistent differences in phenotypic value (e.g. mean calving date) observed later on (Nussey et al. 2005a; Stamps 2016). However, the different individual plastic responses to the amount of precipitation in April were not 'pre-determined' by any of the females attributes early in life tested in this study. One possible explanation would be that the supplemental feeding has hampered the expression of more heterogeneous individual trajectories in regard to climate change (only 2% of the total variation was explained by the variation in individual slope). Alternatively, another unidentified factor could be responsible in determining females' different trajectories. Indeed, the trajectories between females greatly differed, with slopes to the amount of precipitation in April ranging from -1.79 to 1.78. Other sources of variation might be involved, such as 'permanent environment', maternal and indirect genetic effects (Brommer et al. 2008; Dingemanse et al. 2010). Individual differences in slope might be caused by an individual-specific exposure to a combination of climatic conditions permanently affecting a female's plasticity (permanent environment: 'PE' in Dingemanse et al. 2010). We speculate that negative or positive within-individual association between calving date and the amount of precipitation in April might mask trade-offs made at the individual-level between the amount of precipitation in April and a combination of other climatic variables. Understanding the genetic or climatic causes of between-individual heterogeneity in plasticity therefore remains very intricate. As pointed out, empirical support for studies enlightening whether plasticity can vary (or not) as a function of experiences early in life is currently sparse and equivocal (Stamps 2016) but our study will be added to this expanding body of literature.

4.5.4 *Fitness consequences of between-individual heterogeneity in mean calving date and in phenotypic plasticity*

In terms of fitness consequences, the females who had a negative plastic response to the amount of precipitation in April (i.e. advanced their calving dates) gave birth to more calves over their reproductive life (Figure 4.5). It could suggest that females physiologically able to advance their calving dates, despite a higher amount of precipitation in April, could benefit from a high-quality forage at an earlier stage of lactation (Festa-Bianchet 1988), even if more precipitation in

April might cause the onset of spring green-up to be delayed (Pettorelli et al. 2007). In turn, females feeding on the longest possible highest-quality vegetation period (in early spring) could provide their calves with a protein-rich milk and provide greater maternal care being in a high enough body condition to invest towards reproduction (Barboza and Parker 2008; Parker et al. 2009). Even if the reported effect size is quite small (see Figure 4.5), it however points out that if climatic changes were to exacerbate, with more precipitation in April, inter-individual differences in the number of calves produced might become greater and a positive plastic response to the amount of precipitation in April might become maladaptive.

A lower intercept also conferred a reproductive advantage since females with consistently earlier calving dates gave birth to heavier calves (Figure 4.4a), calves with a higher first-summer survival (Figure 4.4b) and to more calves over their reproductive life (Figure 4.4c), as found in other studies (Brommer et al. 2003; Réale et al. 2003; Nussey et al. 2005a). Unfortunately, approximately one third of the calves are slaughtered every autumn as a management practice, therefore we could not estimate long-term fitness consequences on this population. A recent study on roe deer revealed that a higher allocation to reproduction early in life led to an impaired performance later in life with long-term fitness consequences (Lemaître et al. 2018) and an apparent direct fitness benefit of plasticity was found in a wild red deer population with females more plastic to dry autumns having a higher number of calves that survived to 2 years of age (Nussey et al. 2005a). Generally, these results corroborate the assertion that climatic conditions experienced while *in utero* and early in life can determine an individual's phenotypic value and phenotypic plasticity and therefore shape the adult lifetime reproductive success as commonly observed in ungulate species (Kruuk et al. 1999; Post and Stenseth 1999; Forchhammer et al. 2001). However, the underlying physiological mechanisms on why such conditions early in life are able to determine the average phenotype later in life or the average phenotypic plasticity remain unclear. In most ungulate species, a general trend of earlier calving dates following better climatic conditions has been reported (Nussey et al. 2005a; Post and Forchhammer 2008; Moyes et al. 2011) but whether the females differed in the magnitude of their plastic response has received contrasted responses. Our results therefore emphasize the need to better understand the underlying mechanisms leading to the complexity of plastic responses among populations to cope with current climate change (Boutin and Lane 2014).

4.6 Appendices
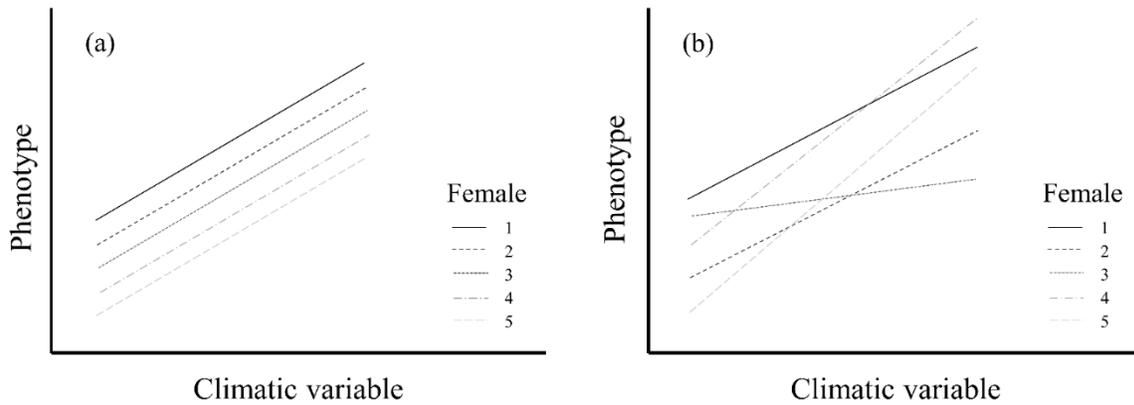
Figure 4.6 Graphical representation of two scenarios of phenotypic plasticity across a climatic gradient for five female phenotypes adapted from Figure 1.2d and Figure 1.2e in Pigliucci (2001): (a) variation in intercept and average plastic response to climatic change without between-individual heterogeneity in plasticity (scenario 1); (b) plastic response to climatic change with between-individual heterogeneity in plasticity (scenario 2; see text for description).

Table 4.4 Four different scenarios explaining when the within- (β_W) and between-individual (β_B) responses of calving date to climatic variability can differ or not in a population. For each scenario, a clear hypothesis was stated, along with its related biological meaning and an example of statistical values that could be obtained.

Plastic response of calving date to a climatic variable (e.g. warmer T° in spring)	**Scenario 1**: combination of within- and between individual hypotheses (Figure 4.1a)	**Scenario 2**: between-individual hypothesis (Figure 4.1b)	**Scenario 3**: within-individual hypothesis (Figure 4.1c)	**Scenario 4**: hypothesis of a within-individual effect in one direction, and a between-individual effect in the opposite direction (Figure 4.1d)
Hypothesis	Do the females found in warmer environments have earlier calving dates and do they individually calf earlier with warmer temperatures?	Do the females that experience warmer temperatures have earlier calving dates?	Do warmer temperatures induce earlier calving dates?	Do warmer temperatures cause earlier calving dates and do females found in colder environments have earlier calving dates?
Biological meaning	Each female calves earlier in response to warmer temperatures and calves later at colder temperatures **and** females with earlier calving dates are found in warmer environments, while females with late calving dates are found in colder environments	At warm temperatures, females always calf earlier, while at low temperatures, females always calf late	Each female calves earlier in response to warmer temperatures and calves later at colder temperatures	Each female calves earlier in response to warmer temperatures and calves later at colder temperatures **but** females with late calving dates are associated with warmer environments, while females with early calving dates are associated with colder environments
Statistical example	$\beta_B = -1$ $\beta_W = -1$ $\beta_B - \beta_W = 0$	$\beta_B = -2$ $\beta_W = 0$ $\beta_B - \beta_W = -2$	$\beta_B = 0$ $\beta_W = -2$ $\beta_B - \beta_W = +2$	$\beta_B = -1$ $\beta_W = +1$ $\beta_B - \beta_W = -2$

Table 4.5 Comparison of linear mixed-effects models of calving date to climatic variables in the Kutuharju area, northern Finland with different random structures and showing deviance estimates and log-likelihood ratio test (LRT) statistics.

Set of models	Models	Log-L	Deviance	*df*	Test	LRT	*P*-value
	Females with ≥ 2 calving dates (n = 392)						
1	0. Year	-6714.5	13429				
	1. Year + ID	-6646.0	13292	1	0 vs. 1	137	< 0.001
	2. Year + ID × T°May$_{within}$	-6644.6	13289	2	1 vs. 2	2.74	0.25
	3. Year + ID × PrecApril$_{within}$	**-6642.3**	**13284**	**2**	**1 vs. 3**	**7.45**	**0.02**
2	0. Year	-6714.9	13430				
	1. Year + ID	-6646.4	13293	1	0 vs. 1	137	< 0.001
	2. Year + ID × T°April-May$_{within}$	-6646.4	13293	2	1 vs. 2	0.04	0.98
	3. Year + ID × PrecApril$_{within}$	**-6642.6**	**13285**	**2**	**1 vs. 3**	**7.60**	**0.02**
	Females with ≥ 3 calving dates (n = 311)						
1	0. Year	-6202.3	12404				
	1. Year + ID	-6137.8	12276	1	0 vs. 1	129	< 0.001
	2. Year + ID × T°May$_{within}$	-6136.6	12273	2	1 vs. 2	2.27	0.32
	3. Year + ID × PrecApril$_{within}$	**-6134.3**	**12268**	**2**	**1 vs. 3**	**7.02**	**0.03**
2	0. Year	-6204.1	12408				
	1. Year + ID	-6138.9	12278	1	0 vs. 1	130	< 0.001
	2. Year + ID × T°April-May$_{within}$	-6138.9	12278	2	1 vs. 2	0.00	1.00
	3. Year + ID × PrecApril$_{within}$	**-6135.3**	**12270**	**2**	**1 vs. 3**	**7.20**	**0.03**
	Females with ≥ 4 calving dates (n = 272)						
1	0. Year	-5822.3	11645				
	1. Year + ID	-5756.8	11514	1	0 vs. 1	131	< 0.001
	2. Year + ID × T°May$_{within}$	-5755.2	11510	2	1 vs. 2	3.23	0.20

	3. Year + ID × PrecApril_{within}	**-5753.4**	**11507**	**2**	**1 vs. 3**	**6.78**	**0.03**
2	0. Year	-5823.6	11647				
	1. Year + ID	-5757.5	11515	1	0 vs. 1	132	< 0.001
	2. Year + ID × T°April-May_{within}	-5757.5	11515	2	1 vs. 2	0.07	0.96
	3. Year + ID × PrecApril_{within}	**-5754.0**	**11508**	**2**	**1 vs. 3**	**6.96**	**0.03**

The same analyses were repeated over different reduced datasets of all females who calved at least 2, 3, 4 (or more) times. The number for the set of models indicates which one of the three base models was used (see text for more details). Random slopes were regressed with the within-individual component (β_W, 'within') of climatic variables. The models in bold text appeared to be the models with the best random structure in explaining variation in calving date.

Chapter 5 The onset in spring and the end in autumn of the thermal and vegetative growing season affect calving time and reproductive success in reindeer

5.1 Abstract

A developing trophic mismatch between the peak of energy demands by reproducing animals and the peak of forage availability has caused many species' reproductive success to decrease. The Match-Mismatch Hypothesis (MMH) is an appealing concept that can be used to assess such fitness consequences. However, concerns have been raised on applying the MMH on capital breeders such as reindeer because the reliance on maternal capita rather than dietary income may mitigate negative effects of changing phenologies. Using a long-term dataset of reindeer calving dates recorded since 1970 in a semi-domesticated reindeer population in Finnish Lapland and proxies of plant phenology; we tested the main hypothesis that the time-lag between calving date and the plant phenology in autumn when females store nutrient reserves to finance reproduction would lead to consequences on reproductive success, as the time-lag with spring conditions would. As predicted, the reproductive success of females of the Kutuharju reindeer population was affected by both the onset of spring green-up and vegetative senescence in autumn as calves were born heavier and with a higher first-summer survival when the onset of the vegetation growth was earlier and the end of the thermal growing season the previous year was earlier as well. Our results demonstrated that longer plant growing seasons might be detrimental to reindeer's reproductive success if a later end is accompanied by a reduced abundance of mushrooms.

5.2 Introduction

The ongoing large changes in climate have already caused unprecedented consequences on the phenology of many plant and animal species. In the Arctic tundra ecosystem, a warming two to three times higher than the increase of the global mean surface temperature (IPCC 2013) has led to longer vegetative growing seasons (Oberbauer et al. 2013); and a 50% increase in the above

ground vegetation biomass (Epstein et al. 2000). In response to these plant phenological changes, many animal species have shifted their timing of reproduction (bird: Visser et al. 1998; Frederiksen et al. 2004; Bourret et al. 2015; amphibian: Blaustein et al. 2001; fish: Asch 2015; mammal: Réale et al. 2003; Moyes et al. 2011; Lane et al. 2012; marine species: review by Poloczanska et al. 2013). However, there is increasing evidence of a mismatch, due to these phenological changes, between the peak of resource demands by reproducing animals and the peak of forage availability (Post and Forchhammer 2008). Although in ruminants, and especially ungulates, the peak of available high-quality forage is of better importance than simply the peak of forage biomass as they are more selective on forage quality than forage quantity (Tveraa et al. 2013). Also, the question on whether potential shifts in timing of reproduction are sufficient to track a rapidly changing environment, is still a debated question with contrasted answers. For instance, climatic changes were shown to affect the reproduction of ungulate species either negatively or positively. Negatively because deep snow cover and 'locked pastures' under an impenetrable layer of ice restrict access to the field layer and to forage during winter for herbivores like *Rangifer* species (Aanes et al. 2000; Tyler 2010); generating reduced reproductive rates down to 49% (Helle and Kojola 2008), major die-offs and population declines (Tveraa et al. 2007). Positively because the timing of flowering was advanced in parallel with earlier snow melting. Also, deep snow may lead to an extended period of access to newly emergent high-quality forage (Post and Stenseth 1999), that was shown to be favorable to both red deer and Soay sheep (Mysterud et al. 2003), to caribou (Forchhammer et al. 2002) and more recently to reindeer (Tveraa et al. 2013). Those contrasted findings highlights the need for a better understanding of how quickly species are able to adapt to their changing environment and if long-term fitness consequences can be detected.

The Match-Mismatch Hypothesis (MMH; Cushing 1990) was developed to address these issues. The MMH is used to estimate the gap between the phenology of a species at the higher level (e.g. grazers) and that of species at the immediate lower level (e.g. vegetation). If there is a time lag between the food requirements and the food availability of the species at the higher level, i.e. a mismatch, then the survival and reproduction rate of this species are expected to be low (Durant et al. 2007). For example, the gosling body mass and structural size at fledging of a snow goose (*Chen caerulescens atlantica*) population was reduced when the trophic mismatch between hatch dates of young and date of peak in plant nitrogen availability was high (> 9 days; Doiron et al. 2015). The MMH is an appealing concept regarding the ongoing climate change as we could

better describe the changes of the time-lag between the peak of resource demands by reproducing animals and the peak of forage availability (Post and Forchhammer 2008). But to date, the MMH has been rarely applied on ungulates and with contradictory results. For instance, the temporal mismatch found between the vegetation peak and the average birth date of the Soay sheep in Hirta, Outer Hebrides in Scotland did not affect the lambs' survival (Durant et al. 2005), while in the Low Arctic Greenland, the increased time lag between the onset of the plant growing season and the caribou's timing of calving has contributed to a reduced production and survival of caribou calves (Post and Forchhammer 2008).

Criticisms have been raised on applying the MMH on capital breeders such as caribou and reindeer (Taillon et al. 2013) because the reliance on maternal body reserves rather than dietary income to ensure foetal development could act as a buffer against negative effects of between-year variability in plant phenology (Veiberg et al. 2016; Gustine et al. 2017), curtailing potential effects of spring phenological mismatches. As such, Veiberg et al. (2016) recently found that the influence of spring phenology was less important than that of maternal winter body condition on reproductive success of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*). As previously documented, the peak of calving time for many *Rangifer* populations usually occurs well (up to three weeks) before the spring green-up (Tveraa et al. 2013; Veiberg et al. 2016; Gustine et al. 2017) in order for the timing of high energetic demands (i.e. lactation) to coincide with the timing of peak nutrient availability/quality in forage species (Klein 1990; Post et al. 2003). An increase in the pre-existing time-lag between parturition time and the emergence of vegetation would then diminish both mother and calf's ability to exploit high-quality forage during a period of high nutritional requirements (i.e. lactation, replenishing winter fat reserves, calf physical growth; Post and Forchhammer 2008), reinforcing the importance of maternal capital for reproduction (Barboza and Parker 2008). Gustine et al. (2017) therefore suggested that it might be more relevant to consider potential lagged effects in the periods when females build up reserves to ensure reproduction in the next breeding season (e.g. in the late summer and autumn; Thompson and Barboza 2014) rather than at parturition. Indeed, the major determinant for calving date was observed to be the conception date (Holand et al. 2002; Clements et al. 2011), inadequate nutrition in autumn would be detrimental to females' body condition and cause a subsequent delay in calving dates (Cook et al. 2004).

To circumvent these issues and following the suggestion made by Gustine et al. (2017), we therefore examined the potential climate-induced lagged effects at the individual-level between calving date and (1) start of vegetation emergence in spring and (2) end of the vegetative growing season in autumn, which is new. We also determined if the potentially lagged effects of plant phenology led to fitness consequences, as recently found in other reindeer populations (Tveraa et al. 2013; Veiberg et al. 2016). Using a long-term dataset of reindeer calving dates recorded since 1970 in a population in Finnish Lapland and proxies of plant phenology, we specifically tested the following three hypotheses: (1) The reported rate of advancement in calving dates (Paoli et al. 2018) would match the rate of change in spring green-up in the study area, with no changes in time-lag over time as already reported in another caribou population (Gustine et al. 2017); (2) The calving time would be more affected by the plant phenology in autumn than in spring, mediated by effects on females' nutrition and body condition at the time of conception (Cook et al. 2004; Veiberg et al. 2016); (3) The time-lag between the end of the vegetative season in autumn and the forthcoming calving time may be expected to diminish over time, because of a reported delay in autumn leaf colouring by up to 2.4 days°C^{-1} in Europe from 1971 to 2000 (Menzel et al. 2006).

5.3 Material and Methods

5.3.1 Study area and reindeer population

Calving dates were obtained from an experimental herd of semi-domesticated reindeer of about 100 animals in every year at the Kutuharju field reindeer research station in Kaamanen (kept by the Reindeer Herders' Association), northern Finland (69°N, 27°E). The study area is composed mainly by open birch and pine forests, bogs and lakes and the landscape varies between 185–370 m above the sea level. The long-term book-keeping of the herd demography and the unique identification of animals fitted with collars and ear tags since their birth allowed reindeer to be individually recognizable and of known age. Most of the year (in summer and during the rut) the herd is free ranging in two large fenced enclosures, the north-west section (Lauluvaara ~ 13.8 km²) and the south-east section (Sinioivi ~ 15 km²). When the mating season is over around late October, the animals are gathered and taken to a winter grazing area (15 km^2) where they can graze freely on natural pastures. In late winter, the animals receive supplemental feed (pellets and hay) in addition to natural forage as part of a common management practice that has started since the 1980s in the northern part of Finland (Helle and Jaakkola 2008). The significant between-years

variability in females' body weight (one-way analysis of variance: $F_{(44, 2,094)}$ = 21.3, P < 0.001) makes us believe that the regular supplemental feeding alone was not able to sustain individuals' body weight at a stable level and therefore females were still dependent upon natural pastures. No detailed information was available on the duration or the amount of supplemental feeding previously given every year to the animals. By the end of winter, females are transferred into a calving enclosure (approximately 0.5 km^2) where newborn calves are captured, weighed, sexed and marked with ear tags. The enclosure was surveyed daily, so that calving date is known for all individuals and has been recorded since 1970. Handling of live mammals and data collection were done in agreement with the Animal Ethics and Care certificate provided by Concordia University (Protocole number 30000303) and by the Finnish National Advisory Board on Research Ethics.

5.3.2   *Calving dates and population variables*

The calving dates from females that have been artificially fed for experimental purpose, anytime during the year preceding the calving season (i.e. more than just the regular extra feeding given in late April) were excluded from the dataset (see Paoli et al. 2018). Given the reported trend of heavier (and older) females giving birth earlier (Cameron et al. 1993; Flydal and Reimers 2002), an artificial feeding by improving the females' physical condition could lead to earlier calving dates, independently from plant phenology. This artificial feeding could therefore buffer the effects of plant phenology on calving date. All calendar dates were converted into Julian days since 1 January for analysis purposes. In total, calving dates spanning over 45 years were available from 1970 to 2015. A lowercase 't' indicated that the variable was estimated from the same calendar year as calving, while a lowercase 't-1' indicated that the variable was estimated from the previous calendar year as calving. The documented effects of females' physical condition, population sex ratio, and population density on calving date (Ropstad 2000; Forchhammer et al. 2001; Flydal and Reimers 2002; Holand et al. 2002; Mysterud et al. 2009) were also controlled for.

The proportion of males during the previous mating season ('PM$_{t-1}$') was estimated as the number of males divided by the number of females over one year of age present in a specific enclosure. Between 1996 and 2013 (except 1998), the proportion of males was estimated per enclosure as the herd was subjected to a number of experiments including manipulation of the proportion of males, leading to the simultaneous use of the two large enclosures, Sinioivi and Lauluvaara. Every year, all animals are gathered in corrals just before the rut period (in September)

and then released in either Sinioivi or Lauluvaara for the entire rutting season. As the identity of the animals involved in any experiment was known, as well as their presence in each enclosure (recorded during the release), every calving date was related to the corresponding proportion of males in that enclosure the previous mating season. In addition to the proportion of males, we also estimated the population density ('$DENS_{t-1}$') per enclosure-year as the total number of individuals present in a specific enclosure during a given year.

All factors linked to physical condition in reindeer interact with each other so that older individuals tend to be heavier (Ropstad 2000). Therefore, an individual body condition index (BCI) was used to allow (1) the effects of individual body weight controlling for age to be taken into account and (2) multicollinearity between these two highly correlated variables to be avoided. This body condition index was estimated by a measure of individual body weight after the effect of age is controlled – the age-specific residual body mass (see Festa-bianchet et al. 1997; Weladji et al. 2003), calculated by subtracting from each individual's body weight the average body weight of all individuals of the same age, across all years. To also account for the reported senescence in female reindeer from this population (Weladji et al. 2010), we extracted the residuals from the linear and quadratic forms of the relationship between females' body weight and females' age. The females' BCI was averaged across three key periods in their reproductive cycle: in autumn ($BCIAutumn_{t-1}$, September-October-November) as a female's conception date (and therefore calving date) is influenced by her physical condition at the time of mating (Clutton-Brock et al. 1982; Adams and Dale 1998; Flydal and Reimers 2002); in winter ($BCIWinter_t$, from December [the previous calendar year] to March [the same calendar year as calving date]) as winter climatic conditions during pregnancy can cause females' nutritional stress and are critical for the fetal growth and development (Barboza and Parker 2008); and in early spring ($BCISpring_t$, April-May) as climatic conditions in April-May were already found to affect calving date (Paoli et al. 2018) and that most of the energy requirements for gestating females occur during the third trimester of pregnancy (Parker et al. 2009).

5.3.3 Plant phenology data

The starting and ending day of the thermal growth season in each year were estimated using daily average temperatures from 1970 to 2015 obtained from three weather stations (Utsjoki, Ivalo airport and Nellim) in northern Finland (68°N, 27°E) downloaded with the 'FMIDownloader' of

the Finnish Meteorological Institute (https://tuomassalmi.com/FMI-weather-downloader/). To obtain the daily average temperatures at our study site with as much reliability as possible, the daily recorded temperature values from the three nearest weather stations were averaged with their weighted mean by the distance from the weather station to our study site. The distance between our study site and each of the weather stations was precisely assessed using their respective GPS coordinates and the Great Circle longitude-latitude calculations tool (http://www.cpearson.com/excel/LatLong.aspx). Then, we defined the onset of the thermal growing season in each year as the last day of the first 5-day period, after the last winter/spring frost, during when the daily mean temperatures all remained above 5°C (Jones et al. 2002; Walther and Linderholm 2006). The last day of frost was defined as the last day in late winter/spring when the minimum temperature was negative ($< 0°C$, Menzel et al. 2003). The end of the thermal growing season was computed as the first day of the first 10-day period when the mean daily temperatures fell below 5°C (Carter 1998; Walther and Linderholm 2006). The length of the thermal growing season ('LTGS') was assessed by the day of end ('ThermalEnd') minus the day of start ('ThermalStart') of the thermal growth season.

Vegetation phenology in the study area was assessed using the phenology of deciduous birch (*Betula pubescens*) as this species is commonly present in the lowland regions of the study area and is the dominant tree species in most parts of the study area (Karlsen et al. 2008). The deciduous growth of birch also allows to well-defined phenophases, phenomena which are not observed easily in conifers, making birch species an ideal phenological indicator (Karlsen et al. 2008). The vegetation phenology data was obtained from the Muddusjärvi station situated at approximately 19.3 km from the study area and monitored by the Natural Resources Institute of Finland (Luke), Finland. Data are part of the Pan European Phenology Project PEP725 and were downloaded through their website (http://www.pep725.eu/index.php) and were available from 1997 to 2015. In the present study, two phenophases were used as indices to reflect respectively the onset in spring and end in autumn of the vegetative growing season: 'onset for sprout of birch leaves' ('VegOnset') and '50% autumnal coloring of birch leaves' ('VegEnd'). Onset of leafing is the date when the first leaves sprout and a 'mouse ear' is visible (BBCH10 code according to Meier 1997). The second phenophase '50% autumnal coloring of birch leaves' is the date when half of the leaves on each trees have turned yellow (BBCH94 code). The chosen birch phenophases represent well the general greening and colouring of the region's vegetation (Karlsen et al. 2008).

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The length of the vegetative growing season ('LVGS') was assessed by the day of VegEnd minus the day of VegOnset of birch. We conducted analyses on two study periods depending on the availabilities of the plant phenology variables: the whole study period (1970–2015) and the last part of the study period (1997–2015). The correlations between the plant phenology variables were assessed using Pearson's correlation test.

5.3.4 Statistical analyses

5.3.4.1 Temporal trends

To evaluate the long-term trends of the population variables (population density and proportion of males) and plant phenology variables in the Kutuharju area, we fitted Linear Models (LMs) with the year of study entered as a covariate (continuous variable) in the models. Variation in calving date, our response variable, was analysed using a Linear Mixed-effects Model (LMM), by running the lmer-function in the R package lme4 (Bates et al. 2015, <www.r-project.org>). Year only was entered as a continuous fixed-effect parameter in the model, and year as a multilevel random effect to control for repeated measures (Kruuk et al. 1999; Milner et al. 1999). Unstandardized value of the temporal trend was reported and the parameter estimate was derived using the restricted maximum likelihood estimates as recommended for mixed effect models (Bolker et al. 2009). The same method was applied for the three metrics of females' body condition index (BCI) as calving date and females' BCI had several values each year. For all models, the temporal trends were considered statistically significant if 95% confidence intervals (CIs) of the parameter estimates excluded 0.

5.3.4.2 Plant phenology variables

We then evaluated whether calving date was affected by the start, end and duration of both the thermal and vegetative growing seasons by running LMMs with the population density ($DENS_{t-1}$) and proportion of males (PM_{t-1}) entered as fixed-effects in a 'basic model' to account for their known effects on calving date, with calving date as the response variable. In total, 9 predictor variables were tested in the models: $ThermalStart_{t-1}$, $ThermalEnd_{t-1}$, $LTGS_{t-1}$, $VegOnset_{t-1}$, $VegEnd_{t-1}$, $LVGS_{t-1}$, $BCIAutumn_{t-1}$, $BCIWinter_t$, and $BCISpring_t$. Given that the plant phenology variables had only one value per year and that we applied the 'detrending' method (see below), only the females' identity was entered as a multilevel random effect in the models to account for

within-individual dependency (Pinheiro and Bates 2000). If statistically significant temporal trends were found for any of the explanatory variables, we applied the 'detrending' method in order to avoid the potential confounding effect of the year on the phenology-calving date relationship, which can happen simply because both variables change across years (Iler et al. 2017). To do so, we extracted the residuals from independent linear regressions with year as the predictor from the population, phenological or calving date variables (Iler et al. 2017). All the predictor variables considered were also centred and standardized ($\bar{X} = 0$, SD = 1) to be on a comparable scale. We also tested the interactions between the metrics of females' BCI (BCIAutumn$_{t-1}$, BCIWinter$_t$, and BCISpring$_t$) and plant phenology variables (ThermalStart$_{t-1}$, ThermalEnd$_{t-1}$, VegOnset$_{t-1}$, VegEnd$_{t-1}$). Since our predictor variables were beforehand centred and standardized, we could directly interpret their main effects even when involved in interactions and thus avoided the potential misinterpretation of main effects between models with and without the interaction term (Gelman 2008; Schielzeth 2010; Grueber et al. 2011).

A model selection was then performed to find combinations from all the explanatory variables used providing the most probable models to explain variation in calving date and this was based both on the Akaike Information Criterion, (AIC) and Akaike weights (AIC weights) to compare the relative performance of the models tested (Anderson et al. 2001; Burnham and Anderson 2002). The delta AICc (Δ_i) was calculated to provide a measure of each model relative to the best model (with the lowest AIC value). All models within a ΔAIC of 2 units were retained as competing models since a substantial evidence was given to the model if $\Delta_i < 2$ (Burnham and Anderson 2002). To account for model selection uncertainty and if more than one model were retained as best models in explaining the data then the estimates of the coefficients of parameters in all models with ΔAIC < 2 were averaged, following the model averaging approach (Schielzeth 2010; Grueber et al. 2011; Mazerolle 2019). The model.avg function in the R package AICcmodavg (Mazerolle 2019, <www.r-project.org>) was used to calculate the model-averaged parameter estimates, as well as their 95% confidence intervals based on our entire list of candidate models. The model selection of mixed models was performed using the maximum likelihood methods (ML), whereas the parameter estimates were obtained from the selected model using the restricted maximum likelihood estimates (REML) as recommended for mixed-effects models (Bolker et al. 2009; Zuur et al. 2010). The effect size of the predictor variables included in the competing models was considered important if the 95% CIs excluded 0 and only the important

variables were further discussed. The analyses were repeated over the two study periods, with a total of 30 models performed for the whole study period and 84 for the last part of the study period.

5.3.4.3 Time-lags

To test our hypotheses of changes in time-lags between calving date and spring or autumn phenology, we first estimated such time-lags in number of days as follow: $TL_{ThermalStart} = calvdate_t - ThermalStart_t$, $TL_{VegOnset} = calvdate_t - VegOnset_t$, $TL_{ThermalEnd} = 365 - ThermalEnd_{t-1} + calvdate_t$, $TL_{VegEnd} = 365 - VegEnd_{t-1} + calvdate_t$. Since the onset of thermal or vegetative growing season occurs after calving in the same calendar year, we simply calculated the difference between ThermalStart$_t$ or VegOnset$_t$ and calvdate$_t$ for TL$_{ThermalStart}$ and TL$_{VegOnset}$ (and given that the plant phenology variables are expressed in Julian days). Given that ThermalEnd$_{t-1}$ and VegEnd$_{t-1}$ were estimated from the previous year to calving, we first calculated the number of days remaining from ThermalEnd$_{t-1}$ or VegEnd$_{t-1}$ respectively until the end of the year ($x = 365 - ThermalEnd_{t-1}/VegEnd_{t-1}$; December 31th being the last day of the year, it is equivalent to the 365th Julian day), and added this number to the number of days until calvdate$_t$ (which is equivalent to the calving date as expressed in Julian days since January 1st; $TL_{ThermalEnd}/TL_{VegEnd} = x + calvdate_t$), to estimate respectively TL$_{ThermalEnd}$ and TL$_{VegEnd}$. The temporal trends in the time-lags were then evaluated by running LMMs with year entered as a continuous fixed-effect parameter in the models, and year as a random effect on the intercept as several values were obtained in each year.

5.3.4.4 Fitness consequences

We also evaluated whether the plant phenology variables or the measures of time-lags could have fitness consequences on calves. To do so, two females' reproductive success attributes were used, such as the birth weight of her calves ('BirthWeight$_t$') and the first-summer survival of her calves ('Surv$_t$'). Given that early-born calves are also heavier (Eloranta and Nieminen 1986), we have corrected the calves' birth weight by their respective calving date, by extracting the residuals of the linear model of calves' birth weight fitted against calves' calving date. The causes of death of a calf excluded from the analyses were those with 'no information' or 'slaughtered'. The values for the survival of a calf ranged from 0: dead during calving season to 1: survived to autumn (at the time of the round-up in September). Then, we performed LMMs for BirthWeight$_t$, with females' identity only entered as a random factor on the intercept and plant phenology

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variables added one by one in the model and their influence assessed by looking at their estimate and the associated 95% CI. The same protocol was used with $Surv_t$ but by fitting Generalized Linear Mixed-effects Models (GLMMs), with a binomial error structure and a logit link. Analyses were performed in R 3.6.0 (R Development Core Team 2019).

5.4 Results

5.4.1 Temporal trends and correlation tests

During the whole study period (1970–2015), the end of the thermal growing season ($ThermalEnd_t$) remained unchanged, whereas the start of the thermal growth ($ThermalStart_t$) occurred earlier over time (Figure 5.1a), resulting in a significant lengthening of the thermal growing season in the study area (Table 5.1). During the last part of the study period (1997–2015), neither the onset of the vegetative growing season ($VegOnset_t$), nor the end in autumn ($VegEnd_t$) changed over time and as a consequence, the $LVGS_t$ did not vary over these years (Table 5.1). During the same study period (1997–2015), however, the start of the thermal growing season has advanced by 15 days, while the end date did not vary (Table 5.1).

The start of the thermal growing season was highly correlated to the start of the vegetative growing season estimated with birch onset of leafing (Figure 5.2 and Table 5.2), with $VegOnset_t$ occurring on average 2.5 days earlier than $ThermalStart_t$. The correlation between the end of the thermal growing season and end of the vegetative growing season in autumn was lower but still significant (Figure 5.2 and Table 5.2), with $VegEnd_t$ being followed by $ThermalEnd_t$ by on average 21 days. The correlation between $LTGS_t$ and $LVGS_t$ was non-statistically significant (Figure 5.2 and Table 5.2). The lack of statistical power by having too few years for the vegetative growing season might explain why no statistically significant temporal trends were detected for either $VegOnset_t$, $VegEnd_t$ or $LVGS_t$ (Table 5.2). Following the reported temporal trends in Table 5.1, the calving date, BCI of females in autumn, winter and spring, $ThermalStart_t$ and $LTGS_t$ were detrended and then standardized for further analyses, while the other variables of the whole study period (proportion of males, population density and $ThermalEnd_t$) were only standardized. The calving date, females' BCI in autumn, winter and spring, population density and $ThermalStart_t$ were detrended for the last study period and then standardized for further analyses, while $ThermalEnd_t$, $LTGS_t$, $VegOnset_t$, $VegEnd_t$, $LVGS_t$ and proportion of males were only

standardized. Calving dates have occurred 6.5 days earlier (Figure 5.1b) during the whole study period and 9.2 days earlier during the last part of the study period.

Table 5.1 Temporal trends of plant phenology variables, mean calving date (calvdate$_t$) and population variables from the reindeer herd of the Kutuharju field reindeer research station in Kaamanen, northern Finland.

Variables		Estimate	SE	95% CI	Total change over the study period
1970–2015					
Thermal growing season	ThermalStart$_t$	-0.24	0.08	**-0.41, -0.08**	**– 11 days**
	ThermalEnd$_t$	0.09	0.13	-0.17, 0.35	+ 4.1 days
	LTGS$_t$	0.34	0.14	**0.04, 0.63**	**+ 15 days**
Calving season	calvdate$_t$	-0.14	0.04	**-0.23, -0.06**	**– 6.5 days**
Population variables	BCIAutumn$_{t-1}$	0.29	0.04	**0.21, 0.38**	**From -8.4 to 4.8**
	BCIWinter$_t$	0.32	0.04	**0.24, 0.39**	**From -8.8 to 5.6**
	BCISpring$_t$	0.31	0.07	**0.16, 0.45**	**From -9.1 to 4.8**
	PM$_{t-1}$	0.0002	0.001	-0.001, 0.002	From 16% to 17%
	DENS$_{t-1}$	-0.04	0.19	-0.42, 0.34	– 1.8 individuals
1997–2015					
Thermal growing season	ThermalStart$_t$	-0.84	0.28	**-1.44, -0.25**	**– 15 days**
	ThermalEnd$_t$	0.04	0.43	-0.86, 0.95	+ 0.8 days
	LTGS$_t$	0.89	0.47	-0.10, 1.87	+ 16 days
Vegetative growing season	VegOnset$_t$	-0.89	0.44	-1.83, 0.06	– 16 days
	VegEnd$_t$	-0.41	0.34	-1.13, 0.30	– 7.5 days
	LVGS$_t$	0.007	0.76	-1.65, 1.66	+ 0.12 days
Calving season	calvdate$_t$	-0.51	0.13	**-0.77, -0.25**	**– 9.2 days**
Population variables	BCIAutumn$_{t-1}$	0.36	0.08	**0.21, 0.52**	**From -1.8 to 4.8**
	BCIWinter$_t$	0.38	0.06	**0.26, 0.50**	**From -1.3 to 5.5**
	BCISpring$_t$	0.40	0.13	**0.13, 0.66**	**From -2.4 to 4.8**
	PM$_{t-1}$	0.006	0.003	-0.0007, 0.01	From 9.5% to 21%
	DENS$_{t-1}$	-1.39	0.30	**-2.02, -0.76**	**– 25 individuals**

The parameter estimates (with SE) from linear models with year as a fixed covariate indicate the direction of the change over time of the variables over the whole study period (1970–2015) or just the last part of the study period (1997–2015). ThermalStart and ThermalEnd were the start and the end, respectively, of the thermal growing season. VegOnset and VegEnd represented, respectively, the onset and the end of the vegetative season, estimated by birch phenology. The length of the thermal growing season is depicted by LTGS, while the length of the vegetative season is

represented by LVGS. BCIAutumn was the females' body condition index (BCI) averaged over the autumn (September-October-November), BCIWinter the females' BCI averaged in winter (from December to March) and BCISpring stood for the females' BCI in spring (April-May, see text for details). PM and DENS were, respectively, the proportion of males in the herd and the population density. The estimates in bold type indicated a statistically significant temporal trend (whose 95% CI excluded 0).

Table 5.2 Correlation coefficients between different plant phenology variables used in the study to understand the effects of plant phenology on calving date of a semi-domesticated reindeer population in Kaamanen, northern Finland from 1970 to 2015.

Variables	r	df	95% CI
ThermalStart$_t$ - ThermalEnd$_t$	0.06	44	-0.24, 0.34
ThermalStart$_t$ - VegOnset$_t$	**0.68**	**13**	**0.26, 0.88**
ThermalStart$_t$ - VegEnd$_t$	0.35	16	-0.14, 0.70
ThermalEnd$_t$ - VegOnset$_t$	0.08	13	-0.45, 0.57
ThermalEnd$_t$ - VegEnd$_t$	**0.55**	**15**	**0.10, 0.82**
VegOnset$_t$ - VegEnd$_t$	-0.001	12	-0.53, 0.53
LTGS$_t$ - LVGS$_t$	0.38	12	-0.19, 0.76

Pearson's correlation tests were used to determine the correlation coefficients between the plant phenology variables. The estimates in bold type indicated a statistically significant correlation between the two variables (whose 95% CI excluded 0). ThermalStart, ThermalEnd and LTGS estimated, respectively, the start, end and length of the thermal growing season in the study area. VegOnset, VegEnd and LVGS depicted, respectively, the onset, end and length of the vegetative growing season in the study area, estimated by birch phenology (see text for details).

The mean calving date was on May 19th, with the earliest reported peak calving date having occurred on May 10th in 2010 and the latest on May 30th in 1973. The average calving occurred 16 days prior to ThermalStart$_t$ (mean = 16.2 days, 95% CI [4.58, 28.5]) and two weeks prior to VegOnset$_t$ (mean = 14.4 days, 95% CI [2.59, 24.1]). The ThermalEnd$_t$ occurred almost four months and half after mean calving date the same calendar year (mean = 134 days, 95% CI [118, 152]), and the end of the vegetative season in autumn almost four months after mean calving date (mean = 115 days, 95% CI [106, 124]).

For the whole study period (1970–2015), a total of 1,644 observations were analyzed and two competing models were selected (Table 5.3). The model-averaged estimates of the two best models revealed that calving date occurred earlier when the proportion of males in the herd (PM$_{t-1}$) was higher and the population density (DENS$_{t-1}$) was lower (Table 5.4), as expected from the literature. Calving dates were also occurring earlier when the start of the thermal growing season the previous calendar year (ThermalStart$_{t-1}$), as well as the end of the previous thermal growing season (ThermalEnd$_{t-1}$) were earlier (Figure 5.1a, b) and when the body condition index of females in winter (BCIWinter$_t$) was higher (Figure 5.1c, Table 5.4). The interaction term between ThermalEnd$_{t-1}$ and BCIWinter$_t$ was also statistically significant, indicating that a later ThermalEnd$_{t-1}$ by compromising the females' BCI in winter (Figure 5.1d) contributed to delay the calving dates the following calving season (Table 5.4).

For the last part of the study period (1997–2015), a total of 606 observations were analyzed and two competing models were also selected (Table 5.3). The model averaging showed that an earlier onset (VegOnset$_{t-1}$) and end (VegEnd$_{t-1}$) of the vegetative growing season the previous calendar year resulted in earlier calving dates the next calving season (Figure 5.1e, f, Table 5.4). Also, a higher females' BCI in spring (BCISpring$_t$) just before the calving season induced earlier calving dates (Figure 5.1g) and the statistically significant interaction term between BCISpring$_t$ and VegOnset$_{t-1}$ indicated that a later VegOnset$_{t-1}$ the previous spring season by compromising the females' BCISpring$_t$ the next year (Figure 5.1h) lead to late calving dates (Table 5.4).

Among the four measures of time-lags, none presented a statistically significant temporal trend, meaning that the time lags between calving date and start of the thermal (ThermalStart$_t$) and

vegetative (VegOnset$_t$) growing season remained unchanged over the years, as well as between calving date and end of the thermal (ThermalEnd$_{t-1}$) and vegetative (VegEnd$_{t-1}$) growing season, being for one or the other of the two study periods.

Table 5.3 Competing linear mixed-effects models of the effects of plant phenology on calving date of a semi-domesticated reindeer population in Kaamanen, northern Finland.

Rank	Models	AIC	*df*	AIC weights	ΔAIC
	1970-2015				
1	$zDENS_{t-1} + zPM_{t-1} + dBCIWinter_t \times zThermalEnd_{t-1} + dThermalStart_{t-1}$	4373.78	9	0.71	0.00
2	$zDENS_{t-1} + zPM_{t-1} + dBCIWinter_t \times zThermalEnd_{t-1} + dBCIWinter_t \times dThermalStart_{t-1}$	4375.56	10	0.29	1.78
	1997-2015				
1	$dDENS_{t-1} + zPM_{t-1} + dBCISpring_t \times zVegOnset_{t-1} + zVegEnd_{t-1}$	1658.53	9	0.62	0.00
2	$dDENS_{t-1} + zPM_{t-1} + dBCISpring_t \times zVegOnset_{t-1} + dBCISpring_t \times zVegEnd_{t-1}$	1659.50	10	0.38	0.98

The analyses were repeated over the two study periods: the whole study period (1970–2015) and the last part of the study period (1997–2015). All models included the female identity as a random factor on the intercept, as well as the population density (DENS) and the proportion of males in the herd (PM) as fixed effects. A lowercase 'd' in front of the variable indicated that the variable was used 'detrended', while a lowercase 'z' indicated that the variable was used standardized. ThermalStart and ThermalEnd represented, respectively, the start and end of the thermal growing season. The onset and end of the vegetative growing season were depicted by VegOnset and VegEnd, respectively. BCIWinter was the body condition index (BCI) of females averaged over the winter (from December to March), while BCISpring was the BCI of females, averaged in spring (April-May). A cross 'x' indicated an interaction term between the two variables. The models presented in the table are the competing models retained in explaining calving date, i.e. with ΔAIC < 2 (see text for details).

Table 5.4 Model-averaged estimates of fixed effects from the linear mixed-effects models of calving date of a reindeer population in relation to plant phenology in Kaamanen, northern Finland.

Variable	Estimate	Unconditional SE	Nbr models	95% CI
1970-2015				
$zDENS_{t-1}$	**0.23**	0.03	2	**0.17, 0.29**
zPM_{t-1}	**-0.09**	0.02	2	**-0.14, -0.04**
$dBCIWinter_t$	**-0.20**	0.03	2	**-0.25, -0.14**
$dThermalStart_{t-1}$	**0.10**	0.02	2	**0.05, 0.15**
$zThermalEnd_{t-1}$	**0.12**	0.02	2	**0.07, 0.16**
$dBCIWinter_t \times zThermalEnd_{t-1}$	**0.06**	0.02	2	**0.02, 0.10**
$dBCIWinter_t \times dThermalStart_{t-1}$	-0.01	0.02	1	-0.06, 0.03
1997-2015				
$dDENS_{t-1}$	-0.08	0.07	2	-0.21, 0.06
zPM_{t-1}	-0.06	0.04	2	-0.14, 0.03
$dBCISpring_t$	**-0.33**	0.06	2	**-0.45, -0.22**
$zVegOnset_{t-1}$	**0.10**	0.05	2	**0.0006, 0.20**
$zVegEnd_{t-1}$	**0.47**	0.04	2	**0.38, 0.55**
$dBCISpring_t \times zVegOnset_{t-1}$	**-0.18**	0.06	2	**-0.31, -0.06**
$dBCISpring_t \times zVegEnd_{t-1}$	-0.05	0.04	1	-0.13, 0.04

The estimates in bold type were deemed important (whose 95% CI excluded 0) in explaining calving date. "Nbr models" is the number of models (out of the two best models in Table 5.3) including that variable. The analyses were repeated over the two study periods: the whole study period (1970–2015) and the last part of the study period (1997–2015). All models included the female identity as a random factor on the intercept. A lowercase 'd' in front of the variable indicated that the variable was used 'detrended', while a lowercase 'z' indicated that the variable was used standardized. The predictor variables were the following: population density (DENS), proportion of males in the herd (PM), start and end of the thermal growing season (ThermalStart and ThermalEnd, respectively), onset and end of the vegetative growing season (VegOnset and VegEnd, respectively), body condition index (BCI) of females averaged over the winter (from December to March, BCIWinter) and BCI of females, averaged in spring (April-May, BCISpring). A cross 'x' indicated an interaction term between the two variables.
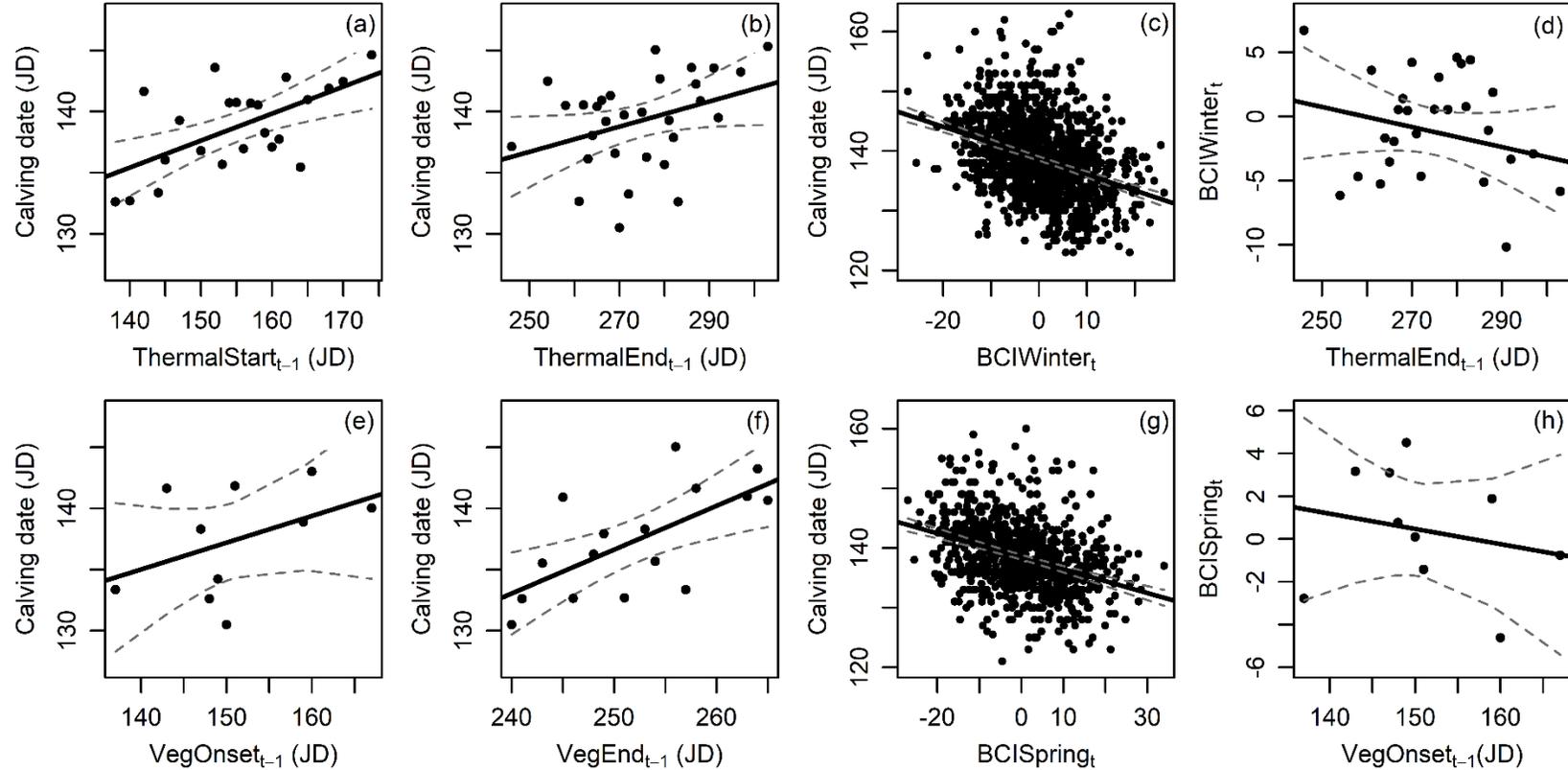
Figure 5.1 Lagged effects of plant phenology on calving date of the Kutuharju reindeer population in Kaamanen, northern Finland. For the whole study period (1970–2015), earlier calving dates were observed when (a) the start (ThermalStart$_{t-1}$) and (b) end (ThermalEnd$_{t-1}$) of the previous thermal growing season were earlier, and when (c) the females' physical condition in winter (December-March) was higher (BCIWinter$_t$). The females' physical condition in winter was deteriorated when ThermalEnd$_{t-1}$ was later (d). For the last part of the study period (1997–2015), earlier calving dates were observed when (e) the onset (VegOnset$_{t-1}$) and (f) end (VegEnd$_{t-1}$) of the previous vegetative growing season were earlier, and when (g) the females' physical condition in spring (April-May) was higher (BCISpring$_t$). A decrease in the females' physical condition in spring was observed when VegOnset$_{t-1}$ occurred later (h). All the dates are expressed in Julian day starting from January 1st (JD). The 95% CI band around the fitted line is also presented. Each point represents the averaged value of the response variable per value of the predictor variable for graphical clarity.

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5.4.3   Fitness consequences

The corrected calves' birth weight (BirthWeight$_t$) was increasing over time ($b = 0.02$, 95% CI [0.01, 0.03]), as well as the calves' first-summer survival (Surv$_t$, $b = 0.06$, 95% CI [0.05, 0.07]). BirthWeight$_t$ was therefore used detrended in the following analyses, while Surv$_t$ was unaltered to preserve its binomial structure. For the whole study period (1970–2015), the BirthWeight$_t$ was higher when the start of the previous thermal growing season (ThermalStart$_{t-1}$) was earlier, when the length of the previous thermal growing season (LTGS$_{t-1}$) was shorter and when the time-lag between calving date and onset of the thermal growing season (TL$_{ThermalStart}$) the previous calendar year was longer (Table 5.5). A longer TL$_{ThermalStart}$ can be due to an earlier calving date or a later ThermalStart$_{t-1}$. Given that ThermalStart$_{t-1}$ was occurring earlier over time and that BirthWeight$_t$ was positively affected by ThermalStart$_{t-1}$, it would indicate that an earlier calving date more likely caused a higher birth weight of calves. The calves' first-summer survival (Surv$_t$) was higher when ThermalStart$_t$ was earlier, when ThermalEnd$_{t-1}$ was earlier and finally when LTGS$_{t-1}$ was shorter (Table 5.5). None of the measures of time-lags (TL$_{ThermalStart}$ or TL$_{ThermalEnd}$) affected Surv$_t$.

For the last part of the study period (1997–2015), heavier new-born calves (corrected by the calving date) were observed when ThermalEnd$_{t-1}$ was earlier, LTGS$_{t-1}$ was shorter, the onset of the vegetative growing season (VegOnset$_{t-1}$) was earlier, and the TL$_{ThermalEnd}$ was longer (Table 5.5). A longer TL$_{ThermalEnd}$ indicates either a later calving date or an earlier ThermalEnd$_{t-1}$. Given that BirthWeight$_t$ is negatively correlated to ThermalEnd$_{t-1}$ and that early-born calves are also heavier ($b = -0.02$, 95% CI [-0.03, -0.02]), it would most likely indicates that an earlier ThermalEnd$_{t-1}$ lead to heavier calves. A higher calves' first-summer survival was observed when VegOnset$_t$ was earlier, the time-lag between calving date and ThermalStart$_t$ (TL$_{ThermalStart}$) was longer and the time-lag between calving date and ThermalEnd$_{t-1}$ (TL$_{ThermalEnd}$) was shorter (Table 5.5). Given that Surv$_t$ was negatively correlated with VegOnset$_t$ and that early-born calves have a higher first-summer survival ($b = -0.06$, 95% CI [-0.07, -0.04]), the positive correlation between TL$_{ThermalEnd}$ and Surv$_t$ would most likely be due to an earlier calving date. A shorter TL$_{ThermalEnd}$ indicates either an earlier calving date or a later ThermalEnd$_{t-1}$. An earlier calving date would more likely contributes to a higher Surv$_t$ as Surv$_t$ was negatively affected by ThermalEnd$_{t-1}$ in the whole study period. As expected from the literature, heavier new-born calves had a higher first-summer survival ($b = 0.94$, 95% CI [0.79, 1.09]).

Table 5.5 Fitness consequences of the lagged effects of plant phenology on the birth weight (BirthWeight$_t$) and first-summer survival (Surv$_t$) of calves of the Kutuharju reindeer herd in northern Finland.

	BirthWeight$_t$			**Surv$_t$**	
	b	**95% CI**		*b*	**95% CI**
1970–2015			**1970–2015**		
dThermalStart$_{t-1}$	-0.07	-0.11, -0.03	dThermalStart$_t$	-0.20	-0.32, -0.07
zTL$_{ThermalStart}$	0.09	0.04, 0.13	zThermalEnd$_{t-1}$	-0.13	-0.25, -0.01
dLTGS$_{t-1}$	-0.04	-0.08, -0.002	dLTGS$_{t-1}$	-0.39	-0.52, -0.26
1997–2015			**1997–2015**		
zVegOnset$_{t-1}$	-0.09	-0.15, -0.02	zVegOnset$_t$	-0.40	-0.71, -0.11
zThermalEnd$_{t-1}$	-0.18	-0.25, -0.12			
zLTGS$_{t-1}$	-0.17	-0.23, -0.10	zTL$_{ThermalStart}$	0.34	0.08, 0.60
zTL$_{ThermalEnd}$	0.20	0.14, 0.27	zTL$_{ThermalEnd}$	-0.31	-0.60, -0.02

The analyses were repeated over the two study periods: the whole study period (1970–2015) and the last part of the study period (1997–2015). All models included the female identity as a random factor on the intercept. A lowercase 'd' in front of the variable indicated that the variable was used 'detrended', while a lowercase 'z' indicated that the variable was used standardized. The predictor variables were the following: start and end of the thermal growing season (ThermalStart and ThermalEnd, respectively), onset of the vegetative growing season (VegOnset), length of the thermal growing season (LTGS), time-lag between calving date and ThermalStart (TL$_{ThermalStart}$) and time-lag between calving date and ThermalEnd the previous calendar year (TL$_{ThermalEnd}$).

5.5 Discussion

As predicted, the time-lag between calving date of the Kutuharju reindeer population and onset of the thermal or vegetative growing season did not change over time. As already reported in other ungulate populations, the onset in spring of both the thermal and vegetative growing season affected calving date (Figure 5.1a, e), with a lagged effect of one year (Table 5.4). Calving date was also affected by the end, in autumn, of the previous thermal and vegetative growing season (Figure 5.1b, f). Although the end of the thermal and vegetative growing season did not significantly change over time (Table 5.1), a delay in ThermalEnd$_{t-1}$ caused females' physical condition in winter to be deteriorated (Figure 5.1d) and then caused a delay in calving date the following calving season (Table 5.4). While an earlier ThermalStart and VegOnset was beneficial to females' reproductive success with an increase in both calves' birth weight and calves' first-summer survival, a delay in ThermalEnd$_{t-1}$ was detrimental (Table 5.5). This is consistent with the suggestion that potential lagged effects of plant phenology arising in late summer and autumn, when females store nutrient reserves to finance reproduction (Barboza and Parker 2008) can also lead to consequences on reproductive success than at parturition due to the capital breeder strategy of *Rangifer* and its reliance on maternal capital (Taillon et al. 2013; Gustine et al. 2017; Williams et al. 2017).

5.5.1 *Keeping up with the onset of spring phenology*

Contrary to temporal trends reported in other northern ecosystems (Oberbauer et al. 2013; Park et al. 2016) and despite warmers temperatures in April and May in our study area over the last 45 years (see Paoli et al. 2018), the VegOnset$_t$ has not advanced (Table 5.1). An earlier ThermalStart$_t$ was, however, reported for the two study periods, with a statistically significant advancement of 11 days from 1970 to 2015 (-0.24 days.yr^{-1}) and of 15 days from 1997 to 2015 (-0.84 days.yr^{-1}, Table 5.1). Despite this temporal trend and as predicted in our first hypothesis, there was no evidence of a developing time-lag between the parturition date and the onset of spring vegetative phenology in this semi-domesticated reindeer population, as previously reported in Alaskan caribou (Gustine et al. 2017). Although the rate of advancement for calving date was much lower for those two study periods, -0.14 days.yr^{-1} for the whole study period and -0.51 days.yr^{-1} for the last part of the study period (Table 5.1), the results indicated that the pace of advancement of reindeer calving date of the Kutuharju herd was so far keeping up with the pace

of advancement in onset of the spring green-up in that area. A high correlation was found between the mean temperature in April-May in our study area and both the onset of the thermal and vegetative growing season (respectively $r = -0.50$, 95% CI [-0.69, -0.24] and $r = -0.86$, 95% CI [-0.95, -0.57]). Moreover, earlier calving dates in the same reindeer population have recently been found to be associated with warmer temperatures in April-May (see Paoli et al. 2018). The mean temperature in April-May being a good predictor of onset of the spring vegetative season, earlier calving dates would have thus concurred with earlier spring green-up. The physiological mechanisms of how such fine adjustment in reindeer calving date is however uncertain. The females' physical condition in spring was improved when the onset of the vegetative growing season one year ago was earlier (Figure 5.1h). A lagged effect of plant phenology in spring the previous year acting on BCISpring$_t$ the next year might thus be involved. Perhaps a compensatory mechanism, as highlighted in numerous species (Rachlow and Bowyer 1991; Cameron et al. 1993; Flydal and Reimers 2002), has favored shortened gestation lengths when females' physical condition in late pregnancy was improved following warmer temperatures in April-May ($b = 0.68$, 95% CI [0.40, 0.97]). On top of that, an earlier VegOnset$_{t-1}$ by allowing the females to calf earlier the previous year might have benefit them as being able to nurse on a high-quality forage for a longer period of time (Festa-Bianchet 1988; Rachlow and Bowyer 1994). As a cascading effect, their body condition the next spring was improved and they could again calf earlier (Figure 5.1g). The previous year's reproductive status has already been shown to affect variation in birth date (Guinness et al. 1978) but this study demonstrates that, as suspected, it was indeed acting through female body condition. Furthermore, a bottom-up trophic effect caused by spring plant phenology the previous year might explain why the effect on females' physical condition in April-May could be observed one year after (as shown for the AO index on reindeer population growth in Aanes et al. 2002).

5.5.2   Calving date constrained by the plant phenology in autumn

Confirming our second hypothesis, the calving date was also affected by ThermalEnd$_{t-1}$ and VegEnd$_{t-1}$ (Figure 5.1b, f). The timing of birth in a Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*) population was shown to be shaped by onset of autumn more than onset of spring and concurs with our findings (Kourkgy et al. 2016). Although this semi-domesticated reindeer population receives supplemental feeding in late winter to buffer the harshness of winter

conditions, it suggests that both wild and domesticated animal populations could also be influenced by the end of the plant growing season in autumn. More studies on autumn phenology are however needed to state this with certainty. The timing of parturition in ungulate species is related to either autumn or over-winter physical condition of females (Cameron et al. 1993; Cook et al. 2004) and it is assumed that variable calving dates might result from nutritionally related differences in gestation length (Bergerud 1975; Berger 1992). In our study, the females' physical condition in winter (from December to March), when females rely on maternal capita to support gestation costs, was improved when the end of the previous vegetative growing season in autumn was later (Figure 5.1d). Caribou and reindeer are capital breeders (Taillon et al. 2013), with females building nutritional reserves in late summer/autumn to finance reproduction (Barboza and Parker 2008). As such, the end of the vegetative season in the autumn by influencing females' physical condition in winter and therefore maternal body stores for foetal development (Barboza and Parker 2008; Williams et al. 2017) would also be of great importance in influencing future calving dates.

Contrary to our third hypothesis, however, the time-lag between calving date and either $ThermalEnd_{t-1}$ or $VegEnd_{t-1}$ did not significantly change over time. Too few years available to measure $VegEnd_{t-1}$ might explain why, despite a high rate of change (-0.41 days.yr^{-1}), the temporal trend was not statistically significant. Furthermore, the correlation of 55% between $ThermalEnd_{t-1}$ and $VegEnd_{t-1}$ confirmed that the autumn phenology is much harder to estimate from climatic variables as temporal change in the autumn seems less apparent and with more heterogeneous patterns (Walther et al. 2002; Walther and Linderholm 2006). The thermal growing season indices can only estimate the real growing season to some extent (Walther and Linderholm 2006), given that the birch phenological data was limited to a shorter period. The use of various indices to estimate the thermal growing season can also lead to remarkable differences in the long-term (Walther and Linderholm 2006). That $VegOnset_{t-1}$ and $VegEnd_{t-1}$ better explained the variation in calving date during the second part of the study period (1997–2015) than $ThermalStart_{t-1}$ and $ThermalEnd_{t-1}$ (Table 5.4) also points out that actual observations on birch phenology are more relevant at depicting biological events than indices of the thermal growing season as some discrepancies might be observed between the thermal and vegetative growing season (Walther and Linderholm 2006).

5.5.3 Fitness consequences

Heavier calves and calves with a better first-summer survival were observed when the start of the thermal growing season was earlier for the whole study period (1970–2015) and when the onset of the vegetation growth was earlier for the last part of the study period (1997–2015). A one-year lagged effect of $ThermalStart_{t-1}$ and $VegOnset_{t-1}$ on $BirthWeight_t$ was observed (Table 5.5), certainly because as stated earlier, an earlier $VegOnset_{t-1}$ or $ThermalStart_{t-1}$ would allow the females to calf earlier the previous year, to free themselves from the 'burden' of lactation earlier in the summer so that they are able to replenish their body fat reserves faster in summer (Skogland 1983). As a calf's birth weight is highly dependent on her mother's food intake and body weight (Bergerud 1975; Cameron et al. 1993; Côté and Festa-Bianchet 2001; Solberg et al. 2007), an earlier $VegOnset_{t-1}$ or $ThermalStart_{t-1}$ would have contributed to improve the females' body weight at the time of calving (Pettorelli et al. 2005) and, in turn, to produce heavier calves. A higher calves' survival was also reported when the onset of spring green-up was earlier the same year ($ThermalStart_t$ or $VegOnset_t$, Table 5.5). Early-born calves are also heavier and then enjoy a higher survival because they benefit not only a longer growing season but also from the high-quality resources available for growth (Bunnell 1982; Festa-Bianchet 1988; Feder et al. 2008). In short summer growth environments, the transfer of energy and protein through maternal milk in sufficient quantity and in a short amount of time is critical for calf's growth and survival (Kumpula and Nieminen 1992; Parker et al. 1990; Sadleir 1969). Ruminants, such as reindeer, are believed to be more selective on forage quality than forage quantity (Tveraa et al. 2013) because females calving earlier produce milk from forage of early phenology, with lower fiber content and higher digestibility (Rachlow and Bowyer 1991). A milk with a higher protein content from a high-quality forage is thus crucial for females' reproductive success (Chan-McLeod et al. 1994; Festa-Bianchet 1988; Rachlow and Bowyer 1994) by increasing the quality and quantity of resources available for calves' growth (Kumpula and Nieminen 1992; Parker et al. 1990). As previously shown in reindeer (Tveraa et al. 2013), the females' reproductive success in our study was thus positively affected by the onset of spring green-up, certainly through a positive effect of forage quality on the females' physical condition during late gestation and, in turn, on calving date and milk production (Chan-McLeod et al. 1994; Rachlow and Bowyer 1991; Cameron et al. 1993).

Despite longer thermal growing seasons benefiting the calves' birth weight and survival (Table 5.5), a 'too late' end of the thermal growing season seemed to negatively affect those

females' reproductive success components (Table 5.5). Indeed, a decrease in calves' birth weight was reported for the last part of the study period (1997–2015) and in calves' first-summer survival for the whole study period (1970–2015) when ThermalEnd$_{t-1}$ was occurring later. This finding seems counter-intuitive given that a later ThermalEnd$_{t-1}$ would favor a longer growing period for the calves before facing their first winter. Since the main determinant of calving date in ungulates is the conception date (Holand et al. 2002; Clements et al. 2011), an inadequate nutrition in autumn would be detrimental to females' body condition and cause a subsequent delay in calving dates (Cook et al. 2004). Late-born calves were then reported to be lighter and with a lower first-summer survival. Mushrooms are an important and preferable source of food for reindeer during the late summer (end of July, beginning of August throughout September) up to early winter (October-December) (Kitti et al. 2006; Inga 2013), with their abundance having a considerable effect on reindeer body condition (JK: personal communication). The ideal growing conditions for mushrooms demand humidity and relatively cool temperatures. A warming trend in September-October ($b = 0.04$, 95% CI [0.02, 0.06]) coinciding with a later ThermalEnd$_{t-1}$ ($r = 0.61$, 95% CI [0.39, 0.77]) might therefore be detrimental to mushrooms development due to heat stress. As a consequence, the mean autumn fruiting date for both mycorrhizal and saprotrophic fungi in Norway is now later (Kauserud et al. 2008, 2012), with an accelerated delay of fruiting in the last 20 years that has coincided with global warming (Kauserud et al. 2008). In those exceptionally warm years, when the mushroom abundance is reduced and delayed due to deteriorated conditions for their growth, females might not be able to gain as much fat as in regular years and a decreased physical condition in autumn was then observed following a later ThermalEnd$_{t-1}$ ($b = -0.06$, 95% CI [-0.09, -0.03]). The level of fatness and protein reserves attained by autumn control conception rate (Cameron et al. 1993; Reimers 1997; Barboza and Parker 2008) and thus affect reproductive effort (Weladji et al. 2002b). The coincidence of warmer temperatures in September-October with a late ThermalEnd$_{t-1}$ would have thus caused an impaired physical condition of females near the breeding time leading to a delay in calving date (Figure 5.1b) and a decrease in calves' BirthWeight$_t$ and Surv$_t$ the following calving season (Table 5.5). In summary and contrary to our expectations, a lengthening of the thermal growing season (Table 5.1), consistent with long-term trends reported in northern ecosystems (Oberbauer et al. 2013; Park et al. 2016) is not necessarily beneficial for reindeer if a later end is accompanied by a reduced abundance of mushrooms. Our study can therefore be added to the growing body of literature on the MMH and how species are

able to adapt to climate change. The consequences of developing lagged effects of plant phenology on species' reproductive success are, however, still much contrasted among ungulates, an area that deserve further investigation.

5.6 Appendices
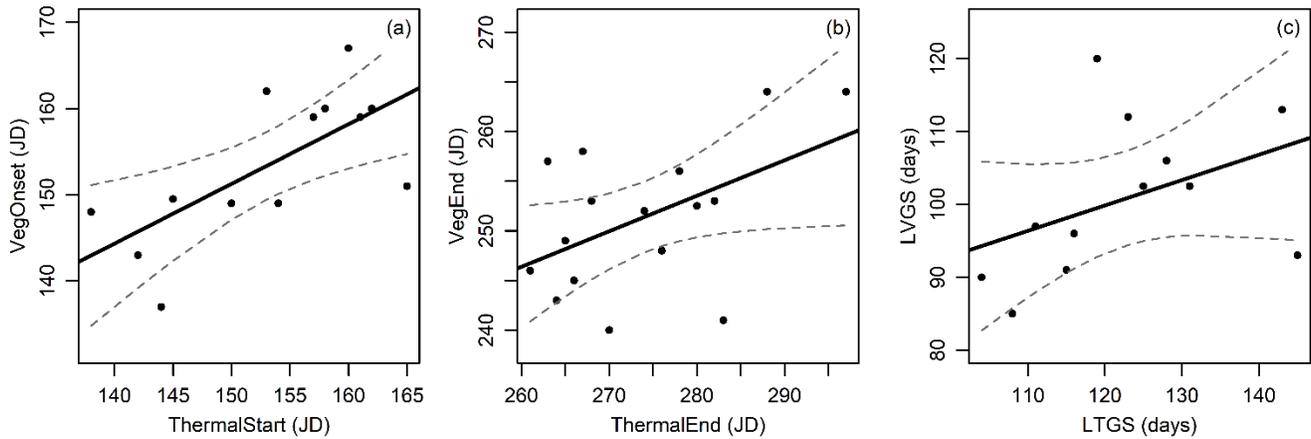
Figure 5.2 Relationship between (a) the start of the thermal growing season (ThermalStart) and the start of the vegetative growing season (VegOnset), (b) the end of the thermal growing season (ThermalEnd) and the end of the vegetative season (VegEnd) and (c) the length of the thermal growing season (LTGS) and the length of the vegetative growing season (LVGS) of the Kaamanen area, northern Finland from 1997 to 2015. The dates are expressed in Julian day (JD). The data on the thermal growing season were obtained from daily average temperatures, while the vegetation phenology was assessed using the phenology of deciduous birch (*Betula pubescens*).

Chapter 6 General Discussion

The objective of this thesis was to study how breeding phenology in reindeer was influenced by climatic variability and its changing environment. For that purpose, I identified the climatic variables influencing the most calving phenology (both calving time and synchrony, Chapter 2) and mating time (Chapter 3). Then, I assessed whether females all adjusted their calving dates in the same way in response to climatic variability and if not, which females' attributes early in life could determine such between-individual heterogeneity (Chapter 4). At last, I tested the match-mismatch hypothesis on reindeer to verify if the rate of advancement in reindeer calving date matched the rates of change in plant phenology at two different periods of the year: in spring and in autumn (Chapter 5). Below, I review the main findings of my research as well as their implications for further studies.

6.1   Breeding phenology in response to climatic variability

In the Arctic ecosystem, where a warming two to three times higher than the increase of the global mean surface temperature was reported (IPCC 2013) and where changes in climate are more pronounced than in lower altitudes (Weladji et al. 2002a), the reproductive phenology of *Rangifer* species has changed (see Chapter 2 and 3). In the present study, I showed that calving dates in the Kutuharju reindeer population have advanced by 6.8 days from 1970 to 2015 (-0.15 days.yr^{-1}, Chapter 2), while the males' timing of rutting activities started 10 days earlier in 2011 than in 1996 (-0.64 days.yr^{-1}, Chapter 3) and the females' copulation dates occurred 11 days earlier in 2013 than in 1996 (-0.72 days.yr^{-1}, Chapter 3). For a species with highly temporally synchronized breeding seasons (most of the conceptions and births occur in a 10-day period, for a 4-5 weeks long mating and calving season, Lent 1966; Dauphiné and McClure 1974; Bergerud 1975; Eloranta and Nieminen 1986), such changes in the reproductive phenology are quite considerable. In other mammal studies, a population of red squirrels advanced breeding by 18 days over 10 years from 1989 to 1998 (-1.18 days.yr^{-1}, Réale et al. 2003), the median birth date of a population of cattle (*Bos taurus* L.) became earlier by 1.0 days.yr^{-1} from 1947 to 2008 (Burthe et al. 2011) and six reproductive phenological traits in a red deer population advanced by between 5 and 12 days across a 28-year study period from 1980 to 2007 (-0.18 to -0.43 days.yr^{-1}, Moyes et al. 2011). In an Alaskan Arctic caribou population, the timing of onset of calving (date of 5% births) has advanced by 3.82 days between 1993 and 2006 (-0.29 days.yr^{-1}, Post and Forchhammer

2008). Several conclusions can be drawn from those studies: (1) the phenology of the mating season is far less studied than the phenology of the birth season; (2) the rates of changes in the reproductive phenology of mammals are species-specific; (3) the climatic-induced changes in the scheduling of reproductive events may be more extensive than previously thought. Indeed, changes in the reproductive phenology following large climatic changes were reported in natural (caribou, red deer, squirrel) or domesticated (cattle, reindeer) populations; seasonal (caribou, red deer, reindeer) or year-round (cattle) breeders; small (squirrel) or large (caribou, cattle, red deer, reindeer) mammals; temperate (cattle, red deer) or Arctic/subarctic (caribou, reindeer, squirrel) species.

It appears however that studies quantifying the phenological changes in reproduction in relation to climatic variability are still scarce in large herbivores, while it could help us better predict the species' viability in a context of extreme climatic variability reported the last decades. The lack of such studies comes from the difficulty to have access to long-term continuous records of reproductive traits on species with relatively long generation times such as reindeer and in most cases, available data are just reaching 20–30 years in duration (Boutin and Lane 2014). I therefore suggest for future studies that (1) the phenological changes in the mating season also have to be considered as mating phenology being the main determinant of the following calving phenology of ungulate species (Holand et al. 2002; Clements et al. 2011); and (2) phenology-associated changes should be reported even if only short-term studies of populations covering less than two decades are available. The projected Earth's global warming of the 21st century is 5-9 times greater than that of the past century (IPCC 2007) and therefore the climate fingerprint (Parmesan and Yohe 2003; Root et al. 2003) of global warming on animal and plant species should be more pronounced in the last decade.

Despite the reproductive timing being mainly triggered by photoperiod in mammalian species, this study also showed that other environmental factors can modulate it (Goldman 2001; Lincoln et al. 2003, 2006; Rosa and Bryant 2003; Bronson 2009). Indeed, the advancement in calving dates concurred with reported climatic trends of warmer temperatures in April-May, and lower precipitation and a reduced snow cover in April in Kaamanen, northern Finland (Chapter 2). Improved females' physical condition in late gestation due to better climatic conditions in early spring probably favored shortened gestation lengths through a compensatory mechanism, as

highlighted in numerous species (Rachlow and Bowyer 1991; Cameron et al. 1993; Flydal and Reimers 2002). On the other hand, the males' timing of rutting activities occurred earlier with a reduced snow cover in late April and a higher amount of precipitation between late April and late June (Chapter 3). A better vegetation productivity in spring and summer induced by the ongoing climatic changes in Finnish Lapland and its 'ripple effect' on improving males' pre-rut body weight possibly explained the advancement in males' mating time. The females' copulation dates occurred earlier with a decreased amount of snowfalls in the third week of January and a decreased maximum temperature between mid- and end of July (Chapter 3). When the snowfalls increased in January, a compensatory mechanism might be involved, where females extended their gestation length in response to winter nutritional deprivation, causing a delay in the timing of births and the subsequent copulation dates. Females conceived later in autumn following a higher maximum temperature in the last two weeks of July, possibly because warmer maximum temperatures in July caused a decrease in forage quality, along with a higher level of insect harassment, in turn degrading the females' foraging conditions. From those results, we therefore showed that the phenological changes in reproduction of reindeer were mainly triggered by climate-induced changes on the individuals' physical condition, at three key periods in the reproductive cycle of reindeer: winter, late winter/early spring and summer. As such, this study enhances our understanding of the environmental factors modulating the timing of reproduction in large herbivores even if the underlying, physiological mechanisms are still not well understood and deserve to be further investigated.

6.2   Between-individual heterogeneity in plasticity of calving date in reindeer

Despite a population-trend of earlier calving dates with a reduced amount of precipitation in April, I found a slightly between-individual heterogeneity in the magnitude of the plastic response of calving date to the amount of precipitation in April (Chapter 4). Among all the females' attributes early in life tested, none could explain this between-individual variability. In the same population, a lengthening of the calving season was observed following an overall warming weather in January, an increasing number of days when mean temperature exceeds 0°C in October-November and a decreasing snow cover in the period from October to November (Chapter 2). We hypothesized that the lengthening of the calving season following better climatic conditions in October-November and warmer temperatures in January may reflect a reduced plasticity among

low-quality mothers (young and light females), so that they are not able to respond as quickly as high-quality mothers (older and heavier females) do, to favorable climatic conditions in autumn and winter (Chapter 2). The variability in calving synchrony might therefore be due to the inter-individual heterogeneity in the plastic response of calving date to improved climatic conditions in October-November and January. In Chapter 4, I hypothesized that a large intraspecific difference in body condition would be responsible for a between-individual heterogeneity in the plastic response of calving date to climatic conditions as females would be at different physiological state to be more or less phenotypically plastic. Unexpectedly, however, I found that the different plastic responses to the amount of precipitation in April were not influenced by a female's physiological condition or by any of the females attributes early in life tested in this study (Chapter 4). The supplemental feeding given to the animals in late winter, by sustaining the females' body weight above a certain threshold, might have helped females to be physiologically able to respond in a similar manner to climatic conditions in spring as I reported individual-level trends of earlier calving dates following warmer temperatures in May and in April-May and with a reduced amount of precipitation in April (Chapter 4). However, the supplemental feeding would cause females with a very low physical condition not to be represented in this population and by homogenizing the intra-specific difference in body condition could have explained why the females' physical condition alone could not explain the between-individual heterogeneity in the plastic responses of females to the amount of precipitation in April. Either way, it therefore appeared that the causes of the inter-individual heterogeneity in phenotypic plasticity of wild or domesticated populations are very intricate and needs further investigations.

The causes of the high level of plasticity for calving date in the Kutuharju reindeer herd were, however, more apparent as females born later than the population average and that also conceived later at their first calving event will give birth consistently later throughout their reproductive life (Chapter 4). Females with a higher physical condition in spring before their first calving season will also have earlier calving dates throughout their lifetime (Chapter 4). These findings thus indicated that a female starting point when facing climatic changes is best predicted by her own phenotypic quality at birth and all the way up to her first calving event. It also supported the assumption that differences among individuals early in life may contribute to consistent differences in phenotypic value (e.g. mean calving date) observed later on (Nussey et al. 2005a; Stamps 2016). Empirical support for studies enlightening whether plasticity can vary with

experiences early in life is currently sparse and equivocal (Stamps 2016), while the maternal-offspring inheritance of genetic and phenotypic components is well established. Understanding what shapes inter-individual heterogeneity in the plasticity of reproductive event (e.g. calving date, mating time) in response to climatic variability is of great importance for animal species as such heterogeneity in plasticity, if genetically-based, could be under selective pressures (Coulson et al. 2003; Réale et al. 2003; Brommer et al. 2005; Nussey et al. 2005b). The individuals better adapted to the ongoing climatic changes would then be 'selected', favoring the resilience of populations to climate change.

6.3   The match-mismatch hypothesis for reindeer

The Match-Mismatch Hypothesis (MMH; Cushing 1990) has become a very 'trendy' concept as a way to test the temporal mismatch between the peak of resource demands by reproducing animals and the peak of resource availability (Durant et al. 2005, 2007; Post and Forchhammer 2008). To date, the MMH has been applied to test the changing time-lag between the peak (or onset) of calving season in *Rangifer* species and the following spring phenology, with its potential consequences on reproductive success (Tveraa et al. 2013; Veiberg et al. 2016; Gustine et al. 2017). However, the present study demonstrated that mismatches arising in late summer and autumn, when females store nutrient reserves to finance reproduction are as relevant to consider in modulating following calving dates as the onset of vegetation growth that occurs up to three weeks after peak parturition in *Rangifer* species (Barboza and Parker 2008). Indeed, the calving dates were found to be affected by both the onset (in spring), as well as by the end (in autumn) of the thermal and vegetative growing season (Chapter 5). As such, the end of the vegetative season in the autumn by influencing females' physical condition in winter and therefore maternal body stores for foetal development (Barboza and Parker 2008; Williams et al. 2017) was as important for calving dates as the onset of spring green-up and its lagged effect on females' physical condition one year after (Chapter 5). Our results therefore emphasized the need to focus on the potential mismatches arising at key periods of the reproductive cycle of the studied species and that capital breeders, such as reindeer (Taillon et al. 2013), despite relying on maternal capita rather than dietary income to finance reproduction, are still sensitive to between-year variability in plant phenology.

6.4 Fitness consequences

In this semi-domesticated reindeer population, assessing the offspring first-winter survival was not feasible because approximately one third of the calves are slaughtered every autumn for meat production. However, the first-summer survival of calves has been monitored and we found that calves who survived the summer had earlier birth dates than calves who died either at birth, after one day, one week or later in the summer (Chapter 2). Across the 45-year study period (1970–2015), we also found that calving dates in female reindeer were estimated to have advanced by 6.8 days (Chapter 2), calves' birth weight to have increased from 4.9 to 6.3 kg ($b = 0.03$, 95% CI [0.02, 0.04]; Figure 6.1a), calves' first-summer survival to have improved from 0.64 to 0.99 ($b = 0.008$, 95% CI [0.004, 0.011]; Figure 6.1b) and calf annual recruitment to have increased from 24 to 83% ($b = 1.34$, 95% CI [0.80, 1.88]; Figure 6.1c). An earlier males' timing of rutting activities and earlier copulation dates in females also induced earlier calving dates the following calving season (Chapter 3). At first sight, it therefore appeared that the reproductive success of females and the population's recruitment rate were improving over time and that climatic changes reported in Finnish Lapland were not impairing reindeer's reproduction.

Yet, an inter-individual heterogeneity in reproductive success could be observed (Chapter 4). Indeed, a reproductive advantage was observed for females born earlier, that conceived earlier at their first calving event and with a higher physical condition in spring before their first calving season as they gave birth consistently earlier throughout their reproductive life (Chapter 4). This "head-start" advantage was maintained throughout their lifetime as they also gave birth to heavier calves, calves with a better first-summer survival and to more calves (Chapter 4). Females who advanced their calving dates in response to an increasing amount of precipitation in April also had a slight reproductive advantage by giving birth to more calves over their reproductive life (Chapter 4). This result first appeared counter intuitive as delaying calving dates when there are more precipitation (snowfalls) in April could be advantageous, allowing the fetus a longer time to grow and develop. From the mother's point of view, however, lengthening the gestation period for too long might increase the risks of death and stillbirth. Based on 227 gestation lengths from 132 different females, I could not find statistically significant correlations between gestation length and the cumulative number of calves that a female produced, the calf's first-summer survival or the calf's birth weight. As the gestation length was not find to affect a female's reproductive

success in this population, another mechanism might be at stake. I also speculated that despite the onset of spring green-up being delayed because of more snowfalls in April, females physiologically able to still advance their calving dates could benefit from a high-quality forage at an earlier stage of lactation, when the reproductive costs are the highest (Clutton-Brock et al. 1989). In this scenario, a bet-hedging strategy might be implicated, where females with a low-risk strategy, by maintaining a constant calving date between years, would minimize the variance in fitness, while females with a high-risk strategy by adjusting their calving date to climatic conditions might have a higher variation in reproductive success. The later strategy seemed to be most advantageous in this herd as females (n = 482) with a higher variation in calving date (given by the coefficient of variation) had on overall more calves born over their reproductive life (r = 0.18, 95% CI [0.08, 0.28]) and calves with a higher birth weight (r = 0.20, 95% CI [0.10, 0.29]) than females with a low-risk strategy (lower variance in calving date). Conditions early in life by shaping a female's lifetime reproductive success would thus have a greater impact on the population's recruitment rate than climatic variation. But if the climatic changes are to exacerbate in the future, some females could become maladapted to their environment and would not be able to compensate by being more phenotypically plastic or by adopting a "risky" strategy.

In that sense, a decrease in females' physical condition in winter was observed following a later end of the thermal growing season. On another hand, a later onset of the vegetative growing season caused the females' physical condition in spring (the year after) to decrease. As a consequence, the females' future reproductive success was lower as lighter newborn calves and calves with a lower first-summer survival the following year were reported (Chapter 5). A possible explanation was that an earlier onset of spring green-up might have allowed females to calf earlier the previous year and to free themselves from the 'burden' of lactation, so that they could replenish their body fat reserves for a longer period of time in summer. Alternatively, the calves born from females calving earlier were advantaged as the maternal dietary protein:energy ratio was shown to affect milk protein (Chan-McLeod et al. 1994). Females feeding on a forage of early phenology, with a high protein content might, in turn, produce a rich-protein milk that was shown to favor calves' growth rate in summer (Parker et al. 1990). The weight gain of calves in summer was also dependent on milk production (Kumpula and Nieminen 1992) and a high inter-individual difference in milk production exists in reindeer (Gjøstein et al. 2004). The differences in reproductive success among females (number of calves in Chapter 4, calves' birth weight and

calves' first-summer survival in Chapter 5) might therefore be accounted by inter-individual differences in milk production and to some extent in milk composition (Chan-McLeod et al. 1994; Gjøstein et al. 2004). However, a long thermal growing season is not necessarily beneficial for reindeer if a later end is accompanied by a reduced abundance of mushroom (Chapter 5). Those unexpected results highlight the need to remain cautious when interpreting the effects of climatic variability on species' reproductive phenology and consequent reproductive success. Even if the population is 'doing rather good' overall, an inter-individual heterogeneity in phenotypic plasticity could be covering a portion of the population being disadvantaged in the future if the Earth's climatic changes were to continue and even accelerate (McCarty 2001; IPCC 2013). Furthermore, as the magnitude and frequency of extreme climatic events are being predicted to increase (McCarty 2001; Coumou and Rahmstorf 2012), animal species might not possess the phenotypic plasticity it would require to adapt. I hence recommend that studies on how the reproductive phenology of species is going to be affected by climatic variation should be pursued, especially in the last decade where climatic changes have been the most extremes for at least a millennium (Coumou and Rahmstorf 2012).

6.5 Conclusion

The reproductive phenology of the semi-domesticated reindeer population of the Kutuharju field reindeer research station has changed in response to climatic variables at different key periods in the reproductive cycle of reindeer: in winter for the calving synchrony and females' copulation dates; in late winter/early spring for the calving time and males' timing of rutting activities; in summer for the females' copulation dates and in autumn for the calving synchrony. The main assumption made in the whole thesis was that the observed relationships between phenology and climatic variables in our study population were interpreted as climate-related changes on individuals' physical condition, impinging on the reproductive phenology. One area for future research would therefore be to elucidate the physiological mechanisms causing the reproductive phenology of mammal species to adapt to variation in their environment; and whether climatic variables such as temperature or precipitation could act as signaling cues to time seasonal breeding.

Then, an inter-individual heterogeneity in the plastic response of females' calving date to the amount of precipitation in April allowed to highlight the importance of studying trait-climate relationships at the individual level and to disentangle population-level from individual-level

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plastic responses to climatic variability. As shown in this thesis, an absence of a population-level trend does not necessarily mean that individuals are not able to respond to their changing climate and vice-versa, an absence of an individual-level trend does not mean that the population lacks plasticity of a particular trait to be able to respond to climatic variability. Contrary to our expectations, however, the inter-individual heterogeneity in phenotypic plasticity was small and we could not find what causes it. Another area for future research would therefore be to conduct experiments to understand whether plasticity can vary (or not) as a function of experiences early in life. But such experiments would better be conducted on species with short generation times.

In contrast, a high plasticity in calving date was observed among females of the Kutuharju reindeer herd. Conditions early in life appeared to strongly shape a female's phenotypic value throughout her reproductive life and as a consequence, her future reproductive success. A maternal-offspring inheritance of genetic and phenotypic components was probably involved. The ancestral knowledge of reindeer herders probably already accounted for this fact given that an artificial selection is under way in this population, selecting for individuals with a better reproductive performance (Holand et al. unpublished). Nonetheless, the ancestral knowledge from reindeer husbandry does not include the large changes in climate recorded in the last decades and the results of this thesis could be applied to fill this gap. Especially given that longer vegetative growing seasons could, unexpectedly, be detrimental to reindeer reproduction as highlighted in this thesis.

The take-home message of this thesis was therefore that the reproductive phenology of the Kutuharju herd responded to climatic variability at different periods of the year and reindeer was, so far, keeping track of its changing environment leading to an improvement in females' reproductive success. But a "head-start" benefit was detected such that some females always did better than others did. Despite this reproductive advantage and if climatic changes were to exacerbate, with "too long" vegetative growing seasons for reindeer, negative consequences for the population's reproduction might be observed.

6.6 Appendices
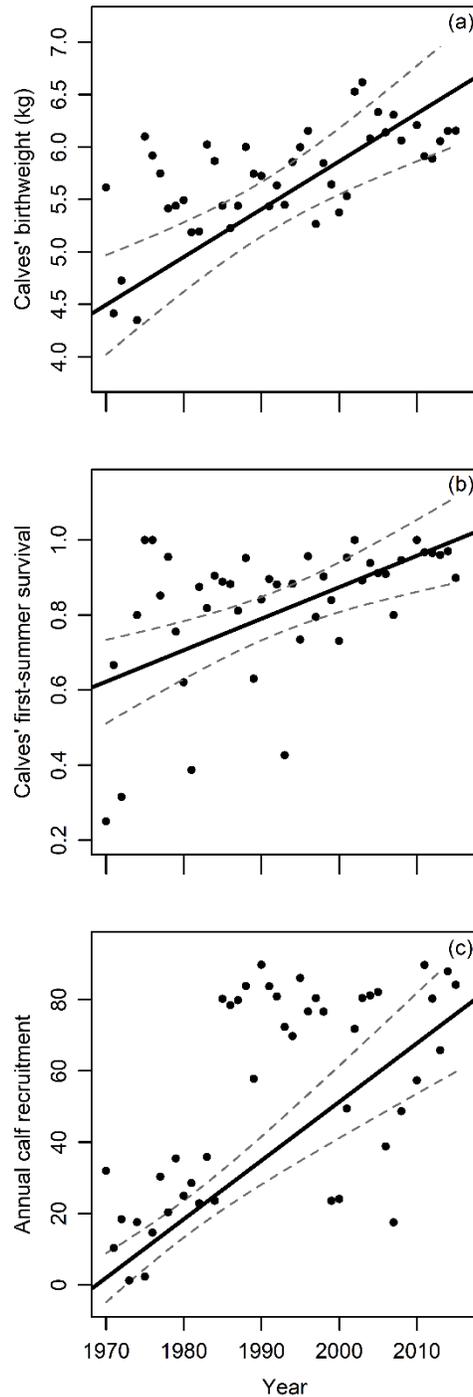
Figure 6.1 Temporal trends of (a) an improvement of calves' birth weight, (b) a better calves' first-summer survival and (c) a higher annual calf recruitment in the Kutuharju reindeer herd from 1970 to 2015 in Finnish Lapland. Fitted line as well as 95% confidence interval band are provided. Data points were weighted by inverse variance (i.e. regression slopes) and each point represents the mean value of the response variable for a specific year. The annual calf recruitment was

calculated as the number of newborn calves divided by the number of mature females each year, converted in percentage. The calves' first-summer survival was averaged per year and could go from 0: born during the calving period to 1: survived to autumn.

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