Climate variation, plant productivity, herbivore performance and population dynamics

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Declaration

I declare that this thesis is entirely my own work. Any other material is accordingly referenced and people who provided help and advice are listed in the acknowledgements.

Ana Isabel Ramos Bento
“A good climate, like a good dinner, is more than the mere sum of its parts.“

-Elton (1924)
Abstract

Prediction is one of the hardest things in ecological science. Predicting the weather is one of the hardest things of all. This is what makes predicting the ecological consequences of climate change so exceptionally demanding. As a first step, we would like to understand the effects of weather variation on the behaviour of those ecological systems for which we have the best long-term data. The Park Grass Experiment at Rothamsted allows us to model the effects of the timing of rainfall and the accumulation of day-degrees in spring on primary productivity in an ungrazed grassland. I use the insights gained from this model to interpret the effects of weather variation in two classic long-term studies of plant-herbivore interactions: the Red Deer on Rum and the Soay Sheep on St Kilda. In both cases, direct effects of extreme weather on animal populations ("killing weather") turn out to be much less important than weather-driven changes in plant production. Because most of the important effects of weather on animal population dynamics act via changes in food availability, it is the interaction between weather and population density that matters more than anything else, rather than weather effects alone. The same weather that would lead to mass starvation at high population densities, might have no measurable impact on animal performance when numbers were low. The analysis is focused on the following questions: which weather variables are most important; when do they have their most important effects; what effect sizes do they generate; and what is the shape of the relationship between the weather variable and the ecological response variable? The answers to these questions will help to guide subsequent analyses of demography and genetics on these two Hebridean Island systems.
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Chapter 1 Introduction

The extent to which weather affects the dynamics of populations is a question that has interested naturalists since the beginning of ecological science. One of the most well known, and long-lived debates in ecology, concerned whether dynamics of wild animal populations were regulated mainly by exogenous environmental factors, like weather (Andrewartha & Birch 1954), or by endogenous density dependence processes, like competition or predation (Nicholson 1933). Although modern thinking usually views endogenous and exogenous factors in a unified way, operating together on a population (e.g. Bjornstad & Grenfell 2001, Goswami et al. 2010), we lack a good working knowledge of the typical importance of weather compared with other factors across many populations. Beyond the fundamental ecological questions, the role of the environment in shaping the dynamics of populations is of interest in applied contexts. This is exemplified by current concerns about effects of climate change, which have sparked an increasing interest in estimating how environmental factors affect populations (e.g. Clements et al. 2010).

The response of species and populations to climate change is likely to be variable and hard to predict (Root et al. 2003, Rozenweig et al. 2008). For instance, the future winter climate in the UK is predicted to become considerably warmer, with precipitation increasing but becoming more variable, both temporally and spatially (IPCC 2007).

Some studies show that species can track interannual shifts in the onset of seasons through phenotypic plasticity (Charmantier et al. 2008) and microevolution (Nussey et al. 2005) while other studies emphasize the limits on these responses (Keith et al. 2008). Not only are mean climate conditions changing, but so are temporal fluctuations in weather (Salinger 2005, IPCC 2007). Previous work shows that increasing interannual variation in population growth rate, due to temporally fluctuating climate conditions, will reduce the long-term stochastic growth rate of a population and increase its risk of extinction (Boyce et al. 2006). Unfortunately,
relatively little is known about how specific vital rates (i.e. survival, growth and reproduction) respond to fluctuations in particular climatic variables, which makes it even more difficult to predict population dynamics (Drake 2005, Melbourne & Hastings 2008). Time series of stage structured population monitoring provide data on the variability of vital rates and make possible the identification of the specific climatic parameters that shape those.

The real breakthrough however, has been the widespread availability of high-speed computing. This has allowed the execution of techniques that would have appeared impossibly tedious to previous generations of analysts repeating the same analysis with literally thousands of different start-dates, end-dates and thresholds to describe the combination of parameter values that maximise the explanatory power of the model.

Traditionally, climate effect studies have focused either on plants’ responses (earlier and longer annual growing season - Chen et al. 2011), changes in biomass production (e.g. Havstrom et al. 1995) using local weather variables (e.g. Callaghan et al. 1997, Pettorelli et al. 2005, Post et al. 2008, Yu et al. 2010, Graae et al. 2011); or on animals without data on plants (e.g. Forchhammer et al. 1998a, b, Coulson et al. 2001, Martinez-Jauregui et al. 2009, Moyes et al. 2011). Consequently, links between responses by vegetation to climatic variability and consequent herbivore demographic responses (such as changes in body size) will remain speculative.

1.1. Climate variability and herbivore population dynamics

Marked seasons are common phenomena in large parts of the globe. This typically involves a pulse of plant growth during the favourable season and an extended unfavourable season with no plant growth, which, at high latitudes, maybe due to temperature and precipitation regime variations. The consequence for large herbivores will be one season with abundant food resources and another season with low food resources.

The large annual variation in plant growth imposes constraints on herbivores, as life history tactics must be adjusted to fit the seasonal pattern of the system. However, a seasonal environment imposes two types of environmental variation on the population dynamics of large herbivores. One type is the predictable within year
variation due to the season, but there is also an unpredictable between-year variation caused by weather fluctuations. Large herbivores adapt to seasonality in a variety of ways. For instance, breeding is timed so that calving (or lambing) is concentrated in the optimal period for offspring survival (e.g. Loudon & Brinklow 1992) and growth is restricted to the period of summer food abundance (e.g. Clutton-Brock & Pemberton 2004). Life in the winter months is focused on survival (Reimers et al. 1983, Adamczewski et al. 1997).

All natural populations experience temporal variation in their environments, which alters the dynamics of the population (Lande et al. 2003). The stability of a large herbivore population is closely linked to two factors: the specific growth rate close to carrying capacity (set by winter resources, in the case of food-limited systems) and the environmental variance among years (Lande et al. 2003). As demonstrated by Clutton-Brock and Coulson (2002), it is clear that the timing of birth relative to the spring flush of plant growth and energetic needs can exert very different effects (e.g. body size).

Variation in winter temperature and snow cover, which in turn affect plant phenology and nutritional value of plants (Mysterud et al. 2003) affect body mass and fecundity. Weather fluctuations operate mainly through cumulative effects on the condition of the mother (Post & Stenseth 1999). Calves born after years of good or bad winters may vary in condition and consequences of this may persist into adulthood. This creates cohort effects on population dynamics (Albon et al. 1992), where the climatic conditions into which a cohort is born influences life-long differences in cohort reproduction and survival.

Density independent weather effects are very important for the food base of animal populations with low intrinsic rates of increase and, thus for population dynamics (Langvatn et al. 1996). This density independent decreases in forage availability may induce density dependent decreases in fecundity, growth and or survival as the animals are forced to forage on a reduced food resource. Soay sheep lambs on St. Kilda are born in April, around one month before the fresh forage begins to be available; and red deer calves on Rum are born in June, later in the season when forage is already accessible. Females of both species use their body reserves to maintain the growth of the lambs and calves in their first postnatal period (Clutton-Brock & Coulson, 2002, Nussey et al. 2005). Detailed knowledge regarding
the way weather affects local populations is often necessary to successfully predict climate impact.

In most studies focused on population in the northern hemisphere, climatic variability is mainly determined by large-scale alternations in the atmospheric mass. The strongest regional expression is the North Atlantic Oscillation (NAO), which affects the direction, magnitude and speed of westerly winds across the Atlantic Ocean (Rogers 1984, Hurrell 1995). This large scale climatic variation influences winter temperature and precipitation patterns over Northern Europe. The variations in local weather variables will have effects on the food supply of large herbivores (Post & Stenseth 1999). The NAO index captures effects of more than one season in a single parameter. Mechanistically, however, several lines of evidence suggest local weather is biologically the most relevant explanatory variable for population dynamics (Sandvik et al. 2008, Martinez-Jauregui et al. 2009).

So, while the fact that weather can and does affect populations is beyond dispute, the problem of how to integrate weather into an understanding of the dynamics of specific populations has generated its own debates. Certain well-studied species have been shown to react to fluctuations in climate and weather through an intricate interplay between demographic traits and combinations of environmental factors (Coulson et al. 2001, Benton, Plaistow & Coulson 2006, Owen-Smith 2010). Including weather variables in analysis of populations offers the potential to clarify other factors affecting them, by explaining part of the variation, and this in turn may improve estimates of density dependence (Ripa & Ives 2007). This highlights the importance of the timing of a stimulus. It is this crucial temporal element that this thesis aims to identify. In practice, there has been little effort to develop methods to evaluate the influence of weather using finer-scale temporal intervals. Yet such methods would highlight the periods when the relationship between weather and demography is strongest and hence suggest the most likely mechanisms responsible for changes in the rates of birth and death.

The situation I address is when a density-independent environmental factor, such as a weather variable, has been measured in a sequence of time intervals. I fit a variety of models in which the response variable is the life-history trait and various weather records at each time interval are used as explanatory variables (this is explained in much more detail in each of the data chapters, also, see van de Pol & Cockburn 2011). Statistical tests of the influence of local weather on plant production
and herbivore demography can be divided into two broad types: time-window associative tests and growing-degree day (GDD) models. A time-window approach typically involves calculating the average weather (i.e. temperature, precipitation and wind speed) during a specified period (usually one or more months) and using linear regression to assess the slope of the relationship between what we want to explain and average weather variable windows across time or space (e.g. Phillimore et al. 2010). Variants on this approach include the application of multiple regression to include several different time-windows (Sparks & Carey 1995) and weighting functions to relax the assumption that all days make an equal contribution (van de Pol & Cockburn 2011). Time-window approaches are especially popular in macroecology (e.g. Roy & Sparks 2000) and long-term studies of animal populations (e.g. Husvy et al. 2010). Strong correlations are often identified even in the absence of a full mechanistic understanding of the effect of temperature on phenology.

The GDD approach incorporates an explicit hypothesis of a linear effect of temperature on development rate via enzyme activity (Bonhomme 2000). The approach owes much to Réaumur's work (1735), in which the idea of heat units as the sum of mean daily temperatures between an arbitrary date of onset and the date of an observed phenological event was proposed. GDD models take on various forms (Wang 1960). In this thesis, I describe a basic form of this model that uses a fixed threshold with daily average temperature data, rather than incorporating within day variation in temperature as most versions do (Cross & Zuber 1971). Starting from a specified time point, daily temperatures above the threshold (or base) temperature are summed and when a specified cumulative number of GDDs has been reached the trait should be expressed. The threshold chosen is the value that minimises the residual deviance for a given window. While the threshold temperature could, in principle, be identified experimentally as the temperature at which development is zero, more often, it is identified statistically and does not necessarily correspond to the temperature where development is zero (Yang et al. 1995, Snyder et al. 1999, Bonhomme 2000). GDD models are most widely used for modelling yields in crop production but have also been used to explore variation in phenological research addressing, for instance, the timing of flowering (Jackson 1966, Clark & Thompson 2010), budburst (Hunter & Lechowicz 1992) and arrival of migratory birds on breeding grounds (Saino et al. 2011).
1.2. Vegetation

Grasslands play an important role worldwide, comprising over 30% of the Earth’s terrestrial surface (Adams et al. 1990). Shoot growth, measured as the change in sward biomass, is a fundamental ecological process, integrating across scales from physiology to community dynamics and ecosystem properties (McMahon & Bonner 1983). An understanding of plant growth is essential to understand ecological processes like plant-herbivore interaction, and plant-environment interactions, as well as local community dynamics (Kobe 1999, Tanner et al. 2005).

Grass is relatively abrasive, low-quality forage (e.g. Robins 1983) whose nutritional content varies over complex spatial and temporal scales (e.g. McNaughton 1985, Jones et al. 2006). Satisfying energetic and nutritional requirements is a difficult challenge for herbivores in grasslands, because of the adverse carbon to nitrogen ratio of their plant food compared to their body tissues - Southwood (1973) called this the ‘nutritional hurdle’. Because grassland is generally low quality and spatio-temporally variable, where herbivores choose to feed and what plant species they select to graze will have a significant impact on whether dietary requirements are met. On the other hand, grazing impacts of herbivores over the seasonal cycle may cause vegetation biomass to expand or contract between the years, with consequent effects on the herbivore population dynamics (Owen-Smith 2002).

Climatic and phenological evidence suggests that, as average annual temperatures have increased, the onset of the plant growing season has advanced and its duration has lengthened across temperate Europe, as well as in Scotland specifically, over the last few decades (Menzel & Fabian 1999, Barnett et al. 2006, Menzel et al. 2006). Earlier and more protracted plant growth should increase food availability to herbivores at key junctures in their annual breeding cycles (Post & Stenseth 1999, Mysterud et al. 2008a). This is likely to be positive for the herbivores, as both plant biomass and nutritional quality will increase (Lenart et al. 2002). It is not trivial what happens when plant productivity goes up. The longer vegetation period predicted by many models will also have a short-term positive effect as the animals will have a longer period for growth and an increased survival during the short winter (Folland et al. 2001). However, it is possible that long-term effects are that animals will eventually suffer same level of density dependence per capita with
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equilibrium going up, it is unclear which effects this will have on population dynamics.

The key theoretical result is that in a food-limited plant-herbivore system there is no necessary relationship between plant productivity (as influenced, for example, by current weather conditions) and the resulting plant biomass. Suppose that the dry mass of plant material is $V$ (vegetation) and the number of herbivores is $N$. The plants are assumed to grow in a logistic manner in the absence of herbivores, reaching a maximum biomass of $K$ (dry mass per unit area). The growth rate of the plants, $r$, is assumed to be a function of weather conditions (mainly temperature and water availability; we assume that soil conditions are essentially constant for the duration of our study). The feeding rate of the herbivores exhibits a functional response: it does not matter for our present argument whether we assume a linear or a saturating numerical response (Crawly 1983), so for simplicity we assume a linear functional response where total offtake is a linear function of the product of herbivore numbers and plant biomass. Plant mass increases as a function of carbon fixation and declines as a result of herbivore feeding:

$$\frac{dV}{dt} = rV \left(\frac{K - V}{K}\right) - \alpha VN$$

The herbivore population increases in proportion to the amount of food eaten and declines as a result of density independent mortality:

$$\frac{dN}{dt} = \beta VN - \gamma N$$

At equilibrium, the herbivore gains are equal to the losses, so we can solve for the equilibrium plant biomass $V^*$:
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\[
V^* = \frac{\gamma}{\beta}
\]

This important result, due originally to Lotka and Volterra, illustrates that the plant's equilibrium biomass is determined entirely by the biology of the herbivores and does not depend on plant growth rate or plant size (Crawley 1983). Increases in plant growth rate, \( r \), or biomass, \( K \) are important, but they affect herbivore equilibrium not plant equilibrium biomass:

\[
N^* = \frac{r \left[ K - \frac{\gamma}{\beta} \right]}{\alpha K}
\]

This counter-intuitive result is reversed only when there is explicit density dependence acting on the herbivores (e.g. herbivore territorially). For our proposes, the point is simply that we should not expect weather conditions that affect plant growth necessarily to lead to increased plant biomass (Crawley 1983).

1.3. Why ungulate populations?

Large herbivores are among the major drivers for forming the shape and function of terrestrial ecosystems. These animals may modify plant productivity (e.g. McNaughton 1985, de Mazancourt et al. 1998), nutrient cycles (e.g. Cohen et al. 2000), plant succession, soil properties, as well as other biota (Nyberg & Persson 2002). Among grazing ungulates, populations may show little variation in size across the years, irregular oscillations, semi-regular oscillations, or dramatic oscillations (Peterson et al. 1984, Fowler 1987, Coulson et al. 2000, Coulson & Clutton-Brock 2002). In some, a stable-point equilibrium between ungulates and their resources is unlikely, and, in this case, large fluctuations in population size will be a typical pattern (Saether 1997). Some large herbivore populations are at the edge of
extinction and great effort is being made to save them. Other species occur in dense populations and cause conflicts with other land use interests. Understanding the role of large herbivores is important for ecology. While many ecological differences contribute to these disparities, the fact that stability varies widely among naturally regulated ungulate populations in the absence of predators (e.g. Clutton-Brock et al. 1997a), suggests that variation in population dynamics may often be caused by interactions between herbivore populations and their food supplies. Thus, we first need to understand the underlying mechanisms that shape their population dynamics. Certain long-term studies on large herbivore populations have made especially influential contributions to our current understanding of population dynamics (e.g. Clutton-Brock et al. 1982, Gaillard et al. 1993, Fiesta-Bianchet 1998, Owen-Smith 1990, Clutton-Brock & Pemberton 2004).

Islands have long been the focus of interest of several researchers, being the natural laboratories for the study of evolutionary and ecological patterns (e.g. MacArthur & Wilson 1963, Ricklefs & Bermingham 2008), not least because of problems of immigration and emigration are eliminated. The level of individual-based data in Soay sheep and Red deer in Rum systems is such that uncertainty caused by measurement error is minimized and therefore considered to be of negligible consequence on the conclusions drawn (Whittaker et al. 2008).

1.4. Studying ungulate populations in the context of climate change

Northern areas are particularly vulnerable to projected climate changes (IPCC 2007). Due to a variety of feedback mechanisms, these areas are likely to respond more rapidly and severely than any other area on Earth (Anisimov et al. 2001). There are multiple paths via which environmental variation can impact herbivore ecology and this makes the identification of drivers challenging. Changes in intensity of environmental variation can alter population fluctuations in cyclic populations (e.g. Reuman et al. 2006). A myriad of approaches has been used to describe associations between environmental variation and ecology, including local weather, large scale patterns of climate and satellite imagery reflecting plant productivity and

Phenology, the study of the timing of recurring natural events, is a tool for assessing climate change impacts on plant and animal growth and development. Several studies have already documented the effect of global warming in inducing advances in leaf unfolding and flowering during recent decades in Europe (Menzel & Fabian 1999, Menzel et al. 2006) and North America (Schwartz & Reiter 2000). Recent meta-analyses provide compelling evidence that the phenology of many temperate plant and animal populations has advanced in response to recent climate warming (Menzel & Fabian 1999, Menzel et al. 2006, Parmesan 2007, Thackeray et al. 2010). Plants respond to the cumulative effects of daily weather over an extended period, so their development stages are effective integrators of climate data. Changing temperatures can force adjustments in crop production and produce ‘ripple effects’ in natural ecosystems. For example, if plants bloom earlier, then insects must try to adjust their life cycles, as well as, other animals that use insects for food. Further, some species can probably respond better, thus gaining an evolutionary advantage. Given such grave consequences, understanding more about interactions during spring ‘greening’ is crucial to improve models, monitor growing season variations and calculate the carbon budget precisely. The overwhelming majority of evidence for such phenological advances in vertebrate systems comes from birds (Berteaux & Stenseth 2006, Parmesan 2006, 2007, Thackeray et al. 2010). Long-term studies of wild birds provide rare insight into the complex interactions between local changes in climate, food availability, breeding phenology and reproductive fitness (Visser et al. 1998, Both & Visser 2001, Winkler et al. 2002, Gienapp et al. 2006, Charmantier et al. 2008) and some of the best evidence for links between rates of phenological change and population growth rates (Both et al. 2006, 2010, Møller et al. 2008). However, recent advances in our understanding of how climate change is affecting the ecological and evolutionary dynamics of avian systems serve to highlight a notable paucity of similar studies in wild mammals (Berteaux & Stenseth 2006, Parmesan 2007, Thackeray et al. 2010). Few studies have even documented phenological responses to climate warming in mammals, let alone investigated the wider ecological or evolutionary consequences of climatic and phenological change (although see Inouye et al. (2000), Adamik & Kral (2008) for examples of the former, and Réale et al. (2003) for an example of both in rodent
populations). Long-lived mammals such as ungulates, are typically highly polygynous and, in temperate regions, experience a long over-winter gestation period separating the mating season and the birth season. This is in stark contrast to species of passerine birds, which have been the overarching focus of studies relating phenology and climate change in wild vertebrates, which are typically monogamous and in temperate zones mate, lay eggs and raise young in quick succession through spring and summer. Clearly, the selective and environmental pressures on phenology are likely to differ markedly between avian and mammalian systems (Inouye et al. 2000, Bertaux & Stenseth 2006).

1.5. The study systems

1.5.1. The Park Grass Experiment

The Park Grass experiment begun by John B. Lawes and Joseph H. Gilbert in 1856, at Rothamsted in Hertfordshire, England, to compare hay yields of unfertilized plots with plots with different combinations of fertilizers. It is the longest running ecological experiment in the world (Tilman et al. 1994).

In the temperate climate on the silty clay loam soil at Rothmasted, processes of soil development and change are slow and require time (Silvertown et al. 2006). Over the 150 years, the different treatments plus atmospheric inputs have resulted in soil acidification, changes in soil organic matter, and phosphorus and potassium enrichment or depletion and these have affected the make up of plant populations (Silvertown et al. 2006).

There are several examples of studies that have used Park Grass as a model system. For instance, the numerous long-term treatments reveal relationships between nutrient availability and grassland biodiversity (Crawley et al. 2005) - one of the best examples of rapid evolution by natural selection under field conditions Anthoxanthum odoratum response to lime applications (Snaydon 1970). Park Grass is of particular interest as it is a perfect system to study ecological processes in the context of an herbivore free system. This is especially relevant to understand in greater detail how local weather variation affects plant productivity. This is of course of great importance when studying herbivore population dynamics.
1.5.2. Soay sheep on the archipelago of St Kilda and Red deer on the isle of Rum

Both island populations of Soay sheep (*Ovis aries*) on St. Kilda and red deer (*Cervus elaphus*) on Rum provide ideal models for the study of plant herbivore dynamics. These two systems are superficially similar but they differ in details. On St. Kilda there are no predators and no competitors. On Rum, however, deer that stray from the study area are occasionally shot and there are some competitors (e.g. goats). The habitats occupied are broadly similar with areas of herb rich or *Agrostis*-dominated grassland at sea level grading into heather dominated communities interspersed with flushes on the slopes of the hills (Clutton-Brock & Pemberton 2004, Clutton-Brock & Albon 1989). The vegetation is relatively unpolluted by atmospheric nutrient inputs (Crawley *et al.* 2004). For the case of Soay sheep, there are no confounding management operations and the population is closed to immigration and emigration. Since these are both food-limited populations we would expect that grazing would have a major impact on plant biomass, spatial structure and botanical composition of the vegetation.

Soay sheep have been individually marked on the island of Hirta in the St Kilda archipelago (See figure 2.1) since 1985 and identification has followed an identical protocol throughout (Clutton-Brock & Pemberton 2004). Three visits are made annually: during lambing (late spring), in August to obtain genetic and morphometric data and during the rut (October – November). An individual is considered a resident of the study area based on approximately 30 censuses throughout a year, such that the probability of re-sighting is considered to be 1 (Clutton-Brock & Pemberton 2004). Vegetation is measured twice a year: in March when food availability is at its minimum and in August, when it is close to its maximum (Crawley *et al.* 2004).

The red deer in the North Block of the Isle of Rum, Scotland, have been under intensive study since the early 1970s. Individual deer are recognized as a result of artificial markings and natural variation and are closely monitored throughout their lifetimes (Clutton-Brock *et al.* 1982). Culling of the population in the 12 km² North Block study area ceased in 1972, since then the breeding phenology and reproductive performance of male and female red deer have been closely monitored (Clutton-Brock *et al.* 1982). Throughout the year, censuses of the study area are
undertaken to monitor the presence and location of individual deer. Vegetation is monitored monthly from April to November, using movable herbivore exclosures that are moved monthly (Albon et al. 1983).

The study populations have much in common, yet important differences between them, coupled to the high-quality data, enables detailed investigation of various hypotheses. Both species experience age-specific changes in performance (Catchpole et al. 2000, Clutton-Brock & Coulson 2002) and have a noticeable birth pulse in spring. There are however differences. A fundamental dissimilarity in the dynamics of these two populations is that red deer appear to be in a fluctuating equilibrium with the vegetation, product of a dynamic interaction between the animals and the plants in which the productivity and composition of vegetation determine the average population density (Crawley 1983). The red deer rapidly increased in abundance after shooting was stopped in the study area and have been relatively constant since 1982. In 1990-2000 population substantially declined rapidly then showed a protracted period of increase. From 2000 the population has fluctuated around the current mean as described in chapter 5.

The dynamics of the Soay sheep population are highly unstable (Grenfell et al. 1992, Grenfell et al. 1998). Soay sheep numbers have increased dramatically during the study period, almost doubling in 25 years. In plant-herbivore interactions, where there are no competing herbivores and no vertebrate predators, we expect the herbivore numbers will be determined by food supply available during winter (Crawley 1983). Understanding the relationship between the herbivores and their resources is therefore a key element in understanding the population dynamics of the sheep. Soay sheep are the sole vertebrate herbivores on St. Kilda; red deer, however, are not the only vertebrates on Rum (Kruuk et al. 1999).

Soay sheep can produce offspring in their first year of life; red deer reproduce much later (around their 3rd birthday). Male Soay sheep rut during October to gain access to females, who conceive in late autumn and give birth from the following April; red deer males rut in November and females give birth in June (Moyes et al. 2011).

Whilst both species are considered to be long-lived (Soay sheep females live up to 16 years and males up to 11 years, whereas red deer females live up to 24 years and males up to 17 years), these marked differences in individual characteristics contribute to form markedly different population dynamics.
1.6. Thesis Outline

Soay Sheep and red deer are warm-blooded, well insulated and generally hardy. There is no reason to suppose that well-fed individuals would suffer any direct negative consequences of weather on St Kilda and Rum. It is never too warm for the animals in summer, and snow never lies for long enough to deprive the animals of food for a significant period. Weather, therefore, is only likely to be an issue for under-nourished animals, especially when they are very young or very old. It is for this reason, that we always include population density as a surrogate for under-nourishment in all of our weather models.

Plants, in contrast, are likely to be temperature and moisture sensitive throughout the growing season. Though, they too must all be hardy to the worst of Hebridean winter weather.

There is a fundamental asymmetry, therefore, in our expectations about weather effects. We would be surprised to find direct weather effects on the animals when the population density was low and the average plane of nutrition was relatively high. But we would be surprised not to find direct effects of weather on plant growth, most especially in determining the length of the growing season (i.e. on the start-date of grass growth in spring and the end-date of grass growth in autumn). Coupling population dynamics with annual variations in climatic conditions will provide us with mechanistic insight into the functional role of individual species in higher order ecological responses to climate change. Such an approach will aid efforts to predict future changes in the populations and communities they are imbedded (Schmitz et al. 2003).

In this thesis, I investigate the influence of interannual variability of weather variables, at specific times of the year and with specific start-dates and window lengths, on vegetation productivity and herbivores performance and ultimately population dynamics.

1.6.1. Aims and Objectives

This thesis is centred on the impacts of weather on population and dynamics and forage availability. The main hypothesis is that at low numbers, direct effects should be negligible on the animal populations. But at high numbers, weather should have an impact on animal condition, both directly through heat loss and indirectly
through food availability. The predominant focus and aims of my thesis are to test whether local weather variables are better predictors of vegetation production and herbivore performance than larger-scale weather indices (chapters 2, 3, 4 and 5). I develop a methodology for constructing time series of weather data, using neighbour islands as a proxy (chapter 2). I quantitatively assess the effects of local climate variability on animal populations (chapters 3 and 4) and plant communities (chapters 3, 4 and 5) to gain an understanding of the fundamental mechanisms regulating herbivore populations and modelling the dynamics of climate-plant-herbivore dynamics.

My thesis is divided into 6 Chapters. For ease of exposition, each chapter is treated as a unitary treatise. Preliminary conclusions drawn are that it is very complex to evaluate how weather influences a system, even if the time series for both weather and populations are very long and uninterrupted. Overall conclusions are drawn in chapter 6.
Chapter 2 Reconstructing local weather time series for the islands of St. Kilda and Rum

Abstract

A new approach to interpolating weather data from local weather stations and gridded observations is introduced and evaluated. This chapter describes the interpolation procedure used for reconstructing the daily weather time series for the islands of St. Kilda and Rum, Scotland. For each of the climatic variables, the choice of model is based on verification statistics and by comparing the observed values with the estimated values at each point. This gives a measure of fit of the method at predicting values when using a proxy station for calibration. The resulting time series provide estimates of seasonal variability as well as year-to-year variability. In both islands, the weather trends observed were in the same direction. There is no significant change in precipitation regimes for either island; however, both Rum and St. Kilda are becoming warmer and less windy, with stronger trends occurring in Rum, with an increase in temperature by at least 1.5°C and a decrease in wind speed by at least 1.88 ms\(^{-1}\) over 47 years. In St. Kilda there was an increase in temperature by at least 0.9°C and a decrease in wind speed by at least 1.65 ms\(^{-1}\) over 55 years. With this knowledge, we might be able to pinpoint the specific drivers for the observed changes in the dynamics and performance of animal populations and plant communities on both islands.
2.1. Introduction

Climate often plays a significant ecological role determining changes in the population dynamics of species (e.g. Coulson et al. 2001, Peñuelas 2001, Stenseth et al. 2002, 2004, Parmesan & Yohe 2003, Parmesan et al. 2006, IPCC 2007, Owen-Smith 2010). Climate is usually a key to understanding the interdependence between environmental and biological factors and is widely used in explaining species interactions (e.g. Durant et al. 2005, Suttle et al. 2007), as well as developing niche models, ecological zones and biodiversity assessments (e.g. Koeppen 1923, Hills 1960, Bailey 1985, Woodward 1987, IPCC 2007).


There are multiple potentially interacting paths via which environmental variation can impact herbivore ecology making the identification of drivers challenging. In addition, there is growing evidence that global warming can affect population dynamics and ecosystem functioning (Saether et al. 2000, Walther et al. 2002, Ozgul et al. 2010). Finally, seasonal variations in local weather conditions may be a potential driver of population dynamics (Ozgul et al. 2004) and these can work in concert with broad long-term climatic phenomena to shape the trajectory of a fluctuating population (Previtali et al. 2009).

Researchers have used diverse approaches to describe the association between environmental variation and ecology, including local weather, large-scale patterns of climate, and satellite imagery reflecting plant productivity and phenology (e.g. Post et al. 1999, Post & Forchhammer 2001, 2002, Owen-Smith 2002, Danell et al. 2006, Martinez-Jauregui et al. 2009).

The most common source of climatic data is the meteorological station, which provides data for a single location. There are three automatic weather stations on St. Kilda, but they were installed relatively recently (in 1999). On Rum, the weather station is even more recent (2011). This means we have to rely on more distant weather stations if we are to investigate weather impacts before those dates.
In the absence of local stations, cruder climatic indices (e.g. North Atlantic Oscillation, Arctic Oscillation and El Niño Southern Oscillation) have been often used in models as descriptors of weather patterns. In the 1990s, those climatic indices that describe large-scale patterns of weather became available and this led to a proliferation of studies reporting far reaching and deep rooted impact of indices like the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) on ecological systems, namely population performance (e.g. Rogers 1997, Milner, Elston & Albon 1999, Post et al. 1999, Catchpole et al. 2000, Coulson et al. 2001, Ottersen et al. 2001, Stenseth et al. 2002, 2004, Clutton-Brock & Pemberton 2004, Forchhammer & Post 2004, Hallett et al. 2004, Coulson et al. 2008). The NAO is one of the major modes of variability of the Northern Hemisphere atmosphere. It is particularly important in winter, when it exerts a strong control on the climate of the Northern Hemisphere. It is also the season that exhibits the strongest interdecadal variability. The NAO is traditionally defined as the normalized sea level pressure difference between a station on the Azores and one on Iceland. For winter, the difference between the normalised sea level pressure over Gibraltar and the normalised sea level pressure over Southwest Iceland is a more useful index of the NAO strength. Positive values of the index indicate stronger than average westerlies over the middle latitudes. The NAO, as a measure of weather severity, has been used in both St. Kilda and Rum because the local weather time series is incomplete especially in the early years. In both islands, it has been assumed that positives values of NAO are associated with wet and stormy weather, meaning bad weather for the animals. Negative values of NAO are associated with cold and dry weather, meaning good weather for the animals.

These, however, are rather crude indices but they have been argued to be better at predicting species demographic processes (Hallett et al. 2004). There are undoubtedly many conceptual problems and practical limitations to using coarse scale indices for predicting ecosystem responses. Sandvick et al. (2008) show that NAO appears to be as good a predictor for population fluctuations of seabirds as local weather variables. However, they conclude that local weather is preferable as it allows for a more mechanistic understanding of the population dynamics.

Given the potential important effects of climate on ecosystems, accurate local weather variables are required more than ever for understanding ecological responses driven by environmental factors. Accurate estimates of meteorological
values such as temperature, precipitation and wind-speed are critical to the performance of biological models. Prediction of the impacts of a changing climate on the distribution and functioning of these systems requires the development of reliable spatially explicit models of current climate, as a first step. Determining spatial relationships in climate conditions, however, is not easy, because long-term average weather observations come from sparse, discrete and irregularly distributed meteorological stations. These discrete data have to be extended spatially and temporally to reflect the continuously and gradually changed climate patterns. This is the case for both St. Kilda and Rum, for which we do not possess complete long-term records.

As is the case across much of the world, the distribution of meteorological stations in Scotland is not uniform, with many remote places having sparse data coverage (especially those that are also sparsely populated, e.g. the Outer Hebrides), while in contrast a clustering of reporting stations can be noted in several of the major metropolitan areas. These gaps in the data must be accounted for in the construction of any spatially and temporally continuous time series. The Met office has an extensive historical database containing daily observations of weather elements back to the 1950’s. These observations come from an irregularly spaced and gradually evolving network of meteorological stations across the UK. This chapter addresses the issue of improving temporal coverage of local climate data in the Scottish islands of St. Kilda and Rum by producing a consistent series of climatic statistics that enables comparisons to be made across space and time and to further our understanding of what drives the dynamics of the herbivore populations, plant communities and plant-herbivore interactions in those islands.

Substantial attention has been given to the application of interpolation techniques to climatic analysis in recent years using a variety of methods (e.g. Daly et al. 2000, Johnson et al. 2000, Jarvis & Stuart 2001a, 2001b, Shang et al. 2001, Lin et al. 2002, Gyalistras 2003, Vicente-Serrano et al. 2003, Perry & Hollis 2005, de Gaetano & Belcher 2006). Given a set of meteorological data, there are a variety of stochastic and deterministic interpolation methods to estimate meteorological variables at un-sampled locations (Meyers 1994). Available interpolation methods for temperature and precipitation regression include geostatistics (e.g. kriging and inverse-distance weighing) and smoothing splines (Agnew & Palutikof 2000, Perry & Hollis 2005), by aspect- and elevation-related
correlations, multiple linear regression, or weighing functions to simulate climatologic functions (e.g. Price et al. 2000, Daly et al. 2002, Jones & Mitchell 2005). Different interpolation methods yield data of varying quality, which can strongly influence modelling results (New et al. 1999, Perry & Hollis 2005). Many studies have been carried out comparing the predictive performance of interpolating methods via cross validation (e.g. Dubois et al. 1998, Vicente-Serrano et al. 2003, Stahl et al. 2006, Hofstra et al. 2008), often on a monthly or annual basis. Very few studies examined the influence of different interpolation methods of modelling results on a daily or sub-daily basis (for recent reviews see Tveito et al. 2006, Kneis & Heistermann 2009, van der Heijden & Haerlandt 2010). Most techniques reviewed are statistical approaches for interpolating climatic data over large regions.

Methods to improve the accuracy of interpolation for daily climatic variables are important when placed within an ecological modelling context, because there is a considerable sensitivity of the underlying ecological system to these variables. With such an abundance of methods, a key issue is the choice of interpolating approach for a given set of input data (Burrough & McDonnell 1998). This is especially true for areas such as mountainous regions or isolated islands, where data collection is sparse and measurements for given variables may differ significantly even at reduced spatial scales (Collins & Bolstad 1996, Jones & Lister 2004). When data are sparse, the underlying assumptions about the variation among sampled points may differ and the choice of interpolation method and parameters may become critical. Understanding the accuracy of spatial interpolation techniques is a first step towards identifying sources of error and qualifying results based on sound statistical judgments (Meyers 1994).

For climate interpolation, regression (e.g. spline and multiple regression) and co-kriging methods appear to be preferable, as they may take into account the climatic dependence on topography by using a trivariate function of latitude and longitude as two independent variables and elevation as a covariate (Attorre et al. 2007). Nevertheless they do not take in to consideration aspect. Although regressions techniques and co-kriging methods yield results with similar accuracy when data density is adequate (Hutchinson & Gessler, 1994), regression interpolation, in practice, is far simpler and more advantageous especially when the distance is relatively short and topography of the places is quite similar (Craven & Wahba 1979, Collins & Bolstad 1996, Hartkamp et al. 1999). Regression techniques
can be utilised to develop relationships between temperature, precipitation and wind at locations of measured climate data (Jones & Lister 2004, Hijmans et al. 2005) and the locations lacking the information that need to be reconstructed. Interpolation algorithms may then be employed to reconstruct the unmeasured weather data and calculate daily microclimate conditions (Jones & Lister 2004). Daily weather conditions are known to influence the growth and development of many biological organisms. It is therefore surprising that relatively few ecological or environmental studies focus on the interpolation of continuous national coverage of daily weather (Jarvis & Stuart 2001a, 2001b).

Both Rum and especially St. Kilda are quite remote, not being normally incorporated in the network of gridded datasets covering the UK. As a result, in this chapter, I generate daily weather time series by calibration and subsequent interpolation using proxy nearby weather stations. I use two different methods: simple linear regression models and generalised additive models (GAMs) - fitting the variable of interest to some linear combination of regressor variables (Myers 1994, Wood 2006, Crawley 2007). The reconstructed weather time series will enhance our ability both to quantify changes in climate and the effects of that variability on both St. Kilda and Rum ecosystems and eventually to forecast the possible impacts of climate change.

2.2. Methods

Here, I present the study areas, describe the relationship between NAO and local weather and describe the methods used to compile and interpolate the climate data. I present two different methods for interpolation in order to illustrate the level of uncertainty in the resulting datasets.

All computations and graphics were done on the open source statistical computing environment R version 2.13.0 (R development Core Team 2011).

2.2.1. The study areas

St. Kilda

The St. Kilda Archipelago (57° 49' N, 8° 34' W), ranging from sea level up to 430 m (Conachair), is the most remote group of islands in Scotland, UK. The four main
islands of the St Kilda archipelago lie 160 km to the northwest of the Scottish mainland (figure 2-1). Hirta, the largest, has a total area of 638 ha and consists of a large, horseshoe-shaped bay facing the southeast surrounded by five of the islands’ main hills.

St. Kilda’s climate is oceanic, though its hills increase its annual rainfall. Annual rainfall is around 1100-1300 mm on the lower ground and snow occurs in winter, but rarely lies for more than a few days. Gales are common and occur from every direction and throughout the year (Clutton-Brock & Pemberton 2004). Three automatic weather stations were installed in the island of Hirta in 1999. Several weather variables are now recorded on a daily basis (minimum and maximum air temperature, average grass temperature, average wind speed, wind direction, maximum wind speed, total precipitation, soil water, total radiation, sunshine hours, growth hours and atmospheric pressure).

**Rum**

Rum (57° 0’ N, 6° 20’ W), is a more mountainous island, ranging from sea level up to the highest peak Askival, at over 810 m (Virtanen et al. 2002). Rum is a 10684 ha nature reserve situated in the Inner Hebrides off the northwestern coast of Scotland (figure 2-1). Like St. Kilda, it has an oceanic climate with mild wet and windy weather for much of the year (Clutton-Brock & Albon 1989). There are no drought periods; the summers and winters are mild, with low inter-annual variability in all the climatic variables (Clutton-Brock & Coulson 2000, Martinez-Jauregui et al. 2009). Up till summer 2011, there were no automatic weather stations in the study area; however, there are some automatic weather stations on other parts of the island. Nevertheless the time series are not continuous and are somewhat unreliable.
Figure 2-1 Two study areas (St Kilda and Rum) and their corresponding candidate proxy stations (Stornoway, Benbecula and Tiree).

2.2.2. The candidate proxy stations

Stornoway Airport
This is the best candidate for being a proxy station for St. Kilda. Stornoway is located in the Outer Hebrides, on the Isle of Lewis (58° 20' N, 6° 37' W), with an elevation of 15 m (figure 2-1). Like much of the British Isles, has an oceanic climate, with little variation in temperature and damp conditions throughout the year. Stornoway is approximately 137 km north east of St Kilda, so even though it is much farther away than Benbecula, it has a very complete daily weather record that dates back from the 1950s.

Benbecula Airport
This is the second best candidate for being a proxy station for St Kilda. Located in the Outer Hebrides, western Isles, Scotland (57° 47' N, 7° 36' W), with an elevation
of six metres (figure 2-1). Benbecula is approximately at 80 km east of St. Kilda, so it would be at first glance the best candidate, however, since 1986 the daily records are very incomplete (see quality control for more details).

**Tiree Airport**

Located in the Inner Hebrides (56° 50’ N, 6° 8’ W), with an average elevation of nine metres (figure 2-1). Tiree is approximately 69 km south west of Rum.

### 2.2.3. Climate data compilation and processing

Climate data were initially collected from a large number of sources.

1) The Global Surface Summary of Day Data (GSOD) version 7 (http://www1.ncdc.noaa.gov/pub/data/gsod/). GSOD data summaries are based on data exchanged under the World Meteorological Organisation (WMO). GSOD reports hourly data by year, month and day. GSOD has data for precipitation, mean temperature, and minimum and maximum temperature. There are large gaps in the geographic distribution of stations with temperature data. For some stations, “adjusted” data that had been through homogeneity control procedures were used (Peterson & Easterling 1994, Easterling & Peterson 1995). The candidate stations available in this database were Benbecula, Stornoway and Tiree. Temperature values were converted to degrees Celsius, precipitation to mm and wind-speed to $\text{ms}^{-1}$.

2) Stornoway station daily dataset compiled by the Climate Research Unit (CRU) for 1949 – 1995. This database includes minimum and maximum temperature, precipitation and wind-speed (from 1957). The CRU did extensive quality control on these data. Temperature values were converted to degrees Celsius, precipitation to mm and wind-speed to $\text{ms}^{-1}$.

3) British Atmospheric Data Centre (BADC). The data held at the BADC is from the Met Office Database-Midas Land Surface Observation Stations Data: (http://badc.nerc.ac.uk/home/). Long-term weather observation data were collected from the BADC for local stations Benbecula, Tiree and Stornoway. The database includes data for minimum and maximum temperature, precipitation and wind speed.

The data collected is hourly for the period of 1961-2009. Temperature was recorded in degrees Fahrenheit before 1961 and in degrees Celsius after that date. All temperature values are stored with a precision of 0.1 °C. I have converted all
temperatures to Celsius. The total amount of precipitation, which reaches the ground over a stated period, is expressed as the depth to which it would cover a horizontal surface. The reported accumulation of rainfall is the sum of the amount of liquid precipitation plus the liquid equivalent of any solid precipitation (that is the liquid obtained by melting snow or ice that has fallen). The unit of rainfall is mm and amounts are measured and reported to the nearest 0.2 mm (and where possible, to the nearest 0.1 mm). Inches were the sole unit of measurement until 1970. Where necessary, I have converted the values to mm. The achievable accuracy of precipitation measurements with rain gauges in current use is about 5% though errors will be larger at exposed sites. The unit of speed used at UK stations is the knot (0.515 ms\(^{-1}\)). The data are reported to the nearest knot. I have converted the observations of wind speed to ms\(^{-1}\).

Most of the files were in hourly data form. These hourly data were converted to daily values and dealt with throw back issues of having the minimum temperature match the correct day and not the next day (referring to data being spread out between day \(n\) and day \(n+1\)), so as to match the measurements taken in the automatic weather stations at the study sites for the period of the validation.

4) Met Office United Kingdom Climate projections (UKCP09) gridded data sets based on surface observations have been generated for a range of climatic variables. The data sets cover the UK at 0.5° by 0.5° resolution and span the period 1914–2006. They are available for daily, monthly and annual timescales (http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/available/daily.html). Regression and interpolation are used to generate values on a regular grid from the irregular station network, taking into account factors such as latitude and longitude, altitude and terrain shape, coastal influence and urban land use (Perry & Hollis 2005a). Again, the data were extracted for Tiree, Benbecula, Stornoway, and, for the first time, data were available for Kinloch in the Isle of Rum. No trustworthy gridded data are available for St. Kilda.

### 2.2.4. Quality control

As a first means of identifying errors in the location of the weather stations, all stations were checked for correspondence between the reported location and the location they mapped in. Time series were plotted to look for errors in values and
these were either corrected or removed.

The time series from GSOD (NOAA) at first seemed the best but they were not reliable and not continuous.

In the case of St. Kilda, the gridded datasets were also eventually ruled out since gridded series for St. Kilda need to be avoided due to St. Kilda being on the outer fringes of the UK landmass. Although very convenient, these datasets would not be expected to produce accurate results, since the values are averaged out and extremes and anomalies are removed (New et al. 2000, Mitchell & Jones 2005). In the case of Rum, gridded datasets were used as additional predictors for the GAM calibrations in the years these were available. The gridded datasets were much shorter and, of course, are interpolations themselves (New et al. 2000, Mitchell & Jones 2005).

Benbecula, as a candidate for St. Kilda proxy, was excluded because the series were too short and intermittent for a proper calibration. Also they had more than seven consecutive days missing in most months in all years, which was problematic for calibrations of rainfall, given its high daily variability. BADC and CRU datasets passed the tests for continuity and accuracy. The chosen proxy stations were not random. Stornoway was chosen as a proxy for St. Kilda and Tiree as a proxy for Rum. This was done understanding the caveats and limitations of the choices. While Benbecula would have been preferable to Stornoway, given its proximity and more similar exposure, the data were too incomplete for validations and subsequent interpolation.

I removed or corrected a large number of errors; obvious typos, clearly wrong coordinates and the wrong conversion between different units.

The final dataset for the Stornoway time series is the result of merging two different sources: BADC (1965-2009) and CRU (1949-1995). For the period where they overlapped, I cross-validated one against the other; this was done by calculating the correlation between the two time series for the overlapping period. The correlation was very high (0.99), so it was reasonable to merge the two datasets, in order to obtain a much longer time series for Stornoway. For the overlapping time period I used the BADC time series (which is more recent and continuous).
2.2.5. Models validation and cross-calibration

Two different methodologies were used for the calibration of both St Kilda and Rum with their respective proxy stations: linear regression models (Draper & Smith 1981) and general additive models (GAMs) (Hastie & Tibshirani 1996, Wood 2006). In each case the variable of interest is regressed against one or more variables from the chosen proxy weather station. Typically when predicting, rather than investigating mechanistic understanding, the principle of parsimony can be relaxed, and there is no penalty to using more complex models such as GAMs, so in this case, there is no need for model simplification (Anderson 2008, Claesken & Hjort 2008).

**Linear regression models**

The St. Kilda weather time series were calibrated by regression relationships from the 11-year overlapping period (1999-2009). The Rum weather time series were calibrated from the regression from the 28-year overlapping period, as well as gridded data (1971-1999). The four variables available for cross-calibration using that period are temperature (minimum and maximum), precipitation and wind-speed.

Simple linear regressions were carried out for each of the four variables every month and year to derive the relationship between the two stations. The linear regressions performed allowed me to calculate two coefficients (slope and intercept) to be used for the interpolation (Draper & Smith 1981, Crawley 2007).

**Pruning the outliers**

In order to look for influential points that distort the regression, pruning of sets of the lowest and highest values was carried out. Pruning extreme values was carried out in order to identify data points that are potentially erroneous but have been overlooked by the quality control from BADC. Therefore pruning is only carried out on the Stornoway data, for the most part. This was done in several steps:

1) By removing the lowest, then the highest and then both.

2) By removing the two lowest, then the two highest and then both.

3) By removing the three lowest, then the three highest and then both.

The resulting regressions and $r^2$ (coefficient of determination) were evaluated and compared. I chose model selection based on $r^2$ because it is used in the context of statistical models whose main purpose is the prediction of future outcomes on the basis of other related information. It is the proportion of variability in a data set that is accounted for by the statistical model (Steel & Torrie 1960). It provides a measure of
how well future outcomes are likely to be predicted by the model. $R^2$ is simply the square of the sample correlation coefficient between the outcomes and the values of the single regressor being used for prediction. The coefficient of determination ranges from 0 to 1.

**Generalised additive models (GAMs)**

In order to optimize the relationships, it was necessary to bring in additional variables. By using General Additive Models (GAMs) we can extend the standard linear regression model (Hastie & Tibshirani 1996, Wood 2006). For the GAM analysis and cross calibration I used the mgcv R package, which estimates penalized generalised linear models including generalised additive models (Wood 2006). The predictor effects are assumed to be linear in the parameters, but the distribution of the responses as well as the link between the predictors and this distribution can be quite general. I used a smoother, which is a tool for summarising the trend of a response measurement $y$ as a function of one or more predictor measurements. It produces an estimate of the trend that is less variable than $y$, hence the name smoother (Hastie & Tibshirani 1996, Wood 2006). An important property of the smoother in GAMs is its non-parametric nature: it does not assume a rigid form for the dependence of $y$ on $x_1, \ldots, x_p$ (Wood 2006). The smoother is useful as it enhances the visual appearance of the scatterplot $y$ vs $x$. It allows estimating dependence of the mean of $y$ on the predictors, and thus, serves as a building block for the estimation of additive models. The GAMs were performed for every month across the years. As with the linear regression, the period used for the cross calibrations was 1999-2009 for St Kilda and 1971-1999 for Rum. Further checks were performed, by assessing the monthly predictions. GAMs with one, two, three or four predictors were also performed and compared.

### 2.2.6. Interpolation

The St. Kilda and Rum time series were interpolated from the equations resulting from the GAMs for each month. Because the calibrations were performed using one proxy weather station only, no other covariates that might affect temperature, precipitation and wind speed were used (e.g. distance) with the risk that this might mask many of the local effects from incorporating topographic variables. In addition,
the standard exposure of UK meteorological stations means that data are preferentially collected from flat and open areas (Jarvis & Stuart 2001a, 2001b).

2.2.7. Trends

Using the reconstructed weather time series, I performed linear regression analysis to investigate trends across the years. This was performed for all the weather variables reconstructed, looking at median and mean monthly values for each month of the year. I then used bootstrapping (by scrambling the times series 10000 times) to test if the slopes of the regressions were significantly different from zero (Effron & Tibshirani 1993, Manly 2007).

2.2.8. The North Atlantic Oscillation (NAO)

An extended version of the index can be derived for the winter half of the year by using a station in the Southwestern part of the Iberian Peninsula (Hurrell 1995). Jones et al. (1997) used early instrumental data to extend this index back to 1823. Therefore for this chapter and subsequent chapters this is the version of index used. On December 2010, the Climate Research Unit (UEA) supplied the normalised monthly values of the NAO index up to November 2010. (See http://www.cru.uea.ac.uk/cru/data/nao/. NA depicts no data available for a specific month).

Winter NAO (wNAO) refers to the December through March average (see Osborn et al. 1999). For the purpose of the analysis carried out in this chapter and subsequent chapters, wNAO of year \(x\) refers to December of year \(x-1\) and January through March of year \(x\). Summer NAO (sNAO) refers to high summer average, July and August (Hurrell, 1995). sNAO of year \(x\) refers to both July and August of year \(x\). This was decided as to avoid discrepancies when using it to analyse in conjunction with Soay sheep population changes (see chapter 4 Methods for more information). Briefly however, the issue is that mortality in February and March of year \(x\) is interpreted in relation to sheep population density measured in August of year \(x-1\).
2.3. Results

2.3.1. Winter NAO as a predictor of St. Kilda local weather variables

Winter NAO is not a good predictor for winter local weather in St. Kilda (as defined as the months of December through March). February precipitation is the only variable that was correlated with wNAO (figure 2-2), but only when using the 11-year data from the automatic weather station (other months not shown). When we use the longer time series 1957-2012 there is no significant correlation (figure 2-3).

![Figure 2-2 Winter NAO predicting St. Kilda February precipitation (mm) using the weather data from the automatic weather station at St. Kilda (1999-2010). $R^2 = 0.61$, positive relationship, $p=0.008$.](image-url)
Figure 2-3 Winter NAO predicting St. Kilda February weather using the weather reconstructed time series (1957-2010) in all four panels. Top left, February minimum temperature; top right, February maximum temperature; bottom left, February precipitation; bottom right, February wind speed. There is not correlation between any of February weather and wNAO.

2.3.2. Winter NAO as a predictor of Rum local weather variables

Winter NAO is a much better predictor for Rum local weather. It is highly correlated with the winter months: December (figure not shown) maximum temperature and precipitation (p=0.003 and p=0.03, respectively); January (figure not shown) temperature (minimum and maximum) and precipitation (p=0.03, p=0.001, p=0.0005, respectively); February (figure 2-6) temperature (minimum and maximum), precipitation and wind speed (p=0.003, p=0.004, p=0.001, p=0.002, respectively); March (figure 2-7) minimum temperature and precipitation (p=0.005 and p=0.005, respectively).
Figure 2-4 Winter NAO predicting February local weather using the reconstructed weather time series (1965-2010) Top left shows February minimum temperature correlation with wNAO, dashed line shows the regression line $p=0.003$. Top right shows February maximum temperature correlation with wNAO, dashed line shows the regression line $p=0.004$. Bottom left shows February precipitation correlation with wNAO, dashed line shows the regression line $p=0.001$. Bottom right shows February wind speed correlation with wNAO, dashed line shows the regression line $p=0.002$. 
2.3.3. Pruning the outliers

I removed values of daily precipitation that were above a set threshold of 45 mm on both island and proxy. These values were checked and believed to be errors that would affect the predictive power of the model. I will only show some illustrative examples of pruning, although this was performed for all month and all years for both St. Kilda and Rum calibrations. From the resulting regressions and $r^2$, pruning never improves the relationship between the two stations. The fact that the relationship between the two islands is never of slope 1 and intercept zero means, that relationship might not be exactly linear, so pruning outliers might not be the best approach.
Maximum temperature

Figure 2-6 Pruning the values from September 2002 maximum temperature. Top left panel shows no pruning. Top middle shows pruning the lowest value (blue); top right pruning of the highest value (yellow). Bottom left, shows pruning of both highest and lowest (red). Bottom middle shows pruning of the 2 lowest and the 2 highest (green). Bottom right panel shows pruning of the 3 lowest and the 3 highest (purple). The resulting changes in $r^2$ and regression line are shown.
Minimum temperature

Figure 2-7 Pruning the values from December 1999 maximum temperature. Top left panel shows no pruning. Top middle shows pruning the lowest value (blue); top right pruning of the highest value (yellow). Bottom left, shows pruning of both highest and lowest (red). Bottom middle shows pruning of the 2 lowest and the 2 highest (green). Bottom right panel shows pruning of the 3 lowest and the 3 highest (purple). The resulting changes in \( r^2 \) and regression line are shown.
Precipitation

In an ideal world, the intercept would be zero and slope would be 1. This is not the case; the slope is always less than 1. And the intercept is different from zero. Stornoway is rainier than St. Kilda. The relationship may also not be linear.

Figure 2-8 Pruning the values from January 2002 precipitation. Top left panel shows no pruning. Top middle shows pruning the lowest value (blue); top right pruning of the highest value (yellow). Bottom left, shows pruning of both highest and lowest (red). Bottom middle shows pruning of the 2 lowest and the 2 highest (green). Bottom right panel shows pruning of the 3 lowest and the 3 highest (purple). The resulting changes in $r^2$ and regression line are shown.
Wind speed

This is surprising. It was expected that St. Kilda would be windier than Stornoway.

![Graphs showing wind speed comparison between Stornoway and St. Kilda for June 2006, with different pruning scenarios.](image)

Figure 2-9 Pruning the values from June 2006 wind speed. Top left panel shows no pruning. Top middle shows pruning the lowest value (blue); top right pruning of the highest value (yellow). Bottom left, shows pruning of both highest and lowest (red). Bottom middle shows pruning of the 2 lowest and the 2 highest (green). Bottom right panel shows pruning of the 3 lowest and the 3 highest (purple). The resulting changes in $r^2$ and regression line are shown.
### 2.3.4. Calibrations using linear regression

The analysis was carried out for all available four variables: minimum and maximum temperature, precipitation and wind speed for both St. Kilda and Rum. Here, I show illustrative examples of the best and worst for each variable at different months. For all the variables examined, slope is not equal to 1 and the intercept is not equal to 0. This means that the correlation between the two islands is not straightforward.

**Maximum temperature**

In this particular case, the intercept is 3.87 and the slope is 0.63 ($F_{1,277} = 534.8$, $p < 0.001$). This means that at low temperatures, in January, St. Kilda is comparatively warmer than Stornoway than at high maximum temperatures. The range of temperatures in Stornoway is bigger; meaning the maximum temperature in St. Kilda is less variable.

![Figure 2-10 January maximum temperature calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid line shows the regression $y = 3.87 + 0.53x$, $r^2 = 0.577$.](image)

For the case of August, as above, the intercept is bigger than 0 and the slope is positive and smaller than 1 ($F_{1,294} = 174.9$, $p < 0.001$).

This means that, In August, at low temperatures, St. Kilda is comparatively warmer than Stornoway than at high maximum temperatures. The range of temperatures in Stornoway is bigger; meaning the maximum temperature in St. Kilda is less variable. The relationship holds even in the less correlated months.
Here, as with maximum temperature, the intercept is not 0 and the slope is positive and smaller than 1. This means that at low temperatures, in February, St. Kilda is comparatively warmer than Stornoway than at high minimum temperatures ($F_{1, 252} = 297, p < 0.001$). The range of temperatures in Stornoway is bigger; meaning the minimum temperature in St. Kilda is less variable.

**Minimum temperature**

Figure 2-11 August maximum temperature calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid line shows regression $y = 0.672 + 0.51x$, $r^2 = 0.37$.

Figure 2-12 February minimum temperature calibrations across the years using Stornoway and St. Kilda data for 1999-2010. The solid line is the regression $y = 3.27 + 0.54$, $r^2 = 0.55$. 

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The relationship holds even in the less correlated months, like August ($F_{1,294} = 136.7$, $p < 0.001$).

![Figure 2-13 August minimum temperature calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid line is the regression $y = 7.48+0.41x$, $r^2 = 0.32$.](image)

**Precipitation**

Here, again, the intercept is not 0 and the slope is positive and smaller than 1. For March, this means that in drier conditions, St. Kilda is comparatively wetter than Stornoway than in wetter conditions ($F_{1,277} = 290.6$, $p < 0.001$).

The precipitation range in Stornoway is wider; meaning the precipitation in St. Kilda is less variable. The relationship holds even in the less correlated months.

![Figure 2-14 March precipitation calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid lines shows regression $y = 0.95+0.91x$, $r^2=0.52$.](image)
The relationship holds even in the less correlated months, like February ($F_{1, 252} = 77.52$, $p < 0.001$).

![Graph of St Kilda Precipitation vs Stornoway Precipitation](image1)

**Figure 2-15** February precipitation calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid line shows regression $y = 2.82 + 0.31x$, $r^2 = 0.23$.

**Wind speed**

The intercept is bigger than 0 and the slope is positive and smaller than 1. This means that in September, Stornoway is comparatively windier than St. Kilda. The range in Stornoway is wider; meaning the average wind speed in St. Kilda is less variable. For every ms$^{-1}$ increase, in average wind speed in Stornoway, average wind speed in St. Kilda only increases by 0.45ms$^{-1}$ ($F_{1, 298} = 496.7$, $p < 0.001$).

![Graph of St Kilda Wind Speed vs Stornoway Wind Speed](image2)

**Figure 2-16** September wind speed calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid line shows regression $y = 0.8 + 0.45x$, $r^2 = 0.63$. 

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The relationship holds even in the less correlated months. Stornoway is windier than St. Kilda. In October, for every ms$^{-1}$ increase, in average wind speed in Stornoway, average wind speed in St. Kilda only increases by 0.37ms$^{-1}$ ($F_{1, 318} = 287.8$, $p < 0.001$).

![Graph showing wind speed calibration across years](image)

**Figure 2-17** October wind speed calibrations across the years using Stornoway and St. Kilda data for 1999-2010. Solid line shows regression $y = 1.7+0.37x$, $r^2 = 0.43$.

### 2.3.5. Calibrations using generalised additive models (GAMs)

For both islands calibrations and cross validations were carried out for all four variables: minimum and maximum temperature (°C), precipitation (mm) and wind speed (ms$^{-1}$). This was done to evaluate comparatively the performance of each interpolation method (Willmott & Robeson 1995). After evaluating predictions using one, two, three and four predictors in the GAMs, I decided to use all four variables as predictors, since the deviance explained was much higher, the more predictors I used. There is no penalty for not going for the simpler most parsimonious model in predictions (Anderson 2008, Claesken & Hjort 2008). I show examples for each variable at different months across the years when using GAMs with all four weather variables from the proxy station as predictors for the calibration between proxy and each weather variable of my systems. Extreme values of precipitation were considered erroneous data and were thus identified and removed with the affected months/variables being rerun.
St. Kilda- Calibrations using two predictors

As expected, when using fewer predictors, the resulting calibration between both islands is not as strong. This is true for all variables. Therefore I will only show one example for illustration purposes.

Figure 2-18 GAM results for predicting St. Kilda November minimum temperature from the two-predictor variables from Stornoway (minimum and maximum temperature). The left panel is a scatter plot of predicted against observed values with a regression line showing the St Kilda prediction against the value observed on St. Kilda on the same day; The next 2 panels show St. Kilda on the y axis and Stornoway on the x axis with a non parametric smoother (solid line) and a 95% confidence interval for the fitted line (dashed lines) for minimum temperature (centre), maximum temperature (right). Deviance explained 0.69.

St. Kilda- Calibrations using four predictors

I show one example for each variable. The following graphs all have the same structure. In the top left is a scatterplot of predicted against observed values; the next four panels, show St. Kilda on the y axis and Stornoway on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for minimum temperature (top centre), maximum temperature (top right), daily rainfall (bottom left) and wind speed (bottom centre).

To look for the most obvious correlation the appropriate panel will change from variable to variables.
Maximum temperature

Figure 2-19 GAM results for predicting St. Kilda January maximum temperature from the four-predictor variables from Stornoway (minimum temperature, maximum temperature, precipitation and wind speed). The top left panel is a scatter plot of predicted against observed values with a regression line showing the St Kilda prediction against the value observed on St. Kilda on the same day; The next 4 panels show St Kilda on the y axis and Stornoway on the x axis with a non parametric smoother (solid line) and a 95% confidence interval for the fitted line (dashed lines) for minimum temperature (top centre), maximum temperature (top right), daily rainfall (bottom left) and wind speed (bottom centre). The deviance explained 0.74.
Minimum temperature

Figure 2-20 GAM results for predicting St. Kilda November minimum temperature from the four-predictor variables from Stornoway (minimum temperature, maximum temperature, precipitation and wind speed). The top left is a scatter plot of predicted against observed values with a regression line showing the St. Kilda prediction against the value observed on St Kilda on the same day; The next 4 panels show St Kilda on the y axis and Stornoway on the x axis with a non parametric smoother (solid line) and a 95% confidence interval for the fitted line (dashed lines) for minimum temperature (top centre), maximum temperature (top right), daily rainfall (bottom left) and wind speed (bottom centre). The deviance explained 0.74.
Precipitation

Figure 2-21 GAM results for predicting St. Kilda February precipitation from the four-predictor variables from Stornoway (minimum temperature, maximum temperature, precipitation and wind speed). The top left is a scatter plot of predicted against observed values with a regression line showing the St Kilda prediction against the value observed on St. Kilda on the same day; The next 4 panels show St Kilda on the y axis and Stornoway on the x axis with a non parametric smoother (solid line) and a 95% confidence interval for the fitted line (dashed lines) for minimum temperature (top centre), maximum temperature (top right), daily rainfall (bottom left) and wind speed (bottom centre). The deviance explained 0.58.
Wind speed

Figure 2-22 GAM results for predicting St. Kilda March wind speed from the four predictor variables from Stornoway (minimum temperature, maximum temperature, precipitation and wind speed). The top left is a scatter plot of predicted against observed values with a regression line showing the St. Kilda prediction against the value observed on St Kilda on the same day; The next 4 panels show St Kilda on the y axis and Stornoway on the x axis with a non parametric smoother (solid line) and a 95% confidence interval for the fitted line (dashed lines) for minimum temperature (top centre), maximum temperature (top right), daily rainfall (bottom left) and wind speed (bottom centre). The deviance explained 0.56.

St. Kilda Monthly predictions
The analysis was carried out for all four variables. I show the best and worst prediction for each variable at different months across the years. Analogous analysis was carried out for Rum but results were similar so I don’t include the figures.
Maximum temperature

Figure 2-23 St. Kilda predicted monthly means. Left panel shows April mean monthly maximum temperature observed and mean monthly predictions with an x=y line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned.

Figure 2-24 St. Kilda predicted monthly means. Left panel shows July mean monthly maximum temperature observed and mean monthly predictions with an x=y line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.
Minimum temperature

![Graph](image)

Figure 2-25 Predicted monthly means. Left panel shows December mean monthly minimum temperature observed and mean monthly predictions with an $x=y$ line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.

![Graph](image)

Figure 2-26 Predicted monthly means. Left panel shows June mean monthly minimum temperature observed and mean monthly predictions with an $x=y$ line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.
Precipitation

Figure 2-27 Predicted monthly means. Left panel shows December mean monthly precipitation observed and mean monthly mean predictions with an x=y line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.

Figure 2-28 Predicted monthly means. Left panel shows September mean monthly precipitation observed and mean monthly mean predictions with an x=y line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.
Wind speed

Figure 2-29 Predicted monthly means. Left panel shows August mean monthly average wind speed observed and mean monthly mean predictions with an x=y line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.

Figure 2-30 Predicted monthly means. Left panel shows May mean monthly average wind speed observed and mean monthly mean predictions with an x=y line (from the GAM calibrations). Right shows the difference between observed and predicted for the daily data and for the monthly means. Extreme precipitation values were pruned. The line in each box represents the 50th percentile.
Rum - GAM Calibrations using all predictors

For Rum calibration and interpolation of wind speed was not possible given that the series available for Rum was too short and intermittent. So for the purpose of analyses in chapter 4, Tiree wind time series is used. I will only show some examples, given that the St. Kilda examples illustrate the same points.

I will show one example for each variable. The following graphs all have the same structure. In the top left is a scatterplot of predicted against observed values; the next eight panels, show Rum on the y axis and proxy on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for Kinloch gridded minimum temperature (top centre), Kinloch gridded maximum temperature (top right); Tiree station weather minimum temperature (second row left centre), Tiree station weather maximum temperature (second row centre), Tiree gridded minimum temperature (second row left), Tiree gridded maximum temperature (Bottom left); daily Kinloch gridded rainfall (bottom centre), Tiree station weather daily rainfall (bottom left).
Maximum temperature

Figure 2-31 GAM results for predicting Rum January maximum temperature from the Tiree weather station minimum and maximum temperature and precipitation predictor variables. Also using gridded data available for Rum and Tiree for the same variables. In the top left is a scatterplot of predicted against observed values; the next eight panels, show Rum on the y axis and proxy on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for Kinloch gridded minimum temperature (top centre), Kinloch gridded maximum temperature (top right); Tiree station weather minimum temperature (second row left centre), Tiree station weather maximum temperature (second row centre), Tiree gridded minimum temperature (second row left), Tiree gridded maximum temperature (Bottom left); daily Kinloch gridded rainfall (bottom centre), Tiree station weather daily rainfall (bottom left). Deviance explained 0.98.
Minimum temperature

![Diagram of GAM results for predicting Rum June minimum temperature from the Tiree weather station minimum and maximum temperature and precipitation predictor variables. Also using gridded data available for Rum and Tiree for the same variables. In the top left is a scatterplot of predicted against observed values; the next eight panels, show Rum on the y axis and proxy on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for Kinloch gridded minimum temperature (top centre), Kinloch gridded maximum temperature (top right); Tiree station weather minimum temperature (second row left centre), Tiree station weather maximum temperature (second row centre), Tiree gridded minimum temperature (second row left), Tiree gridded maximum temperature (Bottom left); daily Kinloch gridded rainfall (bottom centre), Tiree station weather daily rainfall (bottom left). Deviance explained 0.97.]
Chapter 2 Reconstructing local weather time series for the islands of St. Kilda and Rum

Precipitation

Figure 2-33 GAM calibration results for predicting Rum November precipitation from the Tiree weather station minimum and maximum temperature and precipitation predictor variables. Also using gridded data available for Rum and Tiree for the same variables. In the top left is a scatterplot of predicted against observed values; the next eight panels, show Rum on the y axis and proxy on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for Kinloch gridded minimum temperature (top centre), Kinloch gridded maximum temperature (top right); Tiree station weather minimum temperature (second row left centre), Tiree station weather maximum temperature (second row centre), Tiree gridded minimum temperature (second row left), Tiree gridded maximum temperature (Bottom left); daily Kinloch gridded rainfall (bottom centre), Tiree station weather daily rainfall (bottom left). Deviance explained 0.99.
2.3.6. The resulting St. Kilda and Rum weather time series

The predicted St. Kilda and Rum weather time series were derived from the GAM calibration equations where the extremes values were pruned (see figures above). Upon visual inspection the residuals appear to be normally distributed, with zero mean and constant variance, so no further testing is necessary. Kilda reconstructed final time series is composed of the reconstructed weather time series from 1957-1999 and the AWS data from 1999-current (see figures 2-34 and 2-35 for illustration).

![Graph showing temperature over time](image)

Figure 2-34 St. Kilda minimum temperature complete daily time series. Red line shows period 1957-mid August 1999 that corresponds to the reconstructed time series. Black line shows AWS times series for the period from mid August 1999-current.
Figure 2-35 St. Kilda precipitation complete daily time series. Red line shows period 1957-mid August 1999 that corresponds to the reconstructed time series. Black line shows AWS times series for the period from mid August 1999-current. The higher value (>80 mm) in 2004 was not removed, as it was a particular rainy day across all the Hebrides.

For Rum the weather reconstruction had had contributions from many different sources as shown in the figures 2-26 and 2-37 (only showing maximum temperature and precipitations as examples).
Figure 2-37 Rum precipitation complete daily time series. Red line shows period 1965 to 1971 where reconstruction is done using BADC time series for Tiree. Black line is actual Rum at Kinloch BADC weather time series for the period of 1971-1999. Red line, as before, for the period of 1999-2004. Blue line corresponds to interpolation using gridded data for Kinloch for the period of 2004-2007. Green line corresponds to interpolation using gridded data for Tiree for the period of 2007-2010. The orange line corresponds to the newly added AWS at Rum from 2011-current.
2.3.7. Trends

For both St. Kilda and Rum, regression analysis performed on all four variables looking at median and mean monthly possible trends for all 12 months are shown in summary tables 2-2 and 2-3. Some of the trended months are shown for illustration purposes.

St. Kilda

I show some illustrations of trends in weather for the period of 1957-2012. For maximum temperature, 3 months of the year show an upward trend. For minimum temperature, 8 months of the year show an upward trend. For total precipitation, only December shows a trend (downward). For average wind speed, 8 months of the year show a downward trend (see table 2-1 for summary statistics).

![Figure 2-38 St Kilda November daily maximum temperature for the period of 1957-2011. Boxplots show daily values. Solid line shows the linear regression for the monthly mean maximum November temperature over each year (0.02±0.005 SE); dashed line shows the linear regression for the monthly median maximum November temperature over each year (0.02±0.007 SE). November monthly mean maximum temperature has risen about 0.9°C in 55 years.](image-url)
Chapter 2 Reconstructing local weather time series for the islands of St. Kilda and Rum

Figure 2-39 St Kilda December daily total precipitation for the period of 1957-2011. Boxplots show daily values. Solid line shows the linear regression for the monthly mean December daily total precipitation over each year (0.03±0.01 SE); dashed line shows the linear regression for the monthly median December daily total precipitation over each year (0.05±0.01 SE). December daily total precipitation has decreased about 1.65 mm in 55 years.

There is some structure in these time series. This may replay further detailed analysis in due course. One could argue that there is a step function from 1975.

Figure 2-40 St Kilda December average wind speed for the period of 1957-2011. Boxplots show daily values. Solid line shows the linear regression for the monthly mean December average wind speed over each year (0.03±0.005 SE); dashed line shows the linear regression for the monthly median December daily total precipitation over each year (0.03±0.006 SE). December average wind speed has decreased about 1.65 ms\(^{-1}\) in 55 years.
Table 2-1 St. Kilda mean monthly weather trends for the period 1957-2011. Only the months that show a significant trend are shown. Both minimum and maximum temperature trend months show a positive trend. Slope, standard error (S.E.) and p values are related to the linear regression for the monthly mean daily values over each year. ‘+’ sign denotes upward trend; ‘-’ sign denotes a downward trend.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Month</th>
<th>Slope</th>
<th>S.E.</th>
<th>P value</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Maximum temperature</strong></td>
<td>January</td>
<td>0.014</td>
<td>0.007</td>
<td>0.04</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.01</td>
<td>0.004</td>
<td>0.02</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.01</td>
<td>0.006</td>
<td>0.007</td>
<td>+</td>
</tr>
<tr>
<td><strong>Minimum temperature</strong></td>
<td>January</td>
<td>0.017</td>
<td>0.008</td>
<td>0.03</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>0.02</td>
<td>0.008</td>
<td>0.02</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>0.02</td>
<td>0.007</td>
<td>0.01</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.01</td>
<td>0.004</td>
<td>0.003</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>0.01</td>
<td>0.005</td>
<td>0.01</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>0.01</td>
<td>0.005</td>
<td>0.01</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.03</td>
<td>0.008</td>
<td>0.0005</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>0.02</td>
<td>0.007</td>
<td>0.01</td>
<td>+</td>
</tr>
<tr>
<td><strong>Total precipitation</strong></td>
<td>December</td>
<td>0.03</td>
<td>0.01</td>
<td>0.01</td>
<td>+</td>
</tr>
<tr>
<td><strong>Average wind speed</strong></td>
<td>January</td>
<td>-0.02</td>
<td>0.005</td>
<td>0.0006</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>-0.01</td>
<td>0.006</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>-0.01</td>
<td>0.004</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>-0.01</td>
<td>0.004</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>-0.008</td>
<td>0.002</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>-0.013</td>
<td>0.004</td>
<td>0.003</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>-0.01</td>
<td>0.004</td>
<td>0.025</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>-0.03</td>
<td>0.004</td>
<td>1.5e-6</td>
<td>-</td>
</tr>
</tbody>
</table>
Rum

I show some illustrations of trends in weather for the period of 1965-2011. For maximum temperature, 7 months of the year are trended. For minimum temperature, 5 months of the year trended. No trends for total precipitation. For average wind speed, 7 months of the year are trended (see table 2-2 for summary statistics). There is some structure in these time series. This may replay further detailed analysis in due course.

Figure 2-41 Rum November maximum temperature for the period of 1965-2011. Boxplots show daily values. Solid line shows the linear regression for the monthly mean maximum November temperature over each year (0.05±0.001 SE); dashed line shows the linear regression for the monthly median maximum November temperature over each year (0.05±0.01 SE). November monthly mean maximum temperature has risen about 2.35°C in 47 years.
Figure 2-42 April minimum temperature for the period of 1965-2011. Boxplots show daily values. Solid line shows the linear regression for the monthly mean minimum April temperature over each year (0.03 ± 0.01 SE); dashed line shows the linear regression for the monthly median minimum April temperature over each year (0.04 ± 0.01 SE). April monthly mean minimum temperature has risen about 1.4°C in 47 years.

Figure 2-43 December average wind speed for the period of 1965-2011. Boxplots show daily values. Solid line shows the linear regression for the monthly mean December average wind speed over each year (0.04 ± 0.01 SE); dashed line shows the linear regression for the monthly median December average wind speed over each year (0.04 ± 0.01 SE). December monthly mean average wind speed has decreased about 1.88 ms⁻¹ in 47 years.
Table 2-2 Rum significant monthly weather trends for the period 1965-2011. Only the months that show a significant trend are shown. Both minimum and maximum temperature trend months show a positive trend. Slope, standard error (S.E.) and p values are related to the linear regression for the monthly mean daily values over each year. ‘+’ sign denotes upward trend; ‘-’ sign denotes a downward trend.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Month</th>
<th>Slope</th>
<th>S.E.</th>
<th>P value</th>
<th>Sign</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Maximum temperature</strong></td>
<td>February</td>
<td>0.035</td>
<td>0.01</td>
<td>0.006</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>0.024</td>
<td>0.01</td>
<td>0.011</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>0.037</td>
<td>0.01</td>
<td>0.008</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>0.030</td>
<td>0.01</td>
<td>0.031</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.032</td>
<td>0.01</td>
<td>0.019</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>0.023</td>
<td>0.01</td>
<td>0.015</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.045</td>
<td>0.01</td>
<td>2.91x10^{-5}</td>
<td>+</td>
</tr>
<tr>
<td><strong>Minimum temperature</strong></td>
<td>March</td>
<td>0.025</td>
<td>0.01</td>
<td>0.058</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>0.039</td>
<td>0.01</td>
<td>0.003</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.021</td>
<td>0.01</td>
<td>0.021</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>0.031</td>
<td>0.01</td>
<td>0.004</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.043</td>
<td>0.01</td>
<td>0.002</td>
<td>+</td>
</tr>
<tr>
<td><strong>Average wind speed</strong></td>
<td>March</td>
<td>-0.027</td>
<td>0.01</td>
<td>0.058</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>-0.025</td>
<td>0.01</td>
<td>0.018</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>-0.019</td>
<td>0.01</td>
<td>0.034</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>-0.022</td>
<td>0.01</td>
<td>0.033</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>-0.028</td>
<td>0.01</td>
<td>0.029</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>-0.029</td>
<td>0.01</td>
<td>0.015</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>-0.045</td>
<td>0.01</td>
<td>0.001</td>
<td>-</td>
</tr>
</tbody>
</table>
In both islands, when trended, the weather variables show the same sign: Minimum and maximum temperature increasing and average wind speed decreasing.

![Figure 2-44 Proportion of significantly trended months for each weather variable. In green St. Kilda, in blue, Rum.](image)

### 2.4. Discussion

As a result of the spatial interpolation, the St. Kilda and Rum weather time series finally have a complete and homogenous, daily minimum, maximum temperatures, precipitation and wind speed that run from 1957 and 1965 respectively, until 2011 (figures 2-35-2-37). These data are to be incorporated on the Hebrides database. Climate data at this very local scale will allow for more robustness when constructing models for biological systems. Unfortunately, additional independent variables like pressure and sun hours, although highly influential in predictions, especially for precipitation (Jarvis & Stuart, 2001a, 2001b), were not available for the proxy station during the overlap period and were therefore not included in the models, as only recent data are available for these.

In this chapter, the variables were included in the calibration process on the basis of both their strength of relationship and according to their consistency of selection, to account for both average and extreme weather patterns. Stornoway time series has proven to be a very good predictor for St. Kilda, despite being
137 km away. The same can be concluded about Tiree in regards to Rum. Despite the overall similarity in climate patterns, when using linear regressions for the calibration, the differences between the island and its proxy are marked, especially in terms of range and variability (figures 2-10-2-17). The reasons for this have been discussed extensively in New et al. (2002), and in this case, they can be attributed to differences in exposure, since in terms of elevation they are not significantly different. Stornoway is sheltered from the westerly winds. As a result from being on the Isle of Lewis, the largest Hebridean island, it has a more “continental” climate. Looking at the linear regressions, the simpler interpolation technique used, we can see that the cross calibration actually manages to capture most of the relationships between stations. Nevertheless it fails to address the non-linearity of the relationship between variables (figures 2-10-2-21). By looking at the linear regressions we can see that it is on average four degrees warmer in St. Kilda and it is windier and it rains more (figures 2-10-2-17). Pruning values on the linear regressions showed that by removing the highest and or lowest values the model changed at times quite significantly (figures 2-6-2-9), nevertheless it actually did not improve the relationship between island and proxy. It was surprising to see that Stornoway, contrary to expectations is windier than St. Kilda. This could be due to the position of the AWS on St. Kilda; these are relatively sheltered in the study population so this may account for the unintuitive relationship between St. Kilda and Stornoway.

The generalised additive models, although more complex, were able to better capture the relationships between stations for both islands (figures 2-18-2-22 and 2-31-2-33). This is in agreement with the idea that prediction is not driven by parsimony. Figures 2-22-2-25 show the prediction of St. Kilda weather when using all four variables (minimum and maximum temperature, precipitation and wind speed). All the regressor variables contributed significantly to the model, suggesting that the choice of regressor has a significant effect on the resulting accuracies.

GAM calibrations were also tried using fewer predictors. These predictions were not as good (see figure 2-18 for example); therefore it is safe to assume that there is no obvious advantage of model simplification when prediction is the objective. Also, from looking at the GAMs we can conclude that the incorporation of additional covariates is very influential (see both St. Kilda and Rum GAM outputs). This can also be seen by the calibration for Rum, which use many predictors (figures 2-31-2-33). The cross-validation error is reasonably low. Despite the high
variance in predictions of daily weather, the mean monthly predictions are well behaved. This is especially illustrated in the monthly predictions produced by the GAM calibration (see for example 2-23-2-30, only St Kilda shown as an example).

For both St. Kilda and Rum, despite being overall agreement between the island and the proxy time series, the variation between the sites exists (maximum deviance explained for St Kilda was 0.74 and for Rum 0.99). This clearly indicates that we there is some uncertainty about the values. The calibrations do not necessarily capture all the extreme variation that may occur at the study site. This is a common issue seen in the literature (e.g. precipitation in mountainous areas) (New et al. 2002). The differences found likely reflect the difference between a pure statistical and a more mechanistic expert-driven approach to interpolation. Model comparison work focusing on these geographic areas would be useful. Temperature is know to be particularly spatially coherent, but it may be that when interpolating a more noisy variable, such as precipitation, a greater emphasis of process based information will be critical (Wilmott & Matsuura 1995). The extent to which uncertainty should be a problem depends on the application of the data.

The accuracy of the interpolations varies, as it is dependent on the nature of the variable and the density of data available for the calibrations. As expected, spatially more homogenous variables, like temperature, are better predicted, in both the linear regression and models (figures 2-10-2-22 and), whereas, spatially heterogeneous variables like precipitation are most difficult.

As expected, winter NAO is a weak predictor for local weather conditions in St. Kilda (figures 2-2-2-3). To this end, I correlated winter NAO with all the locally measured weather variables from St. Kilda automatic station weather (installed at the end of 1999) and discovered that the only significant correlation of NAO was with February rainfall ($r^2=0.61$, positive relationship; $p=0.008$) and wind speed in February ($r^2=0.56$, positive relationship; $p=0.03$, figure not shown). However, when using the longer weather time series, none of the winter months (December-March) weather variables were correlated with winter NAO. Winter NAO is a good predictor for winter weather in Isle of Rum. It is highly correlated with the winter months: December (figure not shown) maximum temperature and precipitation ($p=0.003$ and $p=0.03$, respectively); January (figure not shown) temperature (minimum and maximum) and precipitation ($p=0.03$, $p=0.001$, $p=0.0005$, respectively); February (figure 2-6) temperature (minimum and maximum), precipitation and wind speed ($p=0.003$,
p=0.004, p=0.001, p=0.002, respectively); March (figure 2-7) minimum temperature and precipitation (p=0.005 and p=0.005, respectively). This could possibly be due to the fact that St. Kilda is farther away from the mainland.

Linear regression models and bootstrapping for each of the islands show evidence of weather trends in both islands, we can see that there is evidence of increasing warming and most obviously decrease of wind intensity (tables 2-1 and 2-2 and figures 2-38-2-43). Precipitation regimes are not trended in either island, apart from one month of the years in St Kilda (December) where we see a slight increase in mean precipitation (figure 2-44).

Apart from better and more input data, there are additional ways in which future research might improve our climate surfaces. If regional interpolations are done in collaboration with climatologists familiar with the area, and within a knowledge-based framework, much more of the known regional climatic peculiarities might be captured. Such an approach could also investigate the value of correcting, or removing data from time periods.

In conclusion, I have made the first attempt in reconstructing the weather time series for St. Kilda and Rum. Both sides now have good, replicated AWS. The value of the present work is in extending the series back in time to the period when this was not the case. There may be potential for improving the results further, e.g. by including further factors into the regression model. This will prove invaluable for the study of climate effects on the Soay sheep and red deer populations and plant community dynamics. While I have made a significant progress, additional efforts to compile and capture climate data are needed to improve spatial and temporal coverage of the available climate data and quality control (Mitchell & Jones 2005) and interpolation methods can be further refined to better use these data.

It is reassuring that the number of months and the sign of the trends are consistent for all variables across both islands.
Chapter 3 The effects of weather and phenology on primary production at the Park Grass Experiment, Rothamsted over 130 years

Abstract
Future climate is forecasted to include greater precipitation variability and more frequent heat waves, but the degree to which the timing of climate variability impacts ecosystems is uncertain. I examined the seasonal impacts of climate variability on 130 years of grass productivity at the Park Grass Experiment, in the South of England. This chapter provides two key contributions to the literature, focusing on the question of when is weather most critical for yield. First, I estimate the relationship between weather and yields over a period of 130 years by splitting this period into sub periods and found that weather impacts change over time. Moreover, this is especially obvious by the different weather predictors affecting first and second yields within a year. I found that spring rainfall affects the sward productivity throughout the growing season, with a carrying over effect on to autumn yield. Not surprisingly, for second yield, the size of the first yield in the same year is very important. For both yields, spring rain and temperature are critical. Second, I explore both linear and non-linear impacts of weather on yield. I am thus have found non-linear relationships of temperature and rainfall on yield. The slope of the decline above an optimum is significantly steeper than the incline below it. If these patterns are general across ecosystems, predictions of ecosystem response to climate change will have to account not only the magnitude of climate variability but also for its timing.
3.1. Introduction

Many studies have focused on the response of species to climate change (Root et al. 2003, Rosenweig et al. 2008). However, not only are the mean climate conditions changing, but also temporal fluctuations in climate (Salinger 2005, IPCC 2007). Plants respond to cumulative effects of daily weather over a protracted period, so their developmental stages are integrators of weather data. One specific measure, the first appearance of spring foliage, is particularly important because it often shows the strongest response to temperature change and is crucial for accurate assessment of processes related to the start and duration of the growing season (Roy & Sparks 1995).

Phenology is the study of the timing of life history events that occur in a seasonal and repeated pattern (Forrest & Miller-Rushing 2010). Changes in phenology have long been regarded as sensitive indicators of climatic change. Observations of key life history events, collected either deliberately or incidentally, extend as far back as the 1700’s in Europe (Sparks & Carey 1995). Since the late 1990’s there has been an increasing recognition of the value of phenological records for documenting and projecting the effects of climate change on the natural world (Walther et al. 2002, Parmesan & Yohe 2003). Many studies have revealed correlations between interannual variation in phenology and climate (e.g. Roy & Sparks 2000, Fitter & Fitter 2002). A combination of the sensitivity of spring phenology to climate and the ease of recording such traits has made spring phenological advances among high latitude species the most commonly documented signature of biotic responses to climate change. Previous studies have shown that ambient temperature is often a correlate and, presumably to some extent, a driver of interannual variation in the timing of plant flowering (Fitter & Fitter, Willis et al. 2008), tree budburst and leafing (Menzel & Fabian 1999), butterfly emergence (Roy & Sparks 2000), amphibian spawning (Beebee 1995), and bird egg-laying (Crick & Sparks 1999). For most studied species the effects of other climatic drivers (e.g. precipitation or sunshine hours) on variation in phenology is often assumed to be comparatively small (Sparks & Yates 1997, Menzel et al. 2006).

Primary productivity in grasslands is known to be highly variable when compared to other systems (Risser et al. 1981, Knapp et al. 1998). Climatic variables such as temperature and precipitation are fundamental determinants of plant
production (e.g. Cashen 1947). Different combinations and seasonal patterns have direct consequences on yields (e.g. Schlenker, Haneman & Fisher 2006). Estimating the effective relationship between weather and yields is a critical first step before more elaborate models can be used to estimate how crops and semi-natural vegetation will respond to climate change. These models will give biased results if the underlying relationship between weather and yields is modelled incorrectly.

In temperate grasslands, evidence suggests that drought events cause reduced biomass production (Sternberg et al. 1999, Grime et al. 2000, Kahmen et al. 2005). Weather patterns play a significant role, both within and between years. Wide fluctuation in grassland standing crop from one year to the next are the direct result of both temperature and precipitation patterns (e.g. Talbot et al. 1939, McNaughton 1968, Pitt 1978). Hence, the ideal ingredients for plant productivity growth should be ‘lots’ of warmth and ‘lots’ of water (e.g. Leith & Whittaker 1975, Field et al. 1998, Scurlock et al. 2002). These weather variables correlate strongly with productivity, but it is widely recognized that the actual effect involves the integration of several environmental variables (Visser et al. 2010). The details however are far from clear (e.g. Suttle et al. 2007). For instance, current rainfall is likely to be more important for summer productivity than for spring because soil moisture levels are likely to be relatively high at the end of winter (Bai et al. 2008). The response of grassland productivity to precipitation variation over time also varies among different ecosystems (Le Houerou 1984, Lauenroth & Sala 1992, Knapp & Smith 2001).

The effect of seasonal changes in the environment on the growth of the grass sward is further complicated by the progression from vegetative to reproductive development. The seasonal pattern of radiation is almost symmetrical about the midsummer solstice (22nd of June in the northern hemisphere) so that the total amount of radiation received during a period close to the equinox in spring (21st March) differs little from the amount received during an equivalent period close to the equinox in the autumn (23rd September). At 52°N, in Rothamsted, daily totals of light energy vary from midwinter to midsummer as a result of changes in both light intensity and day length (Woodward and Sheehy 1983). Of even greater importance to grassland production than the amount of light available is the amount of light actually intercepted by the sward canopy. At 52°N, the maximum light occurs in June whereas the period of maximum air temperature is some 4 weeks later in July.
Similarly, minimum temperatures occur in February not January. As a result of this lag temperature in spring may be lower than at the time of equal light energy receipt in autumn. In the temperate zones the marked seasonal variations in light and temperature are a major cause of variations in the rate of growth of grass. In the late autumn, overwinter and early spring, low temperature and low light energy are major limitations to production and define the length of the growing season (Cooper & Breese 1971). Not surprisingly though, shortage of water, during the growth phase, is the single most important factor limiting crop yields (Begg & Turner 1976). In many situations there is an interaction between water deficits and nutrient deficiency (Garwood and Williams 1967), which is due primarily to the non-availability of nutrients in dry soils horizons. In addition, high temperatures and low humidity that have direct effect on plant processes are often associated with conditions of water deficit, such that, the influence of climatic factors during periods of water shortage are complex.

The Park Grass Experiment (PGE) at Rothamsted is the oldest ecological experiment in the world. It began in 1856 and has been carried out with no interruption since, comparing herbage yields of unfertilised plots and plots with different combinations of fertilizers (Tilman et al. 1994). Park Grass is of particular interest as it is a perfect system to study ecological processes in the context of an herbivore free system. This is especially relevant to understand in greater detail how local weather variation affects plant productivity and as a consequence, of great importance when studying herbivore population dynamics, when we would not necessarily expect any relationship between plant productivity and plant biomass (as explained in chapter 4).

There are various studies of the environmental effects of plots in the Park Grass Experiment. For instance, the numerous long-term treatments reveal relationships between nutrient availability and grassland biodiversity (Crawley et al. 2005). Cashen (1947) and then later Jenkinson et al. (1994) reported that rainfall influenced annual hay yield. Kettlewell et al. (2006) explore the association between the winter North Atlantic Oscillation (NAO) and summer plant growth in the Park Grass experiment, as a proxy for inter-annual weather variation.

In this chapter, I extend the analysis to ask when exactly are temperature and rainfall most important in determining plant productivity and how they interact to
determine biomass in contrasting Spring and Summer growth periods (as reflected in the first and second hay yields).

3.2. Methods

3.2.1. The study site

The Park Grass Experiment started in 1856 at Rothamsted in Hertfordshire to compare hay yields between unfertilised and fertilised plots. The soil was slightly acid (pH 5.4–5.6) and the nutrient status poor. The top 23 cm of soil is a silty clay loam overlying clay-with-flints and is moderately well drained. At the start, the species composition of the herbage appeared uniform across the whole site.

For this chapter, data were obtained for unlimed areas of plots 2, 3 and 12 (see figure 3-1 for plot locations) and, after subdivision for further treatments in 1965, for the unlimed sub-plots (2d, 3d and 12d). Plots 3d and 12d have never received any fertilizer or manure since 1856, and although plot 2d received manure from 1856 to 1863, it has received nothing since then, and can be regarded as a replicate of plot 3.
Soil processes

Soil acidification has greatly affected species composition of the sward. Soils have acidified as a result of applying ammonium sulphate and because of atmospheric N inputs. Fertilizer N inputs have remained constant. However, the input of atmospheric N (as wet and dry deposition) varies, both within and between years, depending on emissions to the atmosphere and rainfall. Goulding et al. (1998) calculated that the annual atmospheric N input totalled c. 10 kg ha\(^{-1}\) at the start of the experiment.

![Plot layout and current treatments of the Park Grass Experiment.](image)

**Figure 3-1 The Park Grass experiment.**
3.2.2. Yield

The unfertilised plots are not affected by grazing and represent semi-natural grassland with cutting and herbage removal twice a year. The yield of dry matter (t/ha) is recorded twice: June and autumn. The date of the first cut varied from the 4th of June in 1980 to 21st of July in 1906 and for the second cut from the 3rd of September in 1875 to 11th of December in 1923. The period of growth between the first and second cuts varied from 83 to 174 days (figure not shown). The date of the first cut was significantly delayed by wet weather in early June (figure 3-2).

![Figure 3-2](image_url) 

Figure 3-2 Date of first cut varying with accumulation of Rain (mm) from the 1st of June up to cut day (ranging from the beginning of June to the end of July). There is variation of more than 20 days in cutting date even in dry years, but June rainfall can account for an extra 15-day delay in cutting in wet years ($F_{1,127}= 131.1, p<2e^{-16}$).

The data, from each plot and every harvest since 1856, are lodged in the online Electronic Rothamsted Archive (ERA: www.era.iacr.ac.uk/parkgrass_1.html). For the purpose of the analysis in this chapter, I refer to them as first and second yields. Due to a change in harvesting protocol from 1960, the yields from 1960 are not directly comparable with the earlier yields.

From 1960 onwards, there was a change in the method of harvesting. Before 1960, first yield represents what was removed from the plot; from 1960 onwards it represents estimated total production from cut sample strips; harvested fresh then oven-dried. Following Poulton (1996), first yields were reduced by 20% to make them comparable with yields before 1959.
Second cut was recorded as zero in 1884, 1885, 1887, 1897-1899, 1911, 1913, 1914, 1921, 1924, 1933, 1964 and 2003. This appeared to be a subjective evaluation, and inclusion of a zero value leads to an extreme outlier in subsequent analysis, I decided to substitute those values for the lowest summer yield value corresponding pre and post protocol change accordingly. To make comparison between years more meaningful, the growth per day over the growth period was calculated by dividing the dry matter yield at the second cut by the number of days since the first cut.

3.2.3. The local weather

The weather data were sourced from Rothamsted local weather station. Although the actual yield study starts in 1856, daily weather data are consistently available only from 1880 for maximum, minimum temperature and precipitation, and for wind speed from 1960 only. The 4 explanatory variables show differing degrees of correlation with each other (table 3-1). Windy wet weather is associated with cold temperatures.

<table>
<thead>
<tr>
<th>Weather variables</th>
<th>Max. Temp</th>
<th>Min Temp</th>
<th>Precipitation</th>
<th>Wind speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Max. Temp</td>
<td>1.00</td>
<td>0.83</td>
<td>-0.04</td>
<td>-0.12</td>
</tr>
<tr>
<td>Min. Temp</td>
<td>.</td>
<td>1.00</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>Precipitation</td>
<td>.</td>
<td>.</td>
<td>1.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Wind speed</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>1.00</td>
</tr>
</tbody>
</table>

3.2.4. North Atlantic Oscillation

For details of this index see Chapter 2 methods.

3.2.5. Data analysis

Analysis was carried out in two parts:
a) Whole study period 1880 - 2010 (yield data are available from 1856, daily weather data available from 1880).
b) Post-protocol-change period 1960-2010: for both parts, I analysed the two yields separately.

**Trends**

I used linear regression to assess whether there were trends in yield. This was done for both the whole study period and for the post-protocol-change study period.

**Critical windows**

I used linear regression to estimate the productivity of the grass sward for the first and second cuts, on the average temperature, total precipitation, average wind speed, accumulated growing day degrees and evapotranspiration over specified time-windows.

For the first yield, I varied both the starting date of the sliding window starting on the first of November in seven day intervals up the 15th of June of the year of collection (days given in ordinal dates, i.e. 1 for 1st January and 365 or 366 for 31st December, depending on leap years) and the duration of the window with lengths varying from 7 days up to 16 weeks in 7-day intervals. The same procedure was carried out for the second yield with windows staring on the 1st of January (to investigate the possibility of historical carry over effects) up to the 15th of November. I compared the predictive power of each variable in different time-windows using the fraction of variation in biomass explained by the model ($r^2$). In addition to using the best combinations according to $r^2$, windows were further selected according to the following rules: the combination of window start and length could not exceed the 15th of June or November of the year collection (in respect to the first or second yield), the windows for wind shorter than 21 days were not considered, and also the windows needed to have a p value < 0.05. The linear regressions used to search for the best windows included linear and quadratic forms of the weather variable in question, and also included “year” as a three level factor, with the following periods: 1880-1918, 1919-1959, 1960-present for the first yield. Visual inspection of the time series suggested these three periods differencing in mean first hay yield. Thresholds were picked by variance minimisation (tree models) and a three level factor defined to categorise these three periods mean yields were each significantly different from each other. I considered fitting a trend to each period but decided in favour of
parsimony (3 parameters rather than 6). This looks trended (down and up). In the most recent section though, the change is related with the protocol change so it is an artefact. This 3-level-factor allowed me to investigate weather effects across the whole time series and interactions between weather and time period.

![Time series of mean first yield for the three unfertilised plots for the period 1880-Present. The horizontal lines are the means for the three different periods. Red line is the mean yield for 1880-1918. The blue line is the mean yield for 1919-1959. The green line is the mean yield for 1960-present.](image)

For the second yield a “year” two-level factor was included to account for the change in protocol for the periods: 1880-1959 and 1960-Present. Visual inspection of the time series suggested these two periods differing in mean second hay yield. These coincide with the change in cutting hay protocol. These periods mean yields were each significantly different from each other. I considered fitting a trend to each but decided in favour of parsimony (2 parameters rather than 4).
I used measures of growing day degrees (GDD) to provide an estimate of local climatic conditions in relation to vegetation growth (Grant et al. 1986, Snyder et al. 1999, Bonhomme, 2000). I use the basic form of GDD that uses only daily average temperature (Cross & Zuber 1971). GDD is estimated as the cumulative sum of the daily mean temperatures above a threshold over a set period (Barnett et al., 2006), the zero-development point of the species in question. While the hypothesized threshold temperature can be identified experimentally, as the temperature at which development is zero, more often it is identified statistically and does not necessarily correspond to the temperature where development is zero (Yang et al. 1995, Snyder et al. 1999, Bonhomme 2000). Despite the potential limitations of GDD, including the nonlinearity of the relationship between development rate and temperature (discussed in detail in Bonhomme, 2000), GDD has been used successfully in horticulture to predict flowering dates and also in agriculture to predict yield. In the yield models, it is the proxy for the development - temperature relationship. Although the norm is to use a threshold of 5°C (following Barnett et al., 2006), here, I used thresholds from 4°C till 10°C. Temperatures below the threshold were treated as contributing zero GDDs. Under most GDD
approaches, once the cumulative GDD criterion is met the phenological event is predicted to occur.

**Evapotranspiration**

To quantify moisture stress, I calculated actual evapotranspiration (Penman 1948, 1949). Evapotranspiration calculations were only incorporated in the models to analyse the period post protocol change, since daily wind data are essential for evapotranspiration calculations, as described in Chapter 5. Data was cross-validated using the evapotranspiration data from electronic Rothamsted archives. Models using evapotranspiration were fitted with this variable on its own, as evapotranspiration is calculated using the basic weather variables, and is therefore strongly correlated with them, leading to biased parameter estimates or significance tests (Freckelton 2002).

**Statistical modelling**

**Linear models used in the whole study period (1880-Present)**

The same methods were used for both first and second yields. The critical windows with the highest $r^2$ for each weather variable were then used in multiple linear regression models for each yield. The mean of the dry matter yield from the three unlimed plots was calculated and used as the response variable. I fitted weather variables both as linear and quadratic terms. This was initially done to explore the functional form of variables. I also fitted an interaction of rain with a measure of growing degree days, to explore the reported-negative interaction between the two and wNAO, since in previous work (e.g. Kettlewell et al. 2006) wNAO appeared to have an effect on productivity. I used stepwise deletion to arrive at the minimal adequate model.

For the first yield model, in addition to the best candidate weather windows, I fitted second yield from the previous. For the second yield model, in addition to the best candidate weather windows, I fitted first yield from the same year as an explanatory variable.
General additive models (GAMs) used in the post protocol change period (1960-Present)

I used GAMs to explore the possible non-linear relationship between yield and the weather predictors (GDD, average temperature, rainfall, wind and evapotranspiration). The predictor effects are assumed to be linear in the parameters, but the distribution of the responses as well as the link between the predictors and this distribution can be quite general. I used a smoother, which is a tool for summarising the trend of a response measurement $y$ as a function of one or more predictor measurements. The GAMs were performed for both first and second yields across the years. Evapotranspiration is always fitted separately from the weather variables, as it is calculated using temperature and wind data. As before, the critical windows with the highest $r^2$ for each weather variable were then used in regression analysis performed with GAMs using the mgcv R package (Wood 2006) for both first and second yields.

3.3. Results

3.3.1. Trends

Weather trends

Overall Rothamsted is getting warmer (with at least 1.38°C increase in minimum temperature and at least 0.88°C increase in maximum temperature over 130 years) and rainier (with at least 0.55mm per month over 130 years). Rothamsted has also been getting windier for the past 51 years, with total run of wind significantly trended for 6 of the 12 months of the year (average wind speed has increased approximately 0.51ms$^{-1}$, in 51 years).
Table 3-2 Temporal trends in minimum and maximum temperature, and in rain for the period 1880-2011 at Rothamsted. Only the months that show significant trends are shown. Slope, standard error (S.E.) and p values refer to the linear regression for the monthly mean daily values against year. ‘+’ sign denotes upward trend. All the significant trends were positive. The greatest effect sizes were for October minimum temperature (up 0.197 degrees per year) and July rain (up 0.00646 mm per year).

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Month</th>
<th>Slope</th>
<th>S.E.</th>
<th>p-value</th>
<th>Signal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum temperature</td>
<td>January</td>
<td>0.011</td>
<td>0.004</td>
<td>0.0061</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>0.0151</td>
<td>0.00288</td>
<td>6.65e-07</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>0.0131</td>
<td>0.0023</td>
<td>7.85e-08</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>0.00922</td>
<td>0.00219</td>
<td>4.59e-05</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>0.00627</td>
<td>0.00191</td>
<td>0.00134</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.00733</td>
<td>0.00198</td>
<td>0.000308</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>0.00915</td>
<td>0.00213</td>
<td>3.34e-05</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>0.0128</td>
<td>0.00235</td>
<td>2.52e-07</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>0.0197</td>
<td>0.00305</td>
<td>1.74e-09</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.0123</td>
<td>0.00305</td>
<td>9.71e-05</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>0.0106</td>
<td>0.00388</td>
<td>0.00695</td>
<td>+</td>
</tr>
<tr>
<td>Maximum temperature</td>
<td>January</td>
<td>0.00875</td>
<td>0.00444</td>
<td>0.0509</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>0.0114</td>
<td>0.00374</td>
<td>0.00286</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>0.00682</td>
<td>0.00335</td>
<td>0.0437</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>0.0147</td>
<td>0.00317</td>
<td>8.1e-06</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.0073</td>
<td>0.00306</td>
<td>0.0186</td>
<td>+</td>
</tr>
<tr>
<td>Precipitation</td>
<td>January</td>
<td>0.00456</td>
<td>0.00222</td>
<td>0.0418</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.00646</td>
<td>0.00244</td>
<td>0.00896</td>
<td>+</td>
</tr>
</tbody>
</table>
December data are show here to illustrate the huge amount of structure, and in this case hints of periodicity, in these time series and this may repay further detailed analysis in due course (e.g. figure 3-3 and figure 3-4).

Figure 3-5 December minimum temperature for the period of 1880-2010. Boxplots show variation in daily values within December each year. Solid line shows the linear regression for the monthly mean minimum December temperature over each year (0.01±0.003 SE); dashed line shows the linear regression for the monthly median minimum December temperature over each year (0.009±0.003 SE). December monthly mean minimum temperature has risen about 1.4°C in 130 years.
Table 3-3 Temporal trends in wind and evapotranspiration over the period 1960-2011 in Rothamsted. Only the months that show a significant trend are shown. Slope, standard error (S.E.) and p values are related to the linear regression for the monthly mean daily values over each year. ‘+’ sign denotes upward trend. All significant trends were positive. The largest effect size for wind speed was in October (as with minimum temperature – see table 3-2). Windiness is positively correlated with minimum temperature (as seen in table 3-1).

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Month</th>
<th>Slope</th>
<th>S.E.</th>
<th>p-value</th>
<th>Signal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind speed</td>
<td>January</td>
<td>0.0163</td>
<td>0.00703</td>
<td>0.0243</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>0.0105</td>
<td>0.00436</td>
<td>0.0105</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>0.015</td>
<td>0.00429</td>
<td>0.000989</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>0.0117</td>
<td>0.00541</td>
<td>0.036</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>0.0108</td>
<td>0.0044</td>
<td>0.0172</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>0.0209</td>
<td>0.00632</td>
<td>0.00178</td>
<td>+</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>April</td>
<td>0.0027</td>
<td>0.00107</td>
<td>0.0148</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>0.0004</td>
<td>0.000198</td>
<td>0.0488</td>
<td>+</td>
</tr>
</tbody>
</table>
Figure 3-6 June average wind speed for the period of 1960-2010. Boxplots show daily values. Solid line shows the linear regression for the monthly mean June average wind speed over each year (0.01±0.004 SE); dashed line shows the linear regression for the monthly median June average wind speed over each year (0.01±0.004 SE). June average wind speed has increased approximately 0.51ms⁻¹ in 51 years.

Yield trends
a) Whole study (1880-Present)
First Yield
There appears to be a down and up trend; although the upward trend is most likely an artefact of change of harvest protocol after 1960 (see figure 3-3).
Second Yield
As with the first yield, there is a clear increase in trend from 1960. Again coinciding with the change in harvest protocol (see figure 3-4).
b) Post Protocol change (1960-Present)
First Yield (Spring Yield)
Spring yield corresponds to the rapid growth phase (figure 3-5). No trend in yield was observed for the time period of 1960-2010.
Chapter 3 Weather, phenology and effects on primary production at the Park Grass Experiment, Rothamsted over 130 years

1.0
1.5
2.0
2.5
3.0
Year
First Yield

Second Yield
There is a marginally significant decrease in biomass by approximately 0.7 t/ha (figure 3-8) for the second cut for the period of 1960-2010 (p = 0.0436).

1.0
1.5
2.0
2.5
3.0
Year
Second Yield

Figure 3-7 Time series of Park Grass unfertilised plots yearly mean first yield (June cut) for the period of 1960-present. No trend in yield is observed for this period.

Figure 3-8 Time series of mean second yield of Park Grass unfertilised plots yearly. The dashed line corresponds to the negative trend in autumn yield for the period of 1960 to 2010. Although the significance is marginal, the effect size is large with a decrease of approximately 0.7 t/ha (p=0.0436) over 50 years.
3.3.2. Critical windows

From all the significant critical windows for each weather variable I show the four with the highest R². Windows are labelled from 1 to 4; 1, being the farthest from the event, and 4 the closest to the event in time.

a) Whole study

I begin by describing the windows and results of fitting those windows. The windows in bold are the ones that remain the minimum adequate models.

First yield critical windows

Best critical windows for all the weather predictors started from mid November to April and the length varied from one to three weeks (Figure 3-9 for GDD, other variables shown in table 3-4).

![Figure 3-9 Growing day degrees best critical windows](image)

Figure 3-9 Growing day degrees best critical windows (as defined by r² from linear regression) as predictors for mean first yield for the period of 1880-Present. Calendar days are shown in Julian days where 1 is the 1st of January of the previous year. Vertical lines depict the bounds for window search. Blue line represents the beginning of November of the year prior to the yield. Red line represents mid June of the yield year.
Table 3-4 Best weather critical windows as predictors for first yield for the whole study period. Windows are labelled 1-4, from the farthest to the closest to the event in time. GDD means growing degree-days. Windows in bold remained in the MAM.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>12.11-29.11</td>
<td>15.11-29.11</td>
<td>20.12-03.01</td>
<td>31.01-11.04</td>
</tr>
<tr>
<td>Threshold 7°C</td>
<td>Threshold 7°C</td>
<td>Threshold 5.5°C</td>
<td>Threshold 7°C</td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td>08.11-06.12</td>
<td>01.11-24.01</td>
<td>22.11-06.12</td>
<td>14.03-11.04</td>
</tr>
<tr>
<td>Precipitation</td>
<td>22.11-29.11</td>
<td>20.12-10.01</td>
<td>24.01-07.02</td>
<td>28.03-04.04</td>
</tr>
</tbody>
</table>

Second yield critical windows

Best critical windows for temperature started in June up to September with lengths of up 2.5 months. For precipitation the best windows start much earlier in the season; they start in April and go up to August, with window length up to 3 months (Figure 3-10 for GDD, other variables shown in table 3-5).

Figure 3-10 Rainfall best critical windows (as defined by \( R^2 \) from linear regression) as predictors for mean second yield for the period of 1880-Present. Days are shown in Julian days where 1 is the 1st of January of the yield year. Vertical red line depicts the upper bound for window search (mid November).
Table 3-5 Best weather critical windows as predictors for second yield for the whole study period. Windows are labelled 1-4, from the farthest to the closest to the event in time. GDD means growing degree days. Windows in bold remained in the MAM.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>18.06-03.09 Threshold 4°C</td>
<td>09.07-13.08 Threshold 5.5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>18.06-03.09</td>
<td>09.07-13.08</td>
</tr>
<tr>
<td>Precipitation</td>
<td>03.04-20.08</td>
<td>28.05-20.08</td>
</tr>
</tbody>
</table>

b) Post Protocol change period (1960-2010)
For this period wind speed is available, in addition to temperature and precipitation, I use the wind speed as a predictor. Calculating a proxy for evapotranspiration prior to 1960 was impossible, so I use evapotranspiration as a predictor for yield only post 1960.

Evapotranspiration calculation
Because evapotranspiration data were available from the electronic Rothamsted archives, I used my approximate method for calculating evapotranspiration (described in chapter 5) to allow cross-validation of this approximation ($r^2 = 0.79$). The non-perfect correlation is due to the fact that in my methodology I make some assumptions about radiation that make the time series less scattered.
Figure 3-11 Evapotranspiration time series across six years. Black circles correspond to the calculation using only wind and temperature time series. Red circles are the actual data from eRA calculator. Here shown six years for illustration only.

**First yield critical windows**

Best critical windows for temperature as measured by growing day degrees start in mid November of the year precious to the yield and go up to April. Window lengths vary from 2 weeks up to 1 month and half. The different thresholds reflect the time of the year and the investment of plants to growth and other physiological activities. Average temperature best windows start in March and go to mid April. Precipitation windows start at end of March and go up to mid June. There was a clear window for wind from february to end of March. Evapotranspiration windows start in November of the year prior to yield and go up to January of the yield year, window lengths.
Table 3-6 Best candidate critical windows for first yield production for the period 1960-2010. Windows are labelled 1-4, from the farthest to the closest to the event in time. GDD means growing degree-days. Windows in bold remained in the MAM.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>15.11-29.11</td>
<td>07.02-21-03</td>
<td>04.04-11.04</td>
</tr>
<tr>
<td></td>
<td><strong>Threshold 8.5°C</strong></td>
<td><strong>Threshold 9.5°C</strong></td>
<td><strong>Threshold 4°C</strong></td>
</tr>
<tr>
<td>Average temperature</td>
<td>07.03-11.04</td>
<td>04.04-11.04</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>28.03-04.04</td>
<td></td>
<td>16.04-11.06</td>
</tr>
<tr>
<td>Wind speed</td>
<td>14.02-28.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>01.11-22.11</td>
<td></td>
<td>27.12-10.01</td>
</tr>
</tbody>
</table>

Second yield critical windows
Best critical windows for temperature start in June and go up to September. Precipitation best windows start in April and go up to August. Wind best windows start in November of the year prior to yield and also from April to May. Evapotranspiration windows run from July up to September.

Table 3-7 Best candidate critical windows that for second yield production for the period 1960-2010. Windows are labeled 1-4, from the farthest to the closest to the event in time. GDD means growing degree-days. Windows in bold remained in the MAM.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>11.06-03.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>threshold 4°C</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td><strong>11.06-03.09</strong></td>
<td>09.07-10.09</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td><strong>03.04-20.08</strong></td>
<td>28.05-20.08</td>
<td></td>
</tr>
<tr>
<td>Wind Speed</td>
<td>15.10-05.11</td>
<td><strong>16.04-14.05</strong></td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>09.07-13.08</td>
<td>16.07-13.08</td>
<td>16.07-03.09</td>
</tr>
</tbody>
</table>
3.3.3. Statistical models

a) Whole study

The predictors for first and second yield are slightly different for the period of 1880-2010.

First Yield

The minimum adequate model shows weather interacting differently at the three time periods. Temperature in the first period is a good example of non-linearity with windows that are not the same length. In addition, show that in November temperature can affect yield positively, while when average temperature is too high in March-April, it has a negative effect on yield. It would be interesting to models these effects of GDD and average temperature in separate models and explore explicitly both linear and non-linear terms. Same average temperature window appears to have opposite effects at different time periods. Precipitation, from November through January, in distinct windows of time has positive effects on yield.
Table 3-8 Weather effects on first yield for the period of 1880-2010. “Period” represents the three distinct periods (see figure 3-3). Only the significant terms are shown ($r^2 = 0.4$).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.00</td>
<td>0.394</td>
<td>1.43e-06 ***</td>
</tr>
<tr>
<td>GDD w.1</td>
<td>0.033</td>
<td>0.009</td>
<td>0.0002 ***</td>
</tr>
<tr>
<td>Average temperature w.1</td>
<td>-0.085</td>
<td>0.04</td>
<td>0.021 *</td>
</tr>
<tr>
<td>Period (1.92e+03,1.96e+03]</td>
<td>-0.344</td>
<td>0.54</td>
<td>0.53</td>
</tr>
<tr>
<td>Period (1.96e+03,2.01e+03]</td>
<td>-0.91</td>
<td>0.50</td>
<td>0.074 .</td>
</tr>
<tr>
<td>Average temperature w.4</td>
<td>-0.003</td>
<td>0.053</td>
<td>0.94</td>
</tr>
<tr>
<td>Precipitation w.1</td>
<td>0.006</td>
<td>0.002</td>
<td>0.009 **</td>
</tr>
<tr>
<td>Precipitation w.2</td>
<td>-0.006</td>
<td>0.003</td>
<td>0.05 *</td>
</tr>
<tr>
<td>Period (1.92e+03,1.96e+03]</td>
<td>-0.070</td>
<td>0.07</td>
<td>0.34</td>
</tr>
<tr>
<td>Average temperature w.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Period (1.96e+03,2.01e+03]</td>
<td>0.124</td>
<td>0.069</td>
<td>0.077</td>
</tr>
<tr>
<td>Period (1.92e+03,1.96e+03]</td>
<td>0.01</td>
<td>0.004</td>
<td>0.016 *</td>
</tr>
<tr>
<td>Precipitation w.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Period (1.96e+03,2.01e+03]</td>
<td>0.007</td>
<td>0.003</td>
<td>0.05 .</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = $ *, $P < 0.01 = $ **, $P < 0.001 = $ ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.
Second Yield

Second yield MAM is much simpler. But again shows the different interaction of weather with time period.

Table 3-9 Weather effects on second yield for the period of 1880-2010. “Protocol” depicts the two periods 1880-1959 and the post protocol change 1960-present. Only the significant terms from the MAM are shown. $r^2 = 0.58$.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.51</td>
<td>1.02</td>
<td>0.61</td>
</tr>
<tr>
<td>Protocol.2</td>
<td>2.8</td>
<td>1.44</td>
<td>0.05*</td>
</tr>
<tr>
<td>Average temperature w.2</td>
<td>-0.03</td>
<td>0.05</td>
<td>0.48</td>
</tr>
<tr>
<td>Precipitation w.1</td>
<td>0.002</td>
<td>0.001</td>
<td>0.005 **</td>
</tr>
<tr>
<td>Protocol.2: Average temperature w.2</td>
<td>-0.16</td>
<td>0.07</td>
<td>0.03 *</td>
</tr>
<tr>
<td>Protocol.2: Precipitation w.1</td>
<td>0.004</td>
<td>0.001</td>
<td>0.01 *</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = *$, $P < 0.01 = **$, $P < 0.001 = ***$. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

b) Post Protocol change (1960-Present)

First Yield

From the two GAMs fitted, the one with weather variables performed substantially better than the model using evapotranspiration (Tables 3-10 and 3-11). A wetter spring will increase yield, whereas, a wetter and cold spring will decrease yield. Interestingly, wet days are normally negatively correlated with temperature. Precipitation has fairly linear effect on yield; temperature however (as GDD) has a clearly non-linear effect on yield (figure 3-12).
Table 3-10 Minimum adequate model (MAM) for GAM with non-parametric predictors for first yield for the period of 1960-Present. Deviance explained 62.5%. Effect sizes can also be seen in figure 3-11.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>F</th>
<th>Effect size</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD w.1</td>
<td>3.449</td>
<td>0.14</td>
<td>0.0116 *</td>
</tr>
<tr>
<td>GDD w.2</td>
<td>4.344</td>
<td>0.136</td>
<td>0.0039 **</td>
</tr>
<tr>
<td>Rain w. 2</td>
<td>12.914</td>
<td>0.8</td>
<td>0.0009 ***</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***$. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

Figure 3-12 GAM for first yield prediction. In the top left is a scatterplot of predicted against observed values; the next three panels, show first yield on the y axis and the different weather predictors on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for Precipitation-window 2(top right), with an effect size of 0.8 between the minimum and maximum values of second yield. GDD-window 1 (bottom left), with an effect size of 0.14 between the minimum and maximum values of second yield GDD-window 3 (bottom right), with an effect size of 0.136 between the minimum and maximum values of second yield.
This evapotranspiration effect is in the opposite direction to Rosenzweig rule (see discussion).

Table 3-11 Minimum adequate model (MAM) for GAM with evapotranspiration predictors for first yield for the period 1960-Present. Deviance explained 15.4%.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>F</th>
<th>Effect size</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evapotranspiration w.2</td>
<td>6.171</td>
<td>0.72</td>
<td>0.00738 **</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: \( P < 0.05 = \ast \), \( P < 0.01 = \ast\ast \), \( P < 0.001 = \ast\ast\ast \). Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

Figure 3-13 GAM for first yield prediction. In the left panel is a scatterplot of predicted against observed values; the right, first yield on the y axis and the evapotranspiration on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line), with an effect size of 0.72 between the minimum and maximum values of second yield.
Second Yield

In addition to the textbook notion that the more rain in the summer the bigger the yield, there is a surprising carry-over effect of spring rain, which has never been shown before (table 3-12). First yield has negative effect on second yield.

Table 3-12 Minimum adequate model (MAM) for GAM with non-parametric predictors for second yield for the period of 1960-Present. Deviance explained 83.4%. Effect sizes can also be seen in figure 3-13.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>F</th>
<th>Effect size</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>First yield</td>
<td>5.088</td>
<td>0.58</td>
<td>0.03 *</td>
</tr>
<tr>
<td>Average temperature w.1</td>
<td>11.626</td>
<td>0.88</td>
<td>0.00157 **</td>
</tr>
<tr>
<td>Precipitation w.1</td>
<td>9.180</td>
<td>0.164</td>
<td>3.92e-07 ***</td>
</tr>
<tr>
<td>Wind speed w.2</td>
<td>3.043</td>
<td>0.54</td>
<td>0.04526 *</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***$. Non-significant effects are not shown. $P$ values for significant effects are taken from the model output of the MAM.
Figure 3-14 GAM for second yield prediction. In the top left is a scatterplot of predicted against observed values; the next four panels, show second yield on the y axis and the different predictors on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line) for first yield of same year (top centre) with an effect size of 0.58 between the minimum and maximum values of second yield. Average temperature-window 1 (top right), with an effect size of 0.88 between the minimum and maximum values of second yield. Rainfall-window 1 (bottom left), with an effect size of 0.164 between the minimum and maximum values of second yield. Wind-window 1 (bottom right), with an effect size of 0.54 between the minimum and maximum values of second yield. Effect sizes of each predictor were calculated using model predict.
Table 3-13 Minimum adequate model (MAM) for GAM with evapotranspiration predictors for second yield for the period 1960-Present. Deviance explained 66%. Effect size can also be seen in figure 3-14.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>F</th>
<th>Effect size</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Second Yield</td>
<td>Evapotranspiration w.2</td>
<td>8.899</td>
<td>2.7</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: * P < 0.05, ** P < 0.01, *** P < 0.001. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

Figure 3-15 GAMs for second yield prediction. In the left panel is a scatterplot of predicted against observed values; the right, first yield on the y axis and the evapotranspiration window 2 on the x axis, with the non parametric smoother (solid line) and the 95% confidence interval for the fitted regression (dashed line), with an effect size of 2.7 between the minimum and maximum values of second yield. Effect sizes of each predictor were calculated using model predict.

3.4. Discussion

Terrestrial primary production is among the most important ecosystem variables that have been studied extensively (e.g. Lieth 1975, Roy et al. 2001, Kettlewell et al. 2006). It has been measured for all the major managed and natural ecosystems in the world (e.g. Scurlock et al. 1999, Cramer et al. 2001) and it is one of the most important output variables from ecosystem models that are compared to observed
data sets (Jager et al. 2000, Del Grosso et al. 2008). In this chapter, I have focused on evaluating above ground productivity using shoot biomass produced during the early and later periods in the growing season and investigate how these are affected by local weather variation.

Throughout the whole period of the study, there is a large difference in dry matter yields (figures 3-3 and 3-4), because of technological change, average yields in the more recent period (1960-present) are about twice of those in the earlier periods. To explore how the weather-yield relationship has changed over time, I split the sample into three time periods for the first yield analysis and two time periods for the second yield analysis. This was done in order to investigate if weather effects remained the same over different periods by controlling for mean hay yield.

Jenkinson et al. (1994) had a similar approach; nevertheless they added both first and second yield and only divided the study into two distinct periods pre and post harvest protocol change. It is important to investigate effects of weather on the whole study period, because if just focusing on yields from 1960 onwards, there is a risk in assuming no trends in yield are observed (figure 3-5), as is the case for the first yield, in keeping with the findings of Jenkinson et al. (1994), who found no trends in the yields of the unfertilised plots from 1960 to 1992. I did find a trend in decreasing production in the second cut (figure 3-6) for that same period (1960-2010), but this could be because I have included a further 18 years of data (p =0.0436).

Earlier statistical studies (e.g. Jenkinson et al. 1994) have examined average temperatures and rainfall over a longer time horizon (e.g. an entire season, months), which can hide extreme events like high temperatures at specific time windows. The existing literature has generally represented the effect of climate on agriculture by using the monthly averages for January, April, July, and October (Schlenker, Haneman & Fisher 2006). However, this approach is not ideal. Plant growth depends on exposure to moisture and heat throughout the growing season, albeit in different ways at different periods in the plant’s life cycle; therefore, including weather variables for April and July, but not May, June, August, or September, can produce a distorted representation of how crops respond to ambient weather conditions. Therefore, it was reassuring that the sliding window approach revealed similar candidate weather critical windows for throughout the whole time period analysis and the post-protocol-change period only (figures 3-7 and 3-8; tables 3-3 to 3-5). For the
first yield, candidate windows varied from November to April. For the second yield candidate windows varied from April to September.

My finer scale approach aids identification of these weather effects, and in particular, the phenology of these effects, which are lost if weather variables are averaged over time. The first yield model confirmed my initial hypothesis that the same critical windows would have different effects (in strength) on yield. On the first yield (table 3-5), GDD at the end of November of the year prior to yield, with a threshold of 7°C, not surprisingly has a positive effect on yield. The threshold is much higher that what could be expected, it could be indicative of an investment on other plant functions (such as frost tolerance/protection, pre-winter storage of reserves, over-winter tiller survival and increase if leaf growth in spring), at lower temperatures. There are cumulative effects overtime on soil pH (acid rain) and doubtless other chemical changes.

Had I not included the three different periods in the regression, I would have not discover that the same window of average temperature (table 3-2, mid March to mid April) actually shows significant but opposing effects in yield for the second and third periods (table 3-5). This might be a good proximate explanation as to why the yields in the period 1919-1959 are lower than the first period and the latter period. Nevertheless, there are other factors I have not considered, such as soil chemistry changes, or atmospheric changes. The same precipitation window (table 3-2, mid December - mid January) has an overall positive effect, although effects at different periods vary in strength. As expected, I found a relationship between 1st yield and temperature and rain - a wetter spring will increase yield. Different weather variables have particular timing and possibly roles in the swards investment in the timing for growth. Of the weather variables that show an effect on sward productivity, only GDD window shows an increasing trend.

The second yield revealed interesting results, in addition to the textbook notion that the more rain in the summer the bigger the yield, there was a negative effect of heat in July – August on yield (possibly denoting a non-linear effect of temperature on yield). This thus demonstrates that summer herbage growth in the Park Grass Experiment is strongly dependent on the availability of soil moisture. Declines in productivity are associated with early summer temperature that can be explained by the reduction in soil moisture that accompanies high temperatures.
(exacerbating water deficit). This is in keeping with the idea that any deficit between the supply of water from the soil and the evaporative demand will affect growth; the greater the deficit the greater the effect. Physiological stress occurs, reducing plant metabolic activity (Leafe et al. 1977, Garwood 1979).

There is a surprising carry over effect of spring rain; in both periods within the whole study, in addition to he expected effect of summer rainfall. This spring effect had never been analysed before (table 3-7). This is interesting given that the leaves of the autumn yield have not, at this point, yet started to grow.

Numerous associations between winter NAO and terrestrial ecosystems mediated through this winter index influence have been reported (e.g. Ottersen et al. 2001). Moreover, Kettlewell et al. (2006) argued that winter NAO was a predictor for summer yield in Park Grass. Consequently, I included the winter index when looking for predictors of yield. However, when using a longer time series, wNAO did not remain in any of the yield models using a longer time series.

As an alternative approach in my search for long-term weather effects on yield, I focused on the latter period of the experiment (1960-2010); first and second cuts were regressed against the best candidate critical weather windows this time using GAMs. This was done in order to investigate the functional form of weather effects, without any apriori assumptions, apart from recognizing that the agronomic literature typically represents the effects of temperature on plant growth in terms of cumulative exposure to heat, while recognizing that plant growth is partly non-linear in temperature.

I found that for the first yield, as I expected, GDD has a non-linear relationship with yield (table 3-8 and figure 3-11). Two GDD windows were highly significant, 7-day window in mid November with a threshold of 8°C and a later 45-day window (07.02-21.03) with a higher threshold (9.5°C). The increase of threshold is most likely due to the fact that during the winter months, temperatures need to be higher for the sward to invest in growth rather than other physiological requirements (such as freezing process). This non-linear relation of temperature on yield (in the form of GDD) is very well captured in figure 3-12, where above a certain point too much heat becomes harmful. The nonlinear relationship is starkly asymmetric, with the slope of the decline above the optimal temperature being much steeper than the slope of the incline below the optimal temperature. Herbage growth was positively correlated with
water supply (rainfall). The precipitation window (16.04-11.06) has a fairly linear relationship with yield, in keeping with the textbook assumption that the more water the higher the yield. This model explained 62.5% of deviance. It performed much better than the model using just evapotranspiration as the predictor for yield (table 3-8 and figure 3-12), highlighting the benefit of using untransformed weather variables whenever possible.

For the second yield, as I found when linearly regressed weather variables the same precipitation window remains in the model, the spring carry-over effect on autumn yields in addition to the non-linear effect of summer rain. This is interesting given that the leaves of the autumn yield have not, at this point, yet started to grow, and so the effect must be mediated through below ground reserves. Average temperature (June to September) had a positive relationship with yield. Moreover, wind is has a small effect from mid April to mid May. Windiness is associated with no frosts. In April, plants start to reduce their cold hardiness, being more sensitive to frosts. It is crucial.

An effect only seen when using the latter part of the study is the negative effect of first yield on second yield. This could be an artefact of a longer first-growth period where biomass includes flowering, and the second yield is the result of reserve depletion. Another explanation is where there could have been phase-shifted by extra commitment to reproduction.

Again the model, using untransformed weather variables, (table 3-12 and figure 3-8) performs better (83.4% deviance explained) then when using evapotranspiration (table 3-8 and figure 3-12) as a predictor (66% deviance explained). The surprising negative effects of evapotranspiration on yield are in disagreement with Rosenzweig’s Rule (1968) where net evapotranspiration has a positive effect on yield. This could just mean that maybe I should have used seasonal aggregations rather than small windows that might be better correlated with biomass.

Overall, my results show that grass production is related to the water supply over the growing season as determined by the rainfall from April to September and that temperatures have a non-linear effect on yields is in keeping with the concept of growing day degrees in which yields are increasing in temperature (for moderate temperatures), but become quickly harmful once temperatures exceed 30°C. This relationship is highly significant. The physiological condition of the plants can
introduce memory effects in the system.

The precipitation relationship results are consistent with the analysis by Sparks & Potts (1999) and Kettlewell et al. (2006) of data from the Park Grass Experiment since 1965. The associations of growth rate to rainfall would be expected in grassland dependent only on natural rainfall for water supply. My results do show that it is apparent that the impacts of climate variability differ throughout the growing season, and climate variability can have minimal impact later in the growing season.

The sharply negative effects of temperatures above the critical temperature threshold hold powerful implications for climate change. If climate change shifts the temperature distribution such that a significantly larger portion of it exceeds the threshold, overall impacts are substantial. Indeed, under warming predictions (IPCC 2007), the high-end of the temperature distribution shifts upward enough so that damaging heat waves are observed more frequently.

Hence it is fair to argue that, in a sward provided with ample water and nutrients, seasonal changes in light energy and temperature play a role in the production of grass, in that they ultimately define the potential of the environment to support grass growth (Jones & Lazenby 1988).

**Conclusion**

Even with such an ideal dataset as PGE the relationship between local weather and herbage growth is noisy. My results support the general idea behind previous models (i.e. precipitation and temperature influence grassland productivity). My approach shows when these variables matter most in affecting yield. Effects are significant from November up to the moth before yield. Breaking up the year into short periods works to get the annual coverage that would otherwise be diluted if averaged over longer periods: specific intervals matter.

It is also clear that grass productivity responds differently to climate variability at different times of the year. This is especially obvious by the different critical windows (with different start times, lengths and thresholds) that affect first and second yields. An appreciation of the factors, which limit grass growth, from season to season, is an essential first step in attempting to overcome limitations by management. In addition, my findings are notable in that for the consistency of the estimated nonlinear temperature effects across time. When dealing with a long-term study it is important to understand whether the relationship with weather remains the
same through time. In this way we can aim to extend the length of the growing season or otherwise modify the seasonal pattern of production to our advantage. Also, in understanding plant productivity, it is possible that the timing of climatic variability is just as important, if not more, than its magnitude.

The null hypothesis would be the weather signals in Park Grass would be the same in Rum and Kilda, where as I have said (you would not necessarily expect to see any correlation between weather and plant biomass because of fluctuating herbivore offtake (see chapter 1).

An important caveat of this analysis was my inability to account for CO₂ concentrations. Plants use CO₂ as an input in the photosynthesis process, so increasing CO₂ levels might spur plant growth and yields. Yield declines stemming from warmer temperatures therefore may be offset by CO₂-fertilization. Although higher CO₂ concentrations may boost yields, the magnitude of the effect is still debated. Long et al. (2006) stressed that existing laboratory studies and field experiments might overestimate this effect. We cannot account for CO₂ effects in regression analysis of observed yields because CO₂ concentrations quickly dissipate throughout the atmosphere, leaving only a gently increasing time trend, which is impossible to statistically disentangle from technological change.

**Future work**

It will be interesting to evaluate the effects of total yield of the year before on present year yield. Is it just that there is a fixed amount per year and if first yield is high does it mean there is less second yield? It will be interesting to test whether longer evapotranspiration windows show the expected relationship with yield, Also, in the whole study model, fit GDD and temperature separately in both linear and non linear forms to explore the relationships with yield. Since it is known that the effects of acidity on crops are mostly marked in dry spells (Cashen 1947), it would be interesting to extend Chapter 3 and investigate the effect of lime and other nutrients input on the response of yield to weather, also on the sward composition, since studies have shown that there is a negative relation between species richness and annual herbage yield (e.g. Jenkinson et al. 1994, Tilman et al. 1994).

In addition, using the relationships found in this chapter as parameters to model yield in the context of climate warming scenarios (using Hadley climate models).
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

Abstract
Weather can influence animal performance and population dynamics directly through energetic costs on thermoregulation, and indirectly by influencing food quantity and quality. This potential complexity is rendered more tractable for Soay sheep (Ovis aries) on St. Kilda, where predators and competitors are absent and disease is seldom detected as an important cause of mortality.
St. Kilda provides an excellent model to investigate direct climate effects and plant herbivore-based effects as drivers of population fluctuations.
The results suggest that most of the weather effects on male and female condition are strongly felt indirectly through variation in plant growth conditions in different seasons.
At age 2, sheep's weight is only affected by density dependence, through most likely availability of food. For the most part mild winter weather seems to increase August weight, most likely through early onset of vegetation growth.
Summer temperature and precipitation affect vegetation quality and quantity, which in turn affect the amount of reserves accumulated by lambs during summer, and their ability to survive their first winter.
I didn't expect and I didn't find any obvious direct negative effects of weather on animals, only at higher densities does weather have an effect. No two population crashes were alike, other than high density. I conclude that density-dependent processes and density-independent climatic variables work in tandem to drive the dynamics of fluctuating populations. My findings also support the growing realization that the interaction between climatic variables and density-dependent factors may be a widespread phenomenon.
4.1. Introduction

Certain mammalian species exhibit high-amplitude annual fluctuations in abundance; yet, their causes have remained poorly understood and are the subject of intense debate (Owen-Smith 2010). A key contention has been the relative role of density-dependent and density-independent processes in governing population dynamics. It is therefore important to understand what drives population growth rates and associated vital rates (survival and recruitment). However, density-dependent and environmental factors can exert variable levels of influence on the population dynamics of a species (e.g. Coulson et al. 2000, Rees & Slade 2008).

A key point of dispute has been the role of density-dependent vs. density-independent mechanisms in driving observed fluctuations: a recurring debate that began with the pioneering work of Lotka, Volterra, and Elton in the 1920s, and climaxed in the 1950s with Nicholson advocating the deterministic (density-dependent) process and Andrewartha and Birch championing the stochastic (density independent) school at the Cold Spring Harbor Symposia in 1957. It is now recognized that both processes can act synergistically within the same population (Turchin 2003).

Temporal variation in the demographic rates that underlie population growth, namely survival (including deaths and emigration) and recruitment (including births and immigration), can be associated with both density-dependent and density-independent processes (e.g. Coulson et al. 2000, Owen-Smith 2010).

Among density-independent processes, much attention has been directed toward climatic forcing in recent years (Grotan et al. 2008, Previtali et al. 2009). It is widely recognized that large-scale climatic phenomena such as the North Atlantic Oscillation (NAO), the Arctic Oscillation, and the El Niño Southern Oscillation (ENSO), can have a far-reaching and deep-rooted impacts on ecological systems (Mysterud et al. 2001, Stenseth et al. 2002, Hallett et al. 2004). Most environmental effects on ungulate populations around the North Atlantic have focused on the response to global climatic variations related to the winter index of the North Atlantic Oscillations (NAO, Hurrell 1995) (red deer Cervus elaphus: Mysterud et al. 2001a; reindeer Rangifer tarandus: Solberg et al. 2001; moose Alces alces and white tailed deer Odocoileus virginianus: Post & Stenseth 1998; Soay and domestic sheep Ovis aries: Mysterud et al. 2001b, Hallet et al. 2004; caribou and muskox Ovibos...
moschatus: Forchhammer et al. 2002). In addition, there is growing evidence that global warming can affect population dynamics and ecosystem functioning (Sæther et al. 2000, Walther et al. 2002, Ozgul et al. 2010). Thus, the response of demographic traits (reproduction and survival) to climate variability will determine whether populations decline or increase under future climate change (Hallet et al. 2004; van de Pol et al. 2010, 2011).

We need to be able to identify the critical time windows during which different climatic drivers affect the expression of traits if we are to predict the future impact of climate change and variability on trait dynamics and on population dynamics. A difficulty, however, is that the environment could be related to a trait in many different ways, since organisms are responding to a history of multidimensional environmental variation. Finally, seasonal variations in local weather conditions may be a potential driver of population dynamics (Ozgul et al. 2004) and these can shape the trajectory of a fluctuating population (Previtali et al. 2009). These approaches rarely attempt to decompose population dynamics into contributions from processes like density dependence and environmental stochasticity operating via variation in demographic rates (but see Lande et al. (2006) and Coulson et al. (2008)).

In ungulates, juvenile survival is typically lower and more variable than adult survival, and is generally thought to be more sensitive to changes in weather and resource availability (Sinclair 1977; Fowler & Smith 1981; Douglas & Leslie 1986; Clutton-Brock et al. 1987; Albon & Clutton-Brock 1988).

Several authors have suggested that weather and density may interact in affecting population dynamics of ungulates, and juvenile survival, in particular (Sauer & Boyce 1983, Picton 1984, Douglas & Leslie 1986, Owen-Smith 1990), but, no study has explicitly tested for interactions between population density and weather variables. Density-climate interactions are particularly relevant to the study of population dynamics. It is generally believed that the effects of weather should be more evident near ecological carrying capacity (Picton 1984, Strong 1984, Sinclair 1989, Coulson et al. 2000), but hypotheses about interactions between density and weather are difficult to test for wild mammals because they require data from years of good and bad weather at high and low population density. Furthermore, as many researchers have pointed out (Clutton-Brock et al. 1987, Forrester 1995, Mysterud et al. 2001. Coulson et al. 2008), density effects are not necessarily linear, and may be evident only when density exceeds a threshold.
Many studies have focused on the impact of an early start of the plant’s growing season on herbivore performance (e.g. Portier et al. 1998, Côté & Festa-Bianchet 2001a, Griffith et al. 2002, Pettorelli et al. 2011). Vegetation conditions in spring and summer are regarded as decisive for the reproductive success and offspring condition of large herbivores (Pettorelli et al. 2006, 2007, Owen-Smith 2002, 2010). Objective ways to determine key periods during the growing season have not often been possible due to limitations of plant data.

The role of annual variation in climate for breeding phenology and performance of plants, amphibians and birds in specific populations has received much attention (e.g. Walther et al. 2002, Stenseth et al. 2002, Parmesan et al. 2006). Clearly, the onset of breeding and the reproductive success in seasonal environments for organisms that are either dormant (such as plants and amphibians, Beebee 1995) or migratory over broad scales (for birds, Slagsvold 1976) is coupled with temperature in late winter and early spring. Large herbivores are active over the entire year and a better understanding of how animal performance (i.e. survival, reproduction or growth) are linked to plant performance and climatic conditions throughout the year is needed if we aim to anticipate the effect of climate change on ungulates. However, up to now, linking climate effects and plant productivity has not been an easy task. First, a detailed knowledge of the distribution and phenology of the different food items during the studied period has only been accumulated in few study sites. Traditional field ecological data on plant species are generally collected at a small spatial scale and vary in their type and reliability (Kerr & Ostrovsky 2003). Furthermore, since such data often come from a single time period during the year, it is difficult to identify the most important period of plant growth to the herbivore.

Hallet et al. (2004) have convincingly demonstrated that previous studies that using local monthly values of rainfall (Catchpole et al. 2000), which is the most common temporal scale used (Weladji et al. 2002), have failed to capture incidents of severe weather that might happen the whole winter. So with that the idea to use critical windows, already used in phenology studies came about, in an effort to understand how climate affect the demographic processes.

Identifying the critical time window during which climatic drivers affect the expression of phenological, behavioural, and demographic traits is crucial for predicting the impact of climate change on trait and population dynamics. Models that try to identify critical climatic windows can be either mechanistic or associative.
Mechanistic models aim to include information about the underlying biological processes that determine the timing or degree of trait expression (Trudgill et al. 2005).

Associative models are not directly based on any particular biological mechanism but rather examine quantitative associations between weather variables and trait expression. As in most associative approaches, the underlying idea is that the climatic time window that best explains or predicts the observed variation in trait expression is likely to have a causal role. By far the most popular associative method is the sliding-window approach (e.g. Estrella et al. 2007; Brommer et al. 2008; Husby et al. 2010). In this method, one calculates the mean of a weather variable over a given time period (e.g., January–March temperature) and then determines the strength of association (i.e., cross-correlation) with the dependent variable of interest. By varying the starting date—reflecting time lags—and the width of the sliding time window—reflecting the duration of the window—one aims to identify the critical climatic period that affects trait expression (i.e., the window producing the highest cross-correlation). I use sliding windows models to hypothesize about time lags and the relative importance of recent and past weather on demographic processes. Using a 26-year data set for the sheep population and a 19-year dataset for the St. Kilda vegetation, I illustrate that the climatic windows identified explain both sheep demographic processes and vegetation productivity. The sliding-window approach clearly has merit: it is simple, reflects the basic characteristics of a critical time window, and allows for time lags. However, there are some limitations. First, the method typically uses arbitrary cut-off points for time periods—usually the first or last day of a month, which may not be biologically realistic (but see Roberts 2008). Second, the method assumes that all days included in the critical time window exert equal influence on trait expression.

The Soay sheep study is unusual in that we have such a detailed biological understanding of the system (Clutton-Brock & Pemberton 2004). The population is food limited (Crawley et al. 2004). The oscillations in abundance shown by these sheep have been related to the seasonal cycle in food abundance (Clutton-Brock & Coulson 2002). The population fluctuates widely, but less so in recent years than in the past.

In this chapter I investigate the effect of local climatic variables on natural population fluctuations by investigating the timing of their influence on Soay sheep
demographic processes. The main question is how does weather affects a population dynamics? This is particularly important because ultimately we want to know how we can disentangle density effects from extrinsic factors like environmental variation.

I specifically investigate the possible causes of population crashes, weather effects on birth and August weight, perinatal and lamb survival, female probability of having lambs, as well as weather signals for spring earliness and growing season. Thus, two sets of weather variables may have indirect effects on sheep dynamics: those determining the size of the forage crop at the end of the growing season; and those affecting the rate of primary production during the winter when green biomass is low. Finally, climate also influences sheep directly by imposing energetic demands, and this in turn influences the food requirements of individuals (Grenfell et al. 1998). It is important to understand the relative importance of climatic variables in the different age and sex categories. I examine how density dependence and climate contribute to fluctuations in population size via age- and sex-specific demographic rates, and how fluctuations in demographic structure influence population dynamics.

4.2. Methods

4.2.1. The study population

Soay sheep are classified as a rare breed (Clutton-Brock & Pemberton, 2004). They are thought to be similar to Neolithic sheep introduced to Britain around 5000 BC, and as such, they probably resemble the original wild sheep. The data for this chapter results from an intensive study (1954 to 2011 with a break from 1965-1984) of the Soay sheep living in the Village Bay area of Hirta, the largest island of the St. Kilda archipelago. The islands are found at 57˚49’N, 08˚34’W which is about 200 km west of the Scottish mainland (See map in chapter 2 methods). They are the most westerly of the Scottish islands to support vegetation. Hirta itself covers about 640 ha, whereas the study area in Village Bay covers about 175 ha.

Hirta has been uninhabited since 1930. The sheep were introduced to Hirta in 1932 after the last of the domestic sheep had been removed. The population is food limited, the animals interact with a complex mosaic of vegetation but they are free from culling and predation and there is no competition from other vertebrate
herbivores (Crawley et al. 2004). From 1985 onwards, virtually all-newborn lambs in Village Bay have been caught and marked each year, using a numbered ear-tag with a unique colour for each year. Data between 1985 and the present have been collected using the same counting protocol and are good estimates of population size (Clutton-Brock & Pemberton 2004). In August, there is a whole-island count, with standard routes to avoid double counting. Between 1962 and 1984 the quality of the population estimates is unknown, and Clutton-Brock & Pemberton (2004) recommended that these data should be excluded from analyses of population dynamics.

The Village Bay study population represents approximately one-third of the whole of the island count. Since 1985, >90% of individuals living within the study area have been caught within days of birth and uniquely marked with ear-tags. A set of ten census of the sheep population is taken three times each year, they followed throughout life with demographic data collected during lambing (March–April), in summer (August), during the rut (October–November), giving about 30 censuses per year. In the spring census, counts are made of the dead and live sheep found (Grenfell et al. 1998), which provide an accurate estimate of the study population and temporary immigration. The age and sex structure of the population in each year is known. Full details of methodological data collection are given in Clutton-Brock & Pemberton (2004).

As well as counts of the whole-island population, the Soay sheep living in the Village Bay catchment of the island have been the focus of an individual-based study since 1985 (Clutton-Brock & Pemberton 2004). The individual-based data have been the focus of a range of analyses to identify individual and population level covariates that influence age- and sex-specific survival and recruitment, with measurements ranging from coat colour morphs, horns, tissue sample for paternity, to age and sex (Clutton-Brock et al. 1991, 1992, 1997, Catchpole et al. 2000, Tavecchia et al. 2005, King et al. 2006).

**Soay sheep life cycle**
Lambs are born in April and May, after the spring growth of grasses, and weaned early in the summer, enabling mothers to recover before the food restrictions of winter. First conception generally occurs at 7-8 months, so that some females
produce their first lamb at just one year of age. Rut occurs in November. Most mortality occurs in February and March, at the end of winter (for more details see Clutton-Brock & Coulson 2002). During the summer months, vegetation biomass increases, as plant productivity exceeds offtake by herbivores. At the end of the main growing season, in the late summer, the biomass of available vegetation depends on the number of sheep, possibly the composition of the population, and weather during the growing season (April to September). At the onset of winter, females are in peak condition (Clutton-Brock & Coulson 2002) although summer weights do vary from year to year (Clutton-Brock & Pemberton 2004). During winter, sheep deplete the standing biomass produced over the summer. Depending on sheep numbers and the size of the standing crop, the biomass may remain at low levels until the start of the next growing season and the sheep may lose body mass for a more or less protracted period in late winter and early spring.

4.2.2. Soay sheep demographics

Population density
A key question is whether model assumptions about the form of the density dependence have large consequences on the weather variables retained in the minimal model, their effect sizes and standard errors, so I use three different forms for the density dependence: N, log (N) and Step Function (N), with a threshold of 1274.1 individuals (Coulson et al. 2008).

Population growth
a) Delta
Delta is defined as logarithmic population change (the difference in log population size in successive years): positive values of delta reflect population increase, negative values reflect population decline, while stationary populations would have delta= 0. So, delta = log (N_{t+1}/N_t). Log is defined as the log base e.

For the purpose of this chapter, population growth is not only evaluated by delta but also through measures of recruitment and survival.
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

Sheep weight trends

a) Birth weight
I investigated trends in birth weight across the years from 1986 to 2011. The actual birth weight had to be estimated as by regressing the weigh of the lamb when measured as a function of how many days after the actual birth the lamb was weighed.

b) August weight
August weight measures result from the catch of individuals from all age classes and both sexes (see Clutton-Brock & Pemberton 2004 for details). For the purpose of this analysis, females and males were analysed separately and subsequently divided into age classes: lambs, yearlings, two year olds, three year olds and finally four year old and above (analysed as one single age class). I analysed at the weight variation in those sex and age classes across the years and tested for possible trends in the long term mean and median.

Survival and recruitment

a) Lambs survival to first birthday Density-dependence in juvenile survival may be difficult to detect if survival is also affected by density-independent factors. I investigated the relationships among weather parameters, population density, and lamb survival to first birthday.

b) Females with lambs and females without lambs Density-dependence in the probability of a female becoming pregnant may be difficult to detect if the probability is also affected by density-independent factors. I investigated the relationships among weather parameters, population density, and number of females with lambs.

4.2.3. The vegetation community

Vegetation sampling is made along transects starting from productive grasslands in Village Bay just above sea level up to about 150 m altitude. Measures of biomass are in taken in March and August (since 1993) from 6 locations on each of 5 transects. The analysis included in this chapter will only focus on measures of biomass taken in the relatively productive inbye grasslands within the Head Dyke. Units are mean dry mass per 0.04m² quadrat, corrected for gap and tussock cover and gap and tussock composition (for full details of the methodology see
Crawley 2004 and Virtanen & Crawley 2010).
I averaged across transects, and the positions within the transects, to get one number for each season (March, August) within each year from August 1993. March and August analyses were carried out separately. For each of these time periods, I analysed several different plant response variables separately. The commoner taxa (Agrostis spp., Holcus lanatus, Festuca rubra, Poa spp., Anthoxanthum odoratum, Ranunculus ficaria, Ranunculus acris, Trifolium repens, Cerastium fontanum) in addition four aggregate measures: dead organic matter, bryophytes, grasses and herbs.

4.2.4. Weather

St. Kilda weather time series
In this chapter, I use the reconstructed weather time series (see chapter 2 for details) that includes daily minimum and maximum temperature (°C), precipitation (mm) and wind speed (m/s) from 1954 till 2000 in addition the data extracted from the automatic weather station in St Kilda from 2001 onwards. From the three automatic weather stations on the island, Signals was the chosen one, because it is at the heart of the study area, most sheep experience Signals’ weather, rather than the rest of the island weather. The 4 explanatory variables show differing degrees of correlation with each other. There is strong negative correlation between maximum temperature and precipitation, and a weaker positive correlation between wind speed and precipitation (table 4-1).

Table 4-1 Cross-correlation of the local weather variables on St. Kilda (1957-2011).

<table>
<thead>
<tr>
<th>Weather variables</th>
<th>Min. Temp</th>
<th>Max. Temp</th>
<th>Precipitation</th>
<th>Wind speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Min. Temp</td>
<td>1.00</td>
<td>0.94</td>
<td>-0.13</td>
<td>-0.33</td>
</tr>
<tr>
<td>Max. Temp</td>
<td>.</td>
<td>1.00</td>
<td>-0.90</td>
<td>-0.36</td>
</tr>
<tr>
<td>Precipitation</td>
<td>.</td>
<td>.</td>
<td>1.00</td>
<td>0.47</td>
</tr>
<tr>
<td>Wind speed</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Weather variables and aggregations

The weather variables used in this chapter were minimum and maximum temperature, precipitation and wind speed. I mostly used the daily values but also aggregates of these values, either as monthly means, windows (explained below) or as season aggregates. For the case of precipitation, in addition to monthly means, accumulation of rain over the same period was also measured.

For the purpose of the initial models for this chapter, the definition of seasons is set according to the life cycle of the Soay sheep. Winter is defined as December through mid March; spring is defined as mid March through end of May. Summer is defined as June through August and autumn is defined as September through November. At times I have shifted these definitions by one to two weeks in order to experiment with different “season” definitions. Thresholds were set for what constitutes a warm, wet or windy day for the end of the seasons. The temperature and precipitation thresholds were set by looking at the long term average and choosing values that were 1 or 2 standard deviations above or below the long-term average. Wind thresholds were set according to definitions of gales (above Beaufort force 7).

Growing day degrees

I used measures of growing day degrees (GDD) to provide an estimate of local climatic conditions in relation to vegetation growth (Grant et al. 1986, Snyder et al. 1999, Bonhomme, 2000). GDD is estimated as the cumulative sum of the daily mean temperatures above a threshold over a set period (Barnett et al., 2006), the zero development point of the species in question. Despite the potential limitations of GDD, including the potential nonlinearity of the relationship between development rate and temperature (discussed in detail in Bonhomme, 2000), GDD has been used successfully in horticulture to predict flowering dates and also in agriculture to predict yield. In the sheep models, I therefore use GDD as a proxy for vegetation growth. Although the norm is to use a threshold of 5°C (following Barnett et al., 2006) Here, I used thresholds from 4°C till 7°C (explained in detail in the critical windows section). As GDD is cumulative, it is essential to have accurate information about the mean daily temperature on every day.
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

Critical Windows

I used linear regression to estimate the each demographic and phenological trait of the sheep, as well as plant phenology (biomass inside and outside the cages) on the average temperature, total precipitation, and average wind, as well as accumulated growing day degrees over a specified time-window. I compared the predictive power of each variable in different time-windows using a proxy for $r^2$: (null deviance-deviance)/null deviance. In addition to using the best combinations according to $r^2$ windows were further selected according to the following rules: the combination of window start and length could not exceed the 1st of May of the birth year, and also the minimum p value of the considered weather variables (linear or quadratic form) needed to be 0.05. The linear regressions used for the search of the best windows included sheep density as measured in the August; linear and quadratic forms of the weather variable in question. The relative importance of different dates is captured in the width of the window.

Lamb survival windows - I varied both the starting date of the sliding window starting in on the 1st of April of the previous year in seven day intervals up the 15th of April of the year of birth (days given in ordinal dates, i.e. 1 for 1st January and 365 or 366 for 31st December, depending on leap years) and the duration of the window with lengths varying from 7 to 112 days in 7-day intervals. I compared the predictive power of each variable in different time-windows using a proxy for $r^2$: (null deviance-deviance)/null deviance. In addition to using the best combinations according to $r^2$ windows were further selected according to the following rules: the combination of window start and length could not exceed the 15th of April of the birth year, and also the minimum p value of the considered weather variables (linear or quadratic form) needed to be 0.05. The linear regressions used for the search of the best windows included sheep density as measured in the previous August; linear and quadratic forms of the weather variable in question. The rational for this, is that sheep population is the single most important driver for productivity in the island, so the weather that remains in models is going to explain the residuals that sheep numbers don’t.

Female reproduction allocation windows - Same procedure as above.

e) Plant productivity windows- I used linear regression to estimate the productivity of each plant species and aggregation of species, on the average temperature, total
precipitation, and average wind and accumulated growing day degrees over a
specified time-window.

For March, I varied both the starting date of the sliding window starting in on
the first of July of the previous year in seven day intervals up the 15th of March of the
year of collection (days given in ordinal dates, i.e. 1 for 1st January and 365 or 366
for 31st December, depending on leap years) and the duration of the window with
lengths varying from 7 to 112 days in 7-day intervals. I compared the predictive
power of each variables in different time-windows using \( r^2 \). In addition to using the
best combinations according to \( R^2 \) windows were further selected according to the
following rules: the combination of window start and length could not exceed the 15th
of March of the year collection, the windows for wind shorter than 21 days they were
not considered, and also the windows needed to have a p value< 0.05. The linear
regressions used for the search of the best windows included sheep density as
measured in the previous August; linear and quadratic forms of the weather variable
in question. The rational for this, is that sheep population is the single most important
driver for productivity in the island, so the weather that remains in models is going to
explain the residuals that sheep numbers don’t.

For August similar procedure was carried out, the starting date of the sliding
window starting in on the first of February of the same year in seven day intervals up
the 15th of August of the year of collection (days given in ordinal dates, i.e. 1 for 1st
January and 365 or 366 for 31st December, depending on leap years) and the
duration of the window with lengths varying from 7 to 112 days in 7-day intervals.
Similar stringency rules were applied; in this case the combination of window start
and length could not exceed the 15th of August of the year collection. The linear
regressions used for the search of the best windows included sheep density as
measured on August of the year of collection; plant biomass of the previous March,
linear and quadratic forms of the weather variable in question.

**The North Atlantic Oscillation**

The NAO is traditionally defined as the normalized sea level pressure difference
between a station on the Azores and one on Iceland. Winter NAO (wNAO) refers to
the December through March average (see Osborn et al. 1999). For the purpose of
the analysis carried out in this project, wNAO of year x refers to December of year x-
1 and January through March of year x. Summer NAO (sNAO) refers to high summer average, July and August (Hurrell 1995). sNAO of year x refers to both July and August of year x. This was decided in order to avoid discrepancies when using it in conjunction with sheep delta. Positive values of the NAO index indicate stronger than average westerlies over the middle latitudes.

The NAO as measure of weather severity has been used in St. Kilda because until recently (see chapter 2 for details) the local weather data were incomplete. It has been assumed that positive values of NAO are associated with wet and stormy weather, what is considered bad weather for the sheep. Negative values of NAO are associated with cold and dry weather, meaning what is considered good weather for the sheep population (e.g. Hallet et al. 2004)

4.2.5. Statistical modelling

Statistical analyses were performed using the software R 2.13.1 for Windows (R Development Core Team, 2011).

A key question is whether the model assumptions about the form of the density dependence have large consequences on the weather variables retained in any minimal model, their effect sizes and standard errors. All sheep demography analysis used three forms of density: N, log(N) and Step Function (N).

Population growth using delta to explain population crashes

I have contrasted three different models for the density dependence where delta = log (N_{t+1}/N_t). The models are delta ~ N, delta ~ log (N) and delta ~ Step Function (N).

Weather patterns

Initially the analysis focused on winter climatic conditions in January, February and March in the years when the population crashed. The idea was to look for patterns of weather in crash years. This was done by exploring departures from the long-term monthly averages: values in the 75\textsuperscript{th} percentile and below or above; values in the 90\textsuperscript{th} percentile and below or above; values somewhere inside the box of a box and whisker plot.
Weather models
I have taken all the data from the first (1959-1969) and second (1985-present) study periods and fitted a variety of linear regression models. In all cases, I began with a complex model containing all weather variables from all winter months and simplified this to obtain a minimum adequate model.

Subsequently, I expanded the weather window to include thirty-seven weather variables (monthly means or aggregates). Using eight variables at a time, I ran every possible combination (approximately 38 million). I did this for each of the three different models of density dependence mentioned above. Variables were removed sequentially one at the time using stepwise deletion based on the Akaike information criterion (AIC) (Crawley 2007), until only the significant terms remained. Using the retained terms in these minimum adequate models, these were run again, this time for every possible permutation (assuming that order matters). The same stepwise deletion procedure was repeated.

Sheep weight (Birth and August weight)
Random forests - Before fitting linear models to look for the weather variables that would explain variation of August weight across the years for all ages and sex classes, I used the random forest algorithm (see Breinam 2011 for details) to perform the choice of the best environmental candidates. All biological plausible, explanatory variables (as daily value, monthly and season aggregations, with and without thresholds, as well as quadratic terms for continuous variables were inputted. Random forests are a machine-learning algorithm, which provide a combination of tree predictors such that the tree depends on the values of a random vector sampled independently and with the same distribution for all the trees in the forest. Because of the random elements in the algorithm results vary slightly between repetitions of the same model. As the variation was low and computational costs high, I report the results of one run only. At the end of a run the explanatory variables are ranked by importance to distinguish those that best explained the variation in the data. The ten highest ranked were then used for initial parameterisation of the linear regression models for each of the sex and age class.
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

Linear models

For both birth weight and August weight regressions, stepwise deletion was performed, where the least significant terms were removed sequentially until all remaining terms were significant at $p < 0.05$ to produce the minimal adequate model (MAM). All MAM’s were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors. For August weight, the variables, used in the linear models, were previously selected by the random forest algorithm. Three regression models were used: one with no weight, one with population as weight, and finally one with $1/\text{variance}$ of population. The results yielded similar weather effects so I only show the regression with population as weight.

Generalised linear models (GLMs)

a) Lamb survival to first year- For the GLMs the weather variables fitted were the most significant critical windows, as well as weather the significant windows for Dead organic matter and grasses, in March and August of the year of birth. The weather windows were fitted instead of the actually biomass measured for those two aggregations, as measured of biomass only start in 1993; and finally the sheep density, as measured on the August count of that same year. All three forms of density were fitted separately. From the stepwise deletion, where the least significant terms were removed sequentially until all remaining terms were significant at $p < 0.05$ to produce the minimal adequate model (MAM). All MAM’s were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors. Models were compared using ANOVA to justify retaining or excluding variables, and Akaike’s information criterion (AIC) used to compare model fit. Where the ANOVA indicated no significant difference between the models ($p > 0.05$) the model with the highest degrees of freedom was retained. Where a significant difference occurred the model with the lowest residual deviance was retained.

b) Proportion of ewes with lambs- Same procedure as for lamb survival
Plant productivity
This analysis was performed on the data from 1994 onwards, separately for March and August.

Linear models
The critical windows with the highest $r^2$ for each weather variable were then used in multiple linear multiple regression models for each species. In March, sheep population numbers of the previous year and the best windows of weather were included in the models. In August, sheep population numbers of the same year, March productivity and the best windows of weather were included in the models.

4.3. Results
The results presented here have two main headings: weather effects on sheep population, and weather effects on plant communities in St. Kilda.

4.3.1. Sheep population dynamics
Sheep numbers in the whole island count in August are shown in figure 3-1. There were never two declines, in the population numbers, in a row. The population has shown a significant upward trend over this period, with an average 39.45 extra sheep per year at the whole-island count in August ($n = 26$ years, $p = 0.0113$; choice of start or end date for the series is not influential, and the upward trend is significant if counts with up to three of the years are trimmed from either end of the full time series). In 1985 sheep numbers were set back to the initial numbers in the 1950's.
Figure 4-1 Time series of sheep numbers (solid symbols) during the first study period (1954-68) and the current study period (1985-2012), showing the trends in population size within the two periods (solid regression lines) and averaged across the two study periods (dashed line). The whole island population is increasing as the years go by. The slope of the whole study period regression line is $39.45 \pm 8.25$ animals per year. We do not understand the change in population trends between the first and second study periods.
4.4. Weather impacts on delta

4.4.1. Crash years

Table 4-2 shows the climatic conditions in January, February and March in the years when the population crashed.

Table 4-2 Weather variables in the winter months of the crash years. The signs reflect a departure from the long-term monthly averages. The ‘-’ indicate values in the 75th percentile and below; the ‘- -’ indicate values in the 90th percentile and below; ‘0’ is somewhere within one standard deviation form the long-term monthly averages. The ‘+’ indicate values in the 75th percentile and above. The ‘++’ indicate values in the 90th percentile and above.

<table>
<thead>
<tr>
<th>Crash Years</th>
<th>Month</th>
<th>Min. Temp.</th>
<th>Max. Temp.</th>
<th>Rain</th>
<th>Wind</th>
</tr>
</thead>
<tbody>
<tr>
<td>1959/60</td>
<td>January</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>January</td>
<td>+</td>
<td>0</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>1966/67</td>
<td>February</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>-</td>
<td>+</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td></td>
<td>January</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td>1988/89</td>
<td>February</td>
<td>0</td>
<td>+</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>-</td>
<td>0</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>January</td>
<td>0</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>1998/99</td>
<td>February</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>January</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>2001/02</td>
<td>February</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

4.4.2. Weather models explaining delta

Winter weather

Linear regression models were used to analyse the whole population time series using the definition of winter as the months of December through February.

In Chapter 2, I correlated winter NAO with all the locally measured weather variables from the three St Kilda stations (installed at the end of 1999), and discovered that the only significant correlation of NAO was with February rainfall \( r^2 = \)
0.61, positive relationship; p = 0.008) and total run of wind in February (r² = 0.56 positive; p = 0.03).

![Figure 4-2](image.png)

Figure 4-2 Average total rainfall during February (mm) in years with different sheep population dynamics. The green bars show February rain in years when the population crashed, and the red bars show the average rainfall in February of non-crash years. The two left-most bars relate to the initial study (1954-1968), the next two bars to the current study period (since 1987), and the right-most bar shows the exceptionally dry February of 1986. Error bars show plus and minus 1 standard error of the mean. Note how much higher February rainfall has become between the first and second study periods in both crash and non-crash years.

In figure 4-3a, I show the relationship between the delta residuals and February minimum temperature, which was one of the variables consistently to appear in the minimum adequate model.
Figure 4-3  a) Shows the significant positive relationship between delta residuals and February minimum temperature (for details see text). b), c) and d) show the relationship between delta and population count in August of the previous year with three different functions fitted: b) uses a linear regression, c) a logarithmic function and d) shows the three-parameter step function centred on the threshold population size of 1274 animals. For the models depicted in b), c), and d) the weather variables included in the maximal model were day-degrees (December through mid March with a threshold of 5°C), December minimum temperature, December maximum temperature, December rainfall, December wind speed, January minimum temperature, January maximum temperature, January rainfall, January wind speed, February minimum temperature, February maximum temperature, February rainfall, February wind speed, March minimum temperature, March maximum temperature, March rainfall, March wind speed and the winter NAO.
4.4.3. All year weather

Linear regression models were used again to analyse the population time series; this time, including possible weather from the whole year. The various combinations produced several models that contained significant variables that were retained in the model, using the different forms of density. The regressions for all the permutations were done using the high performance cluster to for speed.

a) Model with density N

The models resulting from the combinations had AICs ranging from -24 to 33. The models with lowest (-18 to -24) AICs were selected and using stepwise deletion only the significant terms were retained in those models.

A recurring issue with multiple regression arises here. More complex models that use more degrees of freedom are not considered. As an example, consider the following maximal model, which uses 23 degrees of freedom with delta as a function of:

1. Population (-)
2. January.Rain(-)
3. February.Rain (-)
4. February.MaxTemp (+)
5. October.MinTemp(+)
6. December.MinTemp (-)
7. winter.dd (+)
8. previous.spring.rain (+)
9. previous.summer.rain (+)
10. previous.autumn.dd (+)
11. jf.windy.days (-)
12. winter.rainy.days(-)
13. previous.summer.rainy.days (+)
14. previous.summer.rain (-)
15. previous.summer.warm.days (+)
16. jfm.windy.days (-)
17. March.windy.days (-)
18. previous.spring.rainy.days (+)
19. previous.springandsummer.rainy.days ()
20. previous.May.Rain (+)
21. spring.rain (+)
The resulting minimum adequate model, although it uses many more degrees of freedom than the sampled less complex models, has an AIC=-57, which is better than the aforementioned models with AIC=-24.

The model with AIC=-57 has delta as a function of:
1. Population (-)
2. February.Rain (-)
3. February.MaxTemp (+)
4. October.MinTemp (+)
5. December.MinTemp (-)
6. previous.spring.rain (+)
7. previous.summer.rain (+)
8. winter.rainy.days (-)
9. previous.summer.rainy.days (+)
10. jfm.windy.days (-)
11. March.windy.days (-)
12. previous.springandsummer.rainy.days (+)
13. previous.May.Rain (+)
14. spring.rain (+)

b) Model with density log(N)

Same procedure as above. And similar issues as above. The model with AIC=-68 was again better than the models from sampling has delta as a function of:
1. log(Population) (-)
2. December.MinTemp (-)
3. February.MaxTemp (+)
4. February.Rain (-)
5. spring.rain (+)
6. previous.spring.rain (+)
7. jfm.windy.days (-)
8. previous.May.Rain (+)
9. October.MinTemp (-)
10. previous.Maydd (+)
11. previous.summer.rain (+)
12. previous.autumn.dd (+)
13. previous.summer.rainy.days (+)
14. winter.dd(+)
15. previous.springandsummer.rainy.days (+)
16. previous.summer.warm.days (+)

c) Model with density StepFunction(N)
Same procedure as above. The model with AIC=-17 was again better than the models from sampling has delta as a function of:
1. stepfunctiondensity (-)
2. December.MinTemp (-)
3. February.MaxTemp (+)
4. February.Rain (-)
5. spring.rain (+)
6. previous.Maydd (+)
7. jf.windy.days (-)
8. previous.June.Rain (+)

4.4.4. Winter NAO and local weather
In chapter 2, I have already shown that NAO is not a good predictor of St. Kilda local weather (see chapter 2 results). Below, I show the NAO times series. When compared with the Soay sheep population time series (Figure 3-3), there is no clear pattern or relationship observed (figure 4-17).
Figure 4.4 In red, the total sheep numbers on Hirta from the annual whole-island count each August for the second part of the study period (1985-2010). In black, winter NAO for the same period.

Here I show the relationship between NAO and some examples of weather aggregations and investigate further whether wNAO actually predicts particular types of weather across periods of time (figures 4-5 and 4-6).

Figure 4-5 Predicting February and March rainy days (threshold is set to 5 mm per day), using winter NAO.
Figure 4-6 Predicting winter windy days (threshold is set to 8 m/s per day) using winter NAO. Winter is defined as December through mid March.

4.4.5. Weight trends

Weight is a measure of fitness, which affects survival and recruitment.

Birth weight

Age of mother is important for the youngest and oldest mothers. On figure 4-7 we can observe three distinct periods. A decline in birth weight, between 1985 and 1994, followed by a period of little change between 1994 and 2001, and an increase in birth weight since then.

Figure 4-7 Sheep birth weight for the period 1985-2011. The dashed line represents the annual median birth weight and the black line represents the annual mean birth weight.
Critical windows

Below I show the best weather critical windows that affect variance (table 4-3) and median birth weight (table 4-4).

**Table 4-3 Weather critical windows for variance in birth weight. Windows are labelled form 1 through 4 from the farthest to the closest to the event.**

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growing day degrees</td>
<td>20.05-</td>
<td>16.09-04</td>
<td>24.02-</td>
<td>17.03-</td>
</tr>
<tr>
<td>Threshold: 7°C</td>
<td>23.06</td>
<td>.11</td>
<td>28.04</td>
<td>28.04</td>
</tr>
<tr>
<td>Threshold: 7°C</td>
<td></td>
<td></td>
<td>24.02-</td>
<td></td>
</tr>
<tr>
<td>Threshold: 7°C</td>
<td></td>
<td></td>
<td>17.03-</td>
<td></td>
</tr>
<tr>
<td>Average Temperature</td>
<td>20.05-</td>
<td>24.02-</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Temperature</td>
<td>03.06</td>
<td>10.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rain</td>
<td>20.05-</td>
<td>01.07-</td>
<td>02.09-</td>
<td>17.03-</td>
</tr>
<tr>
<td></td>
<td>24.06</td>
<td>12.08</td>
<td>14.10</td>
<td>31.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>27.05-</td>
<td>20.01-</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Wind</td>
<td>10.06</td>
<td>27.01</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4-4 Weather critical windows for median annual birth weight. Windows are labelled form 1 through 4 from the farthest to the closest to the event.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growing day</td>
<td>20.05-</td>
<td>30.12-</td>
<td>06.01-</td>
<td>10.03-</td>
</tr>
<tr>
<td>degrees</td>
<td>05.07</td>
<td>03.02</td>
<td>02.10</td>
<td>28.04</td>
</tr>
<tr>
<td>Threshold:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7°C</td>
<td>7°C</td>
<td>7°C</td>
<td>7°C</td>
<td></td>
</tr>
<tr>
<td>Average Temperature</td>
<td>06.05-</td>
<td>20.01-</td>
<td>24.02-</td>
<td>NA</td>
</tr>
<tr>
<td>Rain</td>
<td>22.04-</td>
<td>20.01-</td>
<td>02.09-</td>
<td>17.03-</td>
</tr>
<tr>
<td></td>
<td>03.06</td>
<td>27.01</td>
<td>14.10</td>
<td>31.03</td>
</tr>
<tr>
<td>Wind</td>
<td>06.05-</td>
<td>23.12-24-</td>
<td>24.02-28-</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>15.07</td>
<td>03</td>
<td>04</td>
<td></td>
</tr>
</tbody>
</table>

The Linear regression models

Table 4-5 shows the weather effects on variance in birth weight. Sheep density has a negative effect on birth weight. Growing day degrees between May and June of the previous year to birth have a positive effect.

Table 4-5 Density and weather effects on variance in birth weight

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheep density</td>
<td>-5.709e-05</td>
<td>2.425e-05</td>
<td>-2.354</td>
<td>0.027469 *</td>
<td>0.4538</td>
<td>23</td>
</tr>
<tr>
<td>GDD 1</td>
<td>3.114e-03</td>
<td>7.890e-04</td>
<td>3.947</td>
<td>0.000641 ***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: \( P < 0.05 = ^* \), \( P < 0.01 = ^{**} \), \( P < 0.001 = ^{***} \). Non-significant effects are not shown. \( P \) values for significant effects are taken from the model output of the MAM.
Table 4-6 shows the weather effects on the median birth weight. Again sheep density has a negative effect on birth weight. Growing days degrees in March to April of birth year have a positive effect on weight and Rain in January has a negative effect on birth weight.

Table 4-6 Density and weather effects on median birth weight yearly

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheep density</td>
<td>-3.033e-04</td>
<td>8.445e-05</td>
<td>-3.592</td>
<td>0.00162 **</td>
<td>0.5322</td>
<td>22</td>
</tr>
<tr>
<td>GDD 4</td>
<td>4.133e-03</td>
<td>1.518e-03</td>
<td>2.722</td>
<td>0.01244 *</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rain 2</td>
<td>-5.290e-03</td>
<td>1.699e-03</td>
<td>-3.114</td>
<td>0.00506 **</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

**August weight**

The analysis was carried out separately for the sexes. The female population was put in to age classes as follows: Age 0 which are the lambs born the March of the August catch. Age 1(yearlings), born the March of the year before, and so on until Age 3. Age 4 and older were put in the same category as the number of individuals was far too small, for them to be evaluated in separate categories. The male population was divided similarly, but the older ages were collapsed from age 3 onwards.

**Females**

Each age class shows a different year on year trend. Figure 4-5 shows the weight for females age 0. Note that year 1989 has a very small sample of individuals. There is a variation in weight between years.
Figure 4-8 Females age 0 August weight from 1989. Not significantly trended over the period 1989-2009.

Figure 4-6 shows August weight for females age 1. Again the year 1989 has small sample of individuals. There is again variation between years.

Figure 4-9 Females August weight Age 1. Not significantly trended over the period 1989-2009.

Figure 4-7 shows August weight for females age 2. Again the year 1989 has small sample of individuals. There is again variation between years.
Figure 4-10 Females August weight Age 2. Not significantly trended over the period 1989-2009.

Figure 4-8 shows August weight for females age 3. Again the year 1989 has small sample of individuals. There is again variation between years.

Figure 4-11 Females August weight Age 3. Not significantly trended over the period 1989-2009.

Figure 4-9 shows August weight for females age 4 and above. There is again variation between years.
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

Figure 4-12 Females August weight Age 4 and above. Not significantly trended over the period 1989-2009.

**Males**

Each age class is shows a different year on year trend. Figure 4-10 shows males age 0. There is a variation in weight between years.

Figure 4-13 Males August weight from 1990 to 2010. Lambs, age 0. Mean weight has been increasing for this age class over the period 1990 to 2010 ($F_{1,19} = 4.77$, $p=0.04$).

Figure 4-11 shows August weight for males age 1. Again the year 1989 has small sample of individuals. There is again variation between years.
Figure 4-14 Males August weight from 1989 to 2010. Yearlings, age 1. Not significantly trended over the period 1989-2009.

Figure 4-12 shows August weight for males age 2. The year 1990 has small sample of individuals. There is again variation between years.

Figure 4-15 Males August weight from 1990 to 2010. Age 2. Not significantly trended over the period 1990-2010.

Figure 4-13 shows August weight for males age 3. The year 19991 has small sample of individuals. There is again variation between years.
Figure 4-16 Males August weight from 1991 to 2010. Age 3 and above. Not significantly trended over the period 1991-2009.

### The linear regression models

Here is only show the weather effects on females (table 4-7). Note that for Age 2, no weather variables appear to affect weight.

**Table 4-7** Female August weight at the different age classes. Weather effects on the female August weight of different age classes using linear regression weighted with population size at each class as weight.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Significant weather variables</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lambs</td>
<td>Previous population density</td>
<td>Negative</td>
</tr>
<tr>
<td></td>
<td>March rain</td>
<td>Positive</td>
</tr>
<tr>
<td>Yearlings</td>
<td>Current population</td>
<td>Negative</td>
</tr>
<tr>
<td>Age 2</td>
<td>Current population density</td>
<td>Negative</td>
</tr>
<tr>
<td>Age 3</td>
<td>Current population density</td>
<td>Negative</td>
</tr>
<tr>
<td></td>
<td>Previous December Maximum Temperature</td>
<td>Negative</td>
</tr>
<tr>
<td></td>
<td>Previous December Rain</td>
<td>Positive</td>
</tr>
<tr>
<td>Age 4+</td>
<td>Previous population density</td>
<td>Negative</td>
</tr>
<tr>
<td></td>
<td>Previous December maximum temperature</td>
<td>Positive</td>
</tr>
<tr>
<td></td>
<td>March maximum temperature</td>
<td>Positive</td>
</tr>
</tbody>
</table>
4.4.6. Survival and recruitment

Below (table 4-8) are the best weather windows for lamb survival. Temperature effects range mostly from May to August the year of birth, with one window for average temperature in January to March (presumably a pre-birth effect on maternal condition). Rain effects are felt in the summer on birth year. Wind effects are from November the year of birth to April (their first winter of life).

Table 4-8 Critical windows for lamb survival to first birthday. Windows are labelled form 1 through 4 from the farthest to the closest to the event.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growing day degrees</td>
<td>10.06-</td>
<td>17.06-</td>
<td>24.06-</td>
</tr>
<tr>
<td></td>
<td>29.07</td>
<td>29.07</td>
<td>05.08</td>
</tr>
<tr>
<td>Threshold:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7°C</td>
<td></td>
<td>7°C</td>
<td>7°C</td>
</tr>
<tr>
<td>Average Temperature</td>
<td>27.05-</td>
<td>17.06-</td>
<td>13.01-</td>
</tr>
<tr>
<td></td>
<td>22.07</td>
<td>29.07</td>
<td>10.03</td>
</tr>
<tr>
<td>Rain</td>
<td>24.06-</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>02.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>04.11-</td>
<td>03.03-</td>
<td>10.03-</td>
</tr>
<tr>
<td></td>
<td>25.11</td>
<td>14.04</td>
<td>14.04</td>
</tr>
</tbody>
</table>

The GLM

Sheep density has a negative effect on lamb survival during the first year. Temperature in June to August has a positive effect on survival. Rain in June to September and wind in November the year of birth have negative effects (table 4-9). In addition a proxy for March biomass has a positive effect in survival. The variable here refer as March Grass Average temperature, corresponds to the best critical window for average temperature that has a positive effect on grass growth. Since data for vegetation starts in 1990, I used the temperature and extended it back to
match the survival time series, this assuming that the relationship between average temperature and grass growth in March didn’t change.

Table 4-9 Sheep density and weather effects on lamb survival to first birthday. Residual deviance 560.38, 25 df. Only the significant effects that remained in the MAM are shown.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheep density</td>
<td>-0.0016316</td>
<td>0.00038</td>
<td>-4.264</td>
<td>0.000379 ***</td>
</tr>
<tr>
<td>GDD w3</td>
<td>0.0161706</td>
<td>0.006817</td>
<td>2.372</td>
<td>0.027826 *</td>
</tr>
<tr>
<td>Rain w1</td>
<td>-0.0134789</td>
<td>0.003966</td>
<td>-3.399</td>
<td>0.002850 **</td>
</tr>
<tr>
<td>Wind w1</td>
<td>-0.6351044</td>
<td>0.235112</td>
<td>-2.701</td>
<td>0.013739 *</td>
</tr>
<tr>
<td>March Grass Avg. temp</td>
<td>0.4694606</td>
<td>0.141598</td>
<td>3.315</td>
<td>0.003452 **</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are indicated by ‘ns’. P values for significant effects are taken from the model output of the MAM.
Table 4-10 shows the effects of weather on lamb survival when fitting log density. Same weather effects are observed. Table 4-10 Log sheep density and weather effects on Lamb survival to first birthday. Residual deviance 543.98, 25 df. Only the significant effects that remained in the MAM are shown.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (Sheep density)</td>
<td>-2.215024</td>
<td>0.5019</td>
<td>-4.413</td>
<td>0.000268***</td>
</tr>
<tr>
<td>GDD w3</td>
<td>0.015118</td>
<td>0.0066</td>
<td>2.288</td>
<td>0.033128 *</td>
</tr>
<tr>
<td>Rain w1</td>
<td>-0.014158</td>
<td>0.0039</td>
<td>-3.615</td>
<td>0.001726 **</td>
</tr>
<tr>
<td>Wind w1</td>
<td>-0.630805</td>
<td>0.2318</td>
<td>-2.722</td>
<td>0.013136 *</td>
</tr>
<tr>
<td>March grasses Avg. temp</td>
<td>0.491013</td>
<td>0.1406</td>
<td>3.493</td>
<td>0.002294 **</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance:  $P < 0.05 = ^*$,  $P < 0.01 = ^{**}$,  $P < 0.001 = ^{***}$. Non-significant effects are indicated by ‘ns’. P values for significant effects are taken from the model output of the MAM.
Table 4-11 shows the effects of weather on lamb survival when fitting a step function for density dependence. Same weather effects are observed, with an added window for Wind from March to April.

**Table 4-11** Step function sheep density and weather effects on Lamb survival to first birthday. Residual deviance 1166.3, 24 df. Only the significant effects that remained in the MAM are shown.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Step function sheep density</td>
<td>-1.947166</td>
<td>0.384</td>
<td>-5.077</td>
<td>6.69e-05 ***</td>
</tr>
<tr>
<td>GDD w2</td>
<td>0.017071</td>
<td>0.006</td>
<td>2.736</td>
<td>0.013118 *</td>
</tr>
<tr>
<td>Rain w1</td>
<td>-0.013633</td>
<td>0.004</td>
<td>-3.732</td>
<td>0.001411 **</td>
</tr>
<tr>
<td>Wind w1</td>
<td>-0.951720</td>
<td>0.273</td>
<td>-3.491</td>
<td>0.002446 **</td>
</tr>
<tr>
<td>Wind w2</td>
<td>2.072495</td>
<td>0.755</td>
<td>2.745</td>
<td>0.012869 *</td>
</tr>
<tr>
<td>March grasses Avg. temp</td>
<td>0.504333</td>
<td>0.124</td>
<td>4.069</td>
<td>0.000654 ***</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are indicated by ‘ns’. P values for significant effects are taken from the model output of the MAM.

**Proportion of females with lambs**

![Proportion of females with lambs](image)

Figure 4-17 Proportion of females that have lambs for the period 1986-2010. Proportion of females with lambs is not trended for this period.
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

Table 4-12 Critical windows for lamb survival to first birthday. Windows are labelled form 1 through 4 from the farthest to the closest to the event.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growing day</td>
<td>03.06-</td>
<td>13.12-</td>
<td>10.02-</td>
<td>24.03-</td>
</tr>
<tr>
<td>degrees</td>
<td>24.06</td>
<td>06.01</td>
<td>24.02</td>
<td>07.04</td>
</tr>
<tr>
<td>Threshold:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4°C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average Temperature</td>
<td>03.06-</td>
<td>24.03-</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>24.06</td>
<td>07.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rain</td>
<td>08.07-</td>
<td>30.09-</td>
<td>03.02-</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>19.08</td>
<td>07.10</td>
<td>17.02</td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>22.07-</td>
<td>30.09-</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>26.08</td>
<td>07.10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The GLM

Table 4-13 shows the proportion of females with lambs is not affected by sheep density. Temperature in December through January with a threshold of 7°C and wind in July - August have a positive effect on the probability of females having lambs.

Table 4-13 Proportion of females with lambs. Residual deviance 543.98, 25 df. Only the significant effects that remained in the MAM are shown.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD w.2</td>
<td>0.15</td>
<td>0.005</td>
<td>3.4</td>
<td>0.003 ***</td>
</tr>
<tr>
<td>Wind w.1</td>
<td>0.25</td>
<td>0.07</td>
<td>3.5</td>
<td>0.002 ***</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: $P < 0.05 = ^{*}$, $P < 0.01 = ^{**}$, $P < 0.001 = ^{***}$. Non-significant effects are indicated by ‘ns’. P values for significant effects are taken from the model output of the MAM.
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

4.5. Plant biomass

March Biomass

The different species are affected by weather at different times of the year (Table 4-14).

The critical windows

Table 4-14 Choosing the critical weather windows associated with variation in plant productivity from September of the previous year until March 15th of the current year growth and senescence. Where an NA is present there were no significant windows for the corresponding variables.

<table>
<thead>
<tr>
<th>Species</th>
<th>Growing day degrees</th>
<th>Average temperature</th>
<th>Total precipitation</th>
<th>Average wind speed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Start date: 29.12</td>
<td>Start date: 01.09</td>
<td>Start date: 27.10</td>
<td>Start date: 24.11</td>
</tr>
<tr>
<td></td>
<td>Length: 42 days</td>
<td>Length: 63 days</td>
<td>Length: 105</td>
<td>Length: 21 days</td>
</tr>
<tr>
<td></td>
<td>Threshold: 7°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Festuca rubra</td>
<td>Start date: 01.12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Length: 28 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poa spp</td>
<td>Start date:01.09</td>
<td>Start date: 01.09</td>
<td>Start date: 12.01</td>
<td>Start date: 11.09</td>
</tr>
<tr>
<td></td>
<td>Length: 63 days</td>
<td>Length: 63 days</td>
<td>Length: 14 days</td>
<td>Length: 63 days</td>
</tr>
<tr>
<td></td>
<td>Start date: 12.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Length: 21 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Threshold: 6°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 29.12</td>
<td>Start date: 01.09</td>
<td>Start date: 10.06</td>
<td>Start date: 20.10</td>
</tr>
<tr>
<td></td>
<td>Length: 49 days</td>
<td>Length: 63</td>
<td>Length: 49 days</td>
<td>Length: 21 days</td>
</tr>
<tr>
<td>Agrostis spp</td>
<td>Start date: 01.12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Length: 70 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>Start date: 01.09</td>
<td>Start date 01.09</td>
<td>Start date: 15.09</td>
<td>Start date: 29.09</td>
</tr>
<tr>
<td></td>
<td>Length: 14 days</td>
<td>Length: 14 days</td>
<td>Length: 21 days</td>
<td>Length: 56</td>
</tr>
<tr>
<td></td>
<td>Threshold: 4°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Start Date 1</td>
<td>Length 1</td>
<td>Start Date 2</td>
<td>Length 2</td>
</tr>
<tr>
<td>-------------------------</td>
<td>--------------</td>
<td>----------</td>
<td>--------------</td>
<td>----------</td>
</tr>
<tr>
<td><em>Anthoxanthum odoratum</em></td>
<td>01.09</td>
<td>49 days</td>
<td>01.09</td>
<td>49</td>
</tr>
<tr>
<td><em>Trifolium repens</em></td>
<td>26.01</td>
<td>42 days</td>
<td>26.01</td>
<td>42</td>
</tr>
<tr>
<td><em>Ranunculus ficaria</em></td>
<td>06.10</td>
<td>63 days</td>
<td>06.10</td>
<td>63</td>
</tr>
<tr>
<td><em>Ranunculus acris</em></td>
<td>09.02</td>
<td>7 days</td>
<td>02.02</td>
<td>35 days</td>
</tr>
<tr>
<td><em>Cerastium fontanum</em></td>
<td>01.12</td>
<td>70 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type</td>
<td>Start date</td>
<td>Length</td>
<td>Threshold</td>
<td></td>
</tr>
<tr>
<td>--------------</td>
<td>------------</td>
<td>--------</td>
<td>-----------</td>
<td></td>
</tr>
<tr>
<td>Grasses</td>
<td>Start date: 5.01</td>
<td>Length: 42 days</td>
<td>6.5°C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 05.01</td>
<td>Length: 21 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 27.10</td>
<td>Length: 42 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herbs</td>
<td>Start date: NA</td>
<td>Length: NA</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 08.12</td>
<td>Length: 21 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 03.02</td>
<td>Length: 21 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bryophytes</td>
<td>Start date: 01.09</td>
<td>Length: 14</td>
<td>7°C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 29.09</td>
<td>Length: 70 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 06.10</td>
<td>Length: 49 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start date: 01.09</td>
<td>Length: 49 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 01.09</td>
<td>Length: 98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dead organic matter</td>
<td>Start date: 03.11</td>
<td>Length: 28 days</td>
<td>4°C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 01.09</td>
<td>Length: 77 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 29.12</td>
<td>Length: 49 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start 05.01</td>
<td>Length: 35 days</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 09.02</td>
<td>Length: 14 days</td>
<td>7°C</td>
<td></td>
</tr>
</tbody>
</table>
The linear models

Not all plant species are affected by sheep density. The timing of their growth is illustrated by the different windows that remain in the models for each species (table 4-15).

Table 4-15 Linear models of weather and sheep density effects on March plant biomass. The initial model for each species and aggregations contained sheep density measured previous year (August whole island count), in addition to the critical windows found for each of the weather variables. Only the remaining significant terms in the model are shown. Where a ‘-’ appears after the explanatory variable, this means a negative correlation. Where a ‘+’ sig appears, this means it is a positive correlation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Minimum adequate model</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Festuca rubra</em></td>
<td>Sheep density (-)+ Average temperature (+)+ wind (-)</td>
<td>0.40</td>
</tr>
<tr>
<td><em>Poa spp.</em></td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Agrostis spp.</em></td>
<td>Sheep density (-)+ first rain window (+)</td>
<td>0.49</td>
</tr>
<tr>
<td><em>Holcus lanatus</em></td>
<td>Sheep density (-)+ first window day degrees (+)</td>
<td>0.47</td>
</tr>
<tr>
<td><em>Anthoxanthum odoratum</em></td>
<td>Sheep density (-)+ rain (+)</td>
<td>0.48</td>
</tr>
<tr>
<td><em>Trifolium repens</em></td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ranunculus ficaria</em></td>
<td>Sheep density (-)+ first window rain (+)+first window wind (+)</td>
<td>0.79</td>
</tr>
<tr>
<td><em>Ranunculus acris</em></td>
<td>Rain (+)+ wind(-)</td>
<td>0.63</td>
</tr>
<tr>
<td><em>Cerastium fontanum</em></td>
<td>Sheep density (-)+ First Rain window (-)+ Second Rain window (-)</td>
<td>0.71</td>
</tr>
<tr>
<td><em>Grasses</em></td>
<td>Sheep density (-)+ first window Average temperature (+)</td>
<td>0.63</td>
</tr>
<tr>
<td><em>Herbs</em></td>
<td>Rain (+)</td>
<td>0.36</td>
</tr>
<tr>
<td><em>Bryophytes</em></td>
<td>First window rain (+)</td>
<td>0.56</td>
</tr>
<tr>
<td><em>Dead organic matter</em></td>
<td>Sheep density (-)+ first day degree window (+)</td>
<td>0.80</td>
</tr>
</tbody>
</table>
August biomass

The different species are affected by weather at different times of the year (Table 4-16).

Table 4-16 Choosing the critical weather windows associated with variation in plant productivity between mid March and mid August of the same year growth and senescence

<table>
<thead>
<tr>
<th>Species</th>
<th>Growing day</th>
<th>Average temperature</th>
<th>Total precipitation</th>
<th>Average wind speed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>degrees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Festuca rubra</strong></td>
<td>Star date: 27.02</td>
<td>Star date: 27.02</td>
<td>Start date: 13.02</td>
<td>Start date: 06.02</td>
</tr>
<tr>
<td></td>
<td>Length: 21 days</td>
<td>Length: 21 days</td>
<td>Length: 7 days</td>
<td>Length: 28 days</td>
</tr>
<tr>
<td></td>
<td>Threshold: 4°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start date: 06.03</td>
<td>Start date: 06.03</td>
<td>Start date: 84 days</td>
<td>Start date: 22.05</td>
</tr>
<tr>
<td></td>
<td>Length: 14 days</td>
<td>Length: 14</td>
<td>Length: 63 days</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Threshold: 4°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Poa spp.</strong></td>
<td>Start date: 06.02</td>
<td>Start date: 06.02</td>
<td>Start date: 06.02</td>
<td>Start date: 03.04</td>
</tr>
<tr>
<td></td>
<td>Length: 21 days</td>
<td>Length: 21 days</td>
<td>Length: 7 days</td>
<td>Length: 49 days</td>
</tr>
<tr>
<td></td>
<td>Threshold: 5.5°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Agrostis spp.</strong></td>
<td>Start date: 27.03</td>
<td>Start date: 03.04</td>
<td>Start date: NA</td>
<td>Start date: NA</td>
</tr>
<tr>
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<td>Length: 35</td>
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<td>Length: NA</td>
</tr>
<tr>
<td></td>
<td>Threshold: 4°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Holcus lanatus</strong></td>
<td>Start date: NA</td>
<td>Start date: NA</td>
<td>Start date: NA</td>
<td>Start date: 20.02</td>
</tr>
<tr>
<td></td>
<td>Length: NA</td>
<td>Length: NA</td>
<td>Length: NA</td>
<td>Length: 49 days</td>
</tr>
<tr>
<td></td>
<td>Threshold: NA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Anthoxanthum odoratum</strong></td>
<td>Start date: 13.03</td>
<td>Start date: 01.05</td>
<td>Start date: 13.03</td>
<td>Start date: 13.03</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td>Threshold: 4.5°C</td>
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</table>
### Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

<table>
<thead>
<tr>
<th>Plant</th>
<th>Start date</th>
<th>Length</th>
<th>Threshold</th>
<th>Start date</th>
<th>Length</th>
<th>Start date</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
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<td>10.07</td>
<td>21</td>
<td>7°C</td>
<td>26.06</td>
<td>21</td>
<td>20.07</td>
<td>7 days</td>
</tr>
<tr>
<td><strong>Ranunculus ficaria</strong></td>
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<td>7°C</td>
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<td>7 days</td>
<td>20.02</td>
<td>7 days</td>
</tr>
<tr>
<td><strong>Ranunculus acris</strong></td>
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<td>7 days</td>
<td>7°C</td>
<td>05.06</td>
<td>35 days</td>
<td>05.06</td>
<td>7 days</td>
</tr>
<tr>
<td><strong>Cerastium fontanum</strong></td>
<td>27.03</td>
<td>35 days</td>
<td>4°C</td>
<td>03.04</td>
<td>35 days</td>
<td>03.04</td>
<td>7 days</td>
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<tr>
<td><strong>Grasses</strong></td>
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<td>14 days</td>
<td>7°C</td>
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<td>14 days</td>
<td>03.07</td>
<td>14 days</td>
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<td>Start date: 06.02</td>
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<td>Start date: 24.04</td>
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<tr>
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<td>06.02</td>
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<td>24.04</td>
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</tr>
<tr>
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<td>Start date: NA</td>
<td>Start date: 13.03</td>
<td>Start date: 03.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>Length: NA</td>
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<td>Length: 35 days</td>
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</tr>
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</tr>
<tr>
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<td></td>
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<tr>
<td>Dead organic matter</td>
<td>Start date: 24.04</td>
<td>Start date: 24.04</td>
<td>Start date: 30.01</td>
<td>Start date: 30.01</td>
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<td>Length: 7 days</td>
<td>Length: 49 days</td>
<td>Length: 49 days</td>
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<td>Threshold: 4°C</td>
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<td>4°C</td>
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<td></td>
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</tr>
<tr>
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<td>Length: 21 days</td>
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<td></td>
</tr>
<tr>
<td>Start date: 06.02</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>
The linear models

As in March, not all species are affected by sheep density. The timing of their growth is illustrated by the different windows that remain in the models for each species (table 4-17).

Table 4-17 Linear models of weather and sheep density effects on August plant biomass. The initial model for all species contained biomass measured in March and sheep density (whole island count) of the same year, in addition to the critical windows found for each of the weather variables. Only the remaining significant terms in the model are shown. Where a ‘-’ appears after the explanatory variable, this means a negative correlation. Where a ‘+’ sign appears, this means it is a positive correlation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Minimum adequate model</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Festuca rubra</em></td>
<td>Sheep density (-) + first window avg. temp (+) + second window avg. temp (-) + first window wind (+) + second window wind (-)</td>
<td>0.88</td>
</tr>
<tr>
<td><em>Poa spp.</em></td>
<td>March Poa (+) + day degree (+) + rain (+) + wind (-)</td>
<td>0.73</td>
</tr>
<tr>
<td><em>Agrostis spp.</em></td>
<td>Sheep density (-) + day degree (+) + Average Temperature (-)</td>
<td>0.56</td>
</tr>
<tr>
<td><em>Holcus lanatus</em></td>
<td>Sheep density (-) + Average temperature (+)</td>
<td>0.31</td>
</tr>
<tr>
<td><em>Anthoxanthum odoratum</em></td>
<td>Sheep density (-) + first and second window day degrees (-) + first window average temp (+) + wind (-)</td>
<td>0.80</td>
</tr>
<tr>
<td><em>Trifolium repens</em></td>
<td>March <em>T. repens</em> (+) + wind (+)</td>
<td>0.60</td>
</tr>
<tr>
<td><em>Ranunculus ficaria</em></td>
<td>First day degree window (+) + Average Temp (-) + wind (+)</td>
<td>0.78</td>
</tr>
<tr>
<td><em>Ranunculus spp</em></td>
<td>Sheep density (-) + second window rain</td>
<td>0.51</td>
</tr>
</tbody>
</table>
As expected March and August biomass are not good predictors for sheep numbers in August (figures 4-15 and 4-16). But they are good responders

<table>
<thead>
<tr>
<th>Plant Type</th>
<th>Predictor</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cerastium fontanum</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Grasses</td>
<td>Sheep density (-) + first window growing day degrees (+)</td>
<td>0.85</td>
</tr>
<tr>
<td>Herbs</td>
<td>Average temperature (-) + rain (-)</td>
<td>0.53</td>
</tr>
<tr>
<td>Bryophytes</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Dead organic matter</td>
<td>March dead organic matter (+) + first window Average temp (-) + first wind window (-)</td>
<td>0.77</td>
</tr>
</tbody>
</table>

**Figure 4-18 March grass biomass and sheep numbers.**
Chapter 4 Modelling the role of climatic variation on plant productivity, herbivore performance and population dynamics of Soay sheep in St. Kilda

4.6. Discussion

Understanding complex temporal dynamics in natural populations is difficult to achieve when trying to show an intuitive picture of change. Knowing which factors contribute the most to variation in the dynamics of a population is therefore critical, in order to forecast change in population abundance in a changing world.

The impact of climatic variation on ecological processes has been the focus of discussion in ecology for almost a century (Elton 1924). After a period when it was believed that complex dynamics were determined primarily by density dependent intrinsic processes (Nicholson 1933), many works have since shown that climatic variation can have an important role either directly or through its interaction with density (Grenfell et al. 1998, Turchin 2003).

The results of this chapter come from a long-term data set on the fluctuating Soay sheep population (figure 3.1) in St. Kilda, and its vegetation. Previous analyses of these data tested the role of changes in sheep survival and reproduction in relation to broad climatic phenomena such as the NAO (Coulson et al. 2001, Hallet et al. 2004). It is now well recognized that the impact of broad climatic phenomena such as the NAO, the Arctic Oscillation, and the ENSO, as well as global climate change can be extensive and deep rooted (Sæther et al. 2000, Stenseth et al. 2002, Walther et al. 2002, Hallett et al. 2004, Ozgul et al. 2010, Yu et al. 2010). Although winter NAO

Figure 4-19 August grass biomass and for sheep numbers.
features so often in models of sheep population dynamics on St Kilda (e.g. Coulson et al. 2001, Hallet et al. 2004), I show in chapter 2 that the winter NAO has no significant relationship with local weather in St Kilda. Furthermore, it doesn’t appear to have any relationship with the population time series (figure 3.2). Weather aggregations for windiness and rain (figures 3.3 and 3.4 are not consistently related with the NAO index. It became clear that the use of such crude indices would not give an accurate portrait of the underlying climatic influence on demographic processes.

**Winter and all year weather effects on delta**

In the food limited population of Soay sheep (*Ovis aries*) considered in this chapter, there are two mechanisms by which weather influences mortality rates: by generating energetic costs on animals in poor condition, and second by moderating vegetation productivity and variable grazing for sheep during winter (e.g. Clutton-Brock et al. 1997, Grenfell I 1998, Illius & Gordon 2002, Owen-Smith 2010).

There was a need to develop a more complex and circumspect crash-predictor other than NAO: high population density is obviously a prerequisite, as is an elderly-biased age structure and low grass productivity (Coulson et al. 2001; Clutton-Brock & Pemberton 2004). As local weather should be a more powerful determinant of the timing of sheep death as long as the mechanism by which it affects ecological processes can be captured in the variables. There have been five population crashes so far (table 4-2). The initial approach was to look at winter weather. At first glance, it appeared that at high-density, populations apparently crash in years with wet Februaries, but not in average or dry Februaries (figure 4-2). Having hypothesised that rainy Februaries should be consistent in all of the crashes, as wet conditions would have an impact in thermoregulation and foraging for food. Figure 4.2 shows the decline in 1966-67 during the initial study period conforming to the wet February hypothesis. For the population decline of 1985-86, February 1986 was the driest ever, with only 16mm of rain measured for the entire month. I confirmed these values by looking at February precipitation in Stornoway and Benbecula for the same time period; the weather stations confirm this result. Armed with this new insight, when looking at recent Februaries when the population was high but did not crash (e.g. 2007 and 2008). It turns out that these two years would clearly have been classed as extremely wet Februaries during the early part of the study (with 152 and 158 mm respectively), and therefore should have crashed if high February rain really was the proximate cause of these extreme population declines. Table 4-2 shows that there is
clearly no single climatic cause for all crashes, but, of course, high population density is a pre-requisite along with a biased age and sex structures (Portier et al. 1998, Coulson et al. 2000, 2001).

As in the study done by Hallet and colleagues (2004), higher than average wind speed in winter is associated with crashes, yet none of the other variables Hallet et al. predicted show an absolutely consistent pattern. Energetically challenging conditions can therefore occur at different times and in different forms in each year, and their effects may be expressed immediately or with a delay (Hallet et al. 2004).

More important is the analysis of the whole time series, rather than just concentrating on crashes. In figure 4-3a, I show the relationship between the delta residuals and February minimum temperature, which was one of the variables consistently to appear in the minimum adequate model (figure 4-3). This means that warmer Februaries are associated with higher rates of population increase and lower rates of population decline. The remaining three panels of figure 4-3 illustrate the differences in the form of density dependence across the three models.

Warmer Decembers are consistently associated with lower values of delta, as are wetter Januaries (and, in one case out of three, wetter Februaries). The only weather variable positively correlated with Delta was February temperature (see figure 4-3a for minimum temperature, maximum temperature not shown). It is important to note that winter NAO (winter North Atlantic Oscillation) did not survive model simplification in any of these cases.

In the Soay sheep system there are various factors that might influence mortality: the timing of a spell of bad weather, as well as previous weather in the winter. If a storm in one week killed all animals that were in poor condition an even stronger storm the following week would have little or no impact on mortality. Consequently any local measure of climate should not only incorporate multiple weather types (temperature, precipitation, wind speed) over a long period, but should also incorporate the effects of any harsh weather earlier in the season in either removing weak animals from the population or in weakening animals in better condition.

**Decomposing population growth in to measure of recruitment and survival**

Previous research on this population has shown that survival and recruitment in different age and sex classes are actually influenced by different climatic drivers (Catchpole et al. 2000, Coulson et al. 2001). So it makes sense to look at the different
demographic processes separately. The hypothesis being, that different drivers will appear causal, depending on the process. Hopefully this highlights that it is typically not only one component of the weather that is important determinant of the ecological processes but rather a combination of the different variables at different time periods that is relevant to animal performance. It is this mechanistic approach to understanding the variation in demographic rates and how these are influenced by climate that drives this approach.

**Birth weight and August weight**

The effect of density dependence and climate operate through body mass in several mammalian taxa (reviewed in Saether 1997, Gaillard *et al.* 2002, Lummaa & Clutton-Brock 2002). Body mass is thus an important state variable for large terrestrial mammalian herbivores (e.g. Bardsen *et al.* 2010). The benefits are generally related to survival and reproduction. Body mass shows temporal variation. This is captured by both annual the variability in birth weight (figure 4-4) as well as by the annual measures of August weight (figures 4-5 to 4-13) showing that temporal variation in both males and females at all age classes. This is not surprising as like many other long-lived ungulates inhabiting northern latitudes, Soay sheep depend on body reserves during winter. Temperate large herbivores accumulate fat during summer and any losses of body mass during the reproductive season can have dramatic results for winter survival (Clutton-Brock *et al.* 1996, Tveraa *et al.* 2003, Pelletier *et al.* 2007).

Given this variability I analysed the birth weights in the context of variability within each year and focusing on the median birth weight across years (tables 4-3 to 4-5). Several critical windows seemed to be influential in the variability of birth weight within year (table 4-5). The results of the linear multiple regression show that sheep density decreased variability (p=0.028) and growing day degrees in May the previous year actually increased variability (p=0.0006) in birth weights on the following year. When we look at the median, again many windows appear to be influential (table 3.3). Multiple regression shows, a negative effect of sheep density (p= 0.0017) and rain (p=0.005) in spring summer prior to the birth on median birth weight. Again, a measure of growing day degrees in the summer prior to birth has a positive effect on birth weight (p=0.012). The period of the climatic conditions, was somewhat surprising as for the most part in the literature, birth body mass seems to be affected by conditions during the later period of pregnancy (Albon *et al.* 1987,
Clutton-Brock *et al.* 1987, 1992, Rose *et al.* 1998, Forchhammer *et al.* 2001). These effects however operate through the same mechanism, maternal condition. Mothers may have been weakened by lack of food and therefore sensitive to any additional demands on their energy budget, such as those imposed by low winter temperatures. Weather may have had a direct adverse effect on their offspring birth weight at high density as new-born lambs may be born lighter because of poor maternal condition during gestation. Maternal nutrition affects birth weight in several ungulate species (Verme 1977, Leader-Williams 1980, Clutton-Brock *et al.* 1987). The several consecutive years of high population may have had a cumulative adverse impact on vegetation and indirectly on maternal condition, increasing the possibility that inclement weather depresses birth weight and increases the variability within year.

Not surprisingly, different weather variables affect sheep of different ages (Coulson *et al.* 2001) These results, whether attributable to density dependence and or density independence, seem to be in accordance with the weeding out of inferior phenotypes at early stages in the same cohort (e.g Forchhammer *et al.* 2001) This is especially clear at age 2 (table 4-7), where sheep’s weight is only affected by density dependence, through most likely availability of food. For the most part mild winter weather seems to increase August weight, most likely through early onset of vegetation growth or reduced heat loss in winter.

**Lamb survival to first birthday**

Long-lived iteroparous species generally show little between year variation in survival for adult animals but juvenile survival is often highly variable (reviewed in Gaillard *et al.* 2000). Weather induced increases in spring forage have been reported previously to increase juvenile survival in several ungulate species (Owen-Smith 1990, Gaillard *et al.* 1997, Portier *et al.* 1998), and this analysis adds to this body of work.

I expected that lamb survival would be negatively affected by population density and that any effects of weather on lamb survival would be most evident at high density. The results exemplify the value of accurate long-term data in understanding the dynamics of ungulate populations and underline the key role played by the weather at different times of year in affecting survival of lambs to first birthday. The strong density-dependence in survival shown by lambs in this population agrees with other studies of ungulates that have generally found that juveniles are more sensitive
to resource availability than adults (Fowler 1987).

Average temperature window in December affecting positively the March grass biomass (also see table 4-9 to 4-11) prior to the lambs birth had a positive effect in their survival, as well as a measure of growing day degrees in the summer of their birth. These appear to be related with an early onset of vegetation growth and an extended growing season throughout the summer. Rain in the summer months and wind in the autumn of the year of birth both have a negative effect on survival, perhaps through increased heat loss.

Surprisingly, however, winter lamb survival was affected by weather during the previous summer and autumn but not by current winter weather. Summer temperature and precipitation presumably affected vegetation quality and quantity, which in turn may affect the amount of reserves accumulated by lambs during summer, and their ability to survive the winter. Poor vegetation growth could negatively affect lamb mass gain directly, by decreasing the quantity or quality of the forage they eat, and, indirectly, by decreasing their mother's ability to produce sufficient milk (Festa-Bianchet 1988b). In analyses of population dynamics, weather is classically considered a density-independent effect (Owen-Smith 1990), but our results show that complex weather-density interactions can affect juvenile survival in Soay sheep. Some weather effects were indeed independent of population density: wet summers always had a negative effect on lamb survival, and windy autumns decreased lamb survival to their first birthday. Therefore, while obviously weather and population density are not causally linked, not all weather variables have strictly density independent effects on population dynamics. This finding underlines the difficulties of predicting juvenile survival in sheep and possibly in other ungulates.

**Females with lambs and females with no lambs**

The proportion of females pregnant (figure 4-12) is positively affected by warm December to January (in the form of GDD). Windy summers (July- August) have a negative effect on calf having (tables 4-12 and 4-13). These results support the idea that ewes increase their reproductive allocation during improved environmental conditions. This result is supported by other studies where females seemed thus to experience a reduced cost in reproduction when the preceding winter was advantageous (e.g. Festa-Bianchet, Gaillard & Jorgenson 1998, Tveraa et al. 2003).

These relationships may also represent an example of the effects of climate operating through variation in food supply. In mammalian herbivores, with long life
spans, individuals favour their own survival over reproduction. The balance between reproduction and survival should depend on environmental conditions affecting the two traits (e.g. Saether 1997, Gaillard & Yoccoz 2003). This trade off is especially important in northern temperate environments where reproduction takes place during the favourable season, whereas survival is constrained in the unfavourable season (Saether 1997). This is not surprising, as reproductive allocation is predicted to reduce the probability of surviving to the next year (Weladji et al. 2008). This reproduction vs. survival trade-off is one of the most studied in ecology (e.g. Reznick 1985, Clutton-Brock 1991, Clutton-Brock et al. 1996, Tavechia et al. 2005).

**Plant productivity**

Previous studies regarding the patterns or consequences of altered phenology have tended to focus on either a few selected species or on satellite imaging that aggregates the entire communities (e.g. Schwartz 2006). However the monitoring of all plant species within a community is a necessary step to continue to improve our understanding of species interactions and how systems as a whole may respond to climate change.

In any study of herbivore performance the key parameters are likely to be annual productivity of the sward, the timing of the onset growth in spring and the quality of the plant production (Crawley 1983); in particular, the net rate of biomass production by the plant communities. The simplest measure of vegetation that combines elements of both quantity and quality of food is the total biomass of green leaf for all the palatable grass species. Table 4-12 and 4-13 show March and August biomass of different plant species, and the critical windows that provide a snapshot of onset of the growing season for the different species considered. For a given species, windows referring to different times of the year overwintering and peak reproductive growth for the March biomass collection and August which is the time of peak biomass for most species. The different threshold for growing days degrees indicate the investment plants other than on growth, such as physiological needs like frost protection in the winter. Winter conditions are known to influence spring and summer plant phenology (e.g. Inouye & McGuire 1991, Walsh et al. 1997) by blooming earlier and for a long period of time (Post & Stenseth 1999). During the winter months, temperature needs to be higher for the plant to invest in growth. Plants that evolved in winter-cold climates fall dormant in the autumn to avoid frost
damage in winter and will only resume growth in spring after their chilling requirements have been fulfilled (Yu et al. 2010).

The windows for the different species overlap at points and grasses in aggregate have wider windows than of the individual species (Table 4-13 to 4-17). Dead organic matter is plant material that died before being eaten. Therefore, here we are looking at weather effects on senescence, so warm weather in June to September increases the rate of senescence, but also the rate of disappearance through decomposition.

The results of the multiple regression for each of the species yield different results (tables 3.12 and 3.14). Sheep density for the most species had a negative effect on biomass in March, except for the bryophytes, which sheep avoid. This wasn’t surprising as productivity of the sward is intrinsically bound by grazing intensity (McNaughton 1993). Ranunculus spp also seem not to be affected by sheep density. Perennials Ranunculus ficaria and Cerastium fontanum, however seem to be particularly sensitive to rain and wind the previous autumn and rain in previous winter respectively (table 3.12). The grasses Agrostis spp, Poa spp and Anthoxanthum odoratum are also affected by previous autumn and winter conditions.

August biomass is dependent on sheep density but in some species on March biomass, as well. The weather affecting them seems to still be the weather suffered in the winter and spring months, perhaps indicating some memory in the system. Weather and density explain most of productivity, the residual might be explain by interspecific competition and or niche differences.

Although grasses and dead organic matter biomass (tables 4-9 to 4-11) have an effect of juvenile survival. It doesn’t seem that biomass can predict population growth in sheep (figures 4-15 and 4-16).

Conclusions

Stenseth et al. (2002, 2004) posit that the interaction between climatic variables and density-dependent factors may be a widespread phenomenon. This chapter add to the findings of other studies (Grenfell et al. 1998, Coulson et al. 2001, Previtali et al. 2009) that support this contention.

Despite the difficulties of interpreting results that include interactive effects, the above findings are fairly intuitive. The strength of density-dependent processes is a function of the distribution of weather events. Furthermore, the complex interaction between climate and survival is mediated through food availability.
I conclude by restating that both density dependence and density-independent climatic variables are important determinants of population fluctuations; it is their synergistic effects that will shape the Soay sheep population overtime.

Future work

It would be interesting to further explore the relationship between birth weight and August weight. Also I would like to investigate weather effects on perinatal death. It would be very interesting to investigate further the possible critical periods for conception. Also, to investigate if body weight is positively correlated with summer May-July rainfall since it may increase the feeding on the most preferred nutritious swards. Is the rate of weight loss greater in years when biomass is low?

Improved winter or spring conditions may lead to increased foetal growth rates and previous studies have suggested parturition dates are partly under offspring control and may be triggered upon attaining a target size (Asher 2007). So in addition to what I have looked at, it will be interesting to explore a wider critical window to include overwinter and spring prior to birth weather periods. It would have been interesting to analyse the weather effects at the sheep individual level, rather than population means. It would have been interesting to explore variations in individual quality, since high quality individuals may better cope with the costs of reproduction. With all the critical periods for productivity established it would be interesting to investigate the plant productivity dynamics in the context of different climate change scenarios.
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

Abstract

Identifying the critical time window during which climatic drivers affect the expression of phenological, behavioural, and demographic traits is crucial for predicting the impact of climate change on trait and population dynamics. Using long-term data sets for both red deer (*Cervus elaphus*) and vegetation in Rum, I illustrate that the climatic window identified by the sliding window method explains most of the phenological variation in deer traits and vegetation productivity. The results suggest that most of the weather effects on male and female phenology traits and condition are strongly felt indirectly through variation in plant growth conditions in different seasons, reflecting differences in the period in which physiological constraints limit the onset of the breeding cycle between the sexes. My findings suggest that the deer condition in the summer prior and autumn of conception have significant effects on parturition date.

Deer density and midsummer (mid August to mid September) have a negative effect on calf survival through first birthday. So it is the condition they are in as they enter winter that defines their probability of survival.

What is most interesting is that the critical periods affecting plant growth are not necessarily immediately before the event, but an integration of weather in the months before. For example, in November, productivity is affected by how warm the previous winter was and on how much rain fell in May July. Unsurprisingly, warm weather has a negative effect on productivity in the summer months. This idea of an optimum could potential have implications with future climate change scenarios.

My results indicate that changes in the timing of precipitation and warming are important drivers in the grassland community in Rum for both plants and red deer. This evidence suggests that climate variation play an important role in the population dynamics of red deer in Rum through food availability and their condition entering winter, but red deer are not affecting plant productivity in the island.
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5.1. Introduction


The onset of the rapid growth phase in plants determined by weather is a common phenomenon in large parts of the globe. This typically involves a pulse of plant growth during the favourable season, and an extended unfavourable season with little or no plant growth, which maybe due to temperature variations or water limitations. The large annual variation in plant growth imposes constraints on herbivores, as life history tactics must be adjusted to fit the seasonal pattern of the system. Seasonal and, unpredictable between-year, variation imposes responses on population dynamics of large herbivores. Large herbivores adapt to seasonality in a variety of ways: breeding is timed so that calving is concentrated in the optimal period for offspring survival (Loudon & Brinklow 1992) and growth is restricted to the period of summer food abundance.

For herbivores, food resources change in amount both intrinsically through vegetation growth and decay, and as a result of consumption. Such changes in food abundance influence the rate of food intake obtained by each individual herbivore (Owen-Smith 2002, 2010). In seasonal environments the production of edible plant material does not take place continuously. Plants regenerate much of their aboveground biomass at the start of a growing season, partly by reallocation from belowground reserves (Crawley 1983). Later, when conditions become adverse, they cease to grow, and progressively shed the senescent parts. Vegetation growth is not only phased seasonally, but also fluctuates in response to variability in weather during seasonal periods. Plants are a renewing resource for only a portion of the year, and a depleting resource for the remainder (Crawley 1997). Hence, no balanced equilibrium between production and consumption is achieved, except perhaps transiently (Crawley et al. 2004).
If shoot growth exceeds the rate of consumption, vegetation biomass accumulates toward the limit set by species composition, underlying water and nutrient resources during the course of the favourable season. During the unfavourable season, plants become a non-renewing resource for herbivores so that animals must subsist on a diminishing capital of vegetation biomass and standing dead tissues (Bailey et al. 1996, Hodgson & Illius 1996). To the extent that herbivore numbers are regulated by winter food availability, the capacity of vegetation to support herbivores depends on the amount of standing vegetation remaining at the end of the growing season. The initial growth rate and magnitude of the reserves translocate from belowground at the start of the growing season influence the peak standing crop for a given herbivore density (Rosenthal & Kotanen 1994). In a seasonal environment, resource depression may be negligible during the growing season when vegetation resources are renewing, but intensifies over the course of the unfavourable season when the resource depletion is progressive, reaching a minimum in February or March.

For large herbivores, biomass gains are related directly to the prevailing food availability but depend also on prior herbivore densities interacting with the resource production over longer periods (Crawley 1997, Olff & Ritchie 1998). For large herbivores, intraspecific competition arises primarily through resource depletion (scramble competition rather than interference). Density dependence in the biomass growth potential emerges from the interaction between resource supplies and consumption over the seasonal cycle, as a whole.

Future climates are predicted to involve greater precipitation variability and more frequent heat waves leading to droughts (IPCC 2007), but the degree to which the timing of climate variability impacts ecosystems is uncertain. An increase in climate extremes would have unambiguously negative effects (e.g. IPCC 2007, Parmesan 2006). However, most climate variability would not be considered extreme and occurs on much shorter time scales throughout the growing season, with temperature and precipitation frequently uncoupled. The response of ecosystems to short term climate variability at different times of the year is thought to vary (e.g. Thackeray et al. 2010), but we know little about the way that timing of short duration climate variability impacts on herbivore population dynamics or plant productivity.
The timing of phenological events influences a wide range of ecological processes, including species demography and dynamics (e.g. Del Grosso et al. 2008; Miller-Rushing et al. 2010), as well as species interactions (e.g. Hegland et al. 2009). Phenological events such as bud leaf burst and flowering, insect emergence and bird migration, are strongly influenced by climate (Root et al. 2005; Parmesan 2006; Rosenzweig et al. 2008). Phenology of both plants and animals has been altered by climate warming over the past 50 years and will be an important mechanism behind ecosystem responses to global change in the future (Morrisette et al. 2009). Phenology of plants and animals is controlled by many cues and mechanisms, making it unlikely that species, communities and ecosystems will respond uniformly to climate change or avoid the effects of altered phenology of some species. Winter chilling, photoperiod and temperature are considered to be the most important cues controlling plant phenology, but exact mechanisms and cues vary with species (Lechowicz 1984, Chuine & Courr 1999, van de Meer et al. 2002, Durant et al. 2007, Korner & Balser 2010). Climate change may alter the timing and reliability of these cues in the future and disrupt the temporal relationship of current phenology events (Reed et al. 2010).

This climate forcing, along with the availability of long-term datasets, has led to the recognition that phenological change is one of the early indicators that species are responding to climate change (Zhou et al. 1995, Sparks and Yates 1997, Menzel & Fabian 1999, Moyes et al. 2011, Thackeray et al. 2010). Recent reviews have shown that spring as whole is arriving earlier, and the onset of autumn is generally occurring later, with spring events changing at an average of 2.3 days per decade and more than 2.5 days per degree Celsius for many species (Menzel et al. 2006a). Although most studies have shown an overwhelming importance of temperature in shaping phenology, additional environmental variables such as precipitation and wind speed may be important for some communities (Crimmins et al. 2008, 2010, Diez et al. 2012).

Determining the critical periods affecting the population dynamics is a first step in predicting the consequences of climate on population dynamics (Hallet et al. 2004, Saether et al. 2004b). It could help gaining a better understanding the relative influences of recruitment and adult survival (Saether 1997, Gaillard et al. 1998, 2000) of the extent to which population dynamics are
affected by environmental conditions during the breeding season and non-breeding seasons. In general, ungulate biomass is greater in sites with greater precipitation (Fritz & Duncan 1994), suggesting that if changes in the timing or magnitude of precipitation increase plant production, herbivore performance should also increase. Yet herbivore growth is limited also by plant nutritional quality (Van Soest 1994, Cote & Festa-Bianchet 2001). If changes in the magnitude and timing of precipitation or temperature alter plant quality (e.g. through changes in plant species composition of the biomass), these effects could override the consequences of climatic variability on the total quantity of food available to the herbivores.

Quantification of the costs of reproduction is also fundamental to our understanding of the evolution of reproductive tactics. The cost-benefit approach introduced by Williams (1966) identified costs in many taxa (e.g. Weladji et al. 2008).

Variability in phenological responses to climate has important implications for species’ abilities to adapt to novel environmental conditions and patterns of interaction within communities (Parmesan 2007). In many taxa the majority of births occur within a short time window that coincides with periods of maximum food availability (e.g. Visser et al. 1998, Clements et al. 2011).

Birth weight is a major factor influencing lifetime fitness (Clutton-Brock et al. 1996, Kruuk et al. 1999) and the consequences of weather conditions during pregnancy may have long-term effects on the dynamics of populations (Albon et al. 1992). Long-lived iteroparous species, like the red deer on the Isle of Rum, generally show little between-year variation in survival for adult animals, whereas juvenile survival is highly variable (reviewed in Gaillard et al 2000). The underlying causal mechanisms are likely to differ, but the effect of density-dependence and climate operate primarily through body mass in several mammalian taxa (reviewed in Saether 1997, Gaillard et al. 2000, Lummaa & Clutton-Brock 2002). Body mass, at birth is therefore an important state variable for large terrestrial mammalian herbivores, (e.g. Bardsen et al. 2010). Temperate large herbivores accumulate fat during summer, and any losses of body mass during the reproductive season can have dramatic consequences for winter survival (e.g. Clutton-Brock et al. 1996, Tveraa et al. 2003, Pelletier et al. 2007). In these seasonal environments, both density dependence and
climatic processes affect individuals differently through the seasons, where late winter conditions may have profound effects on survival and reproduction (e.g. Patterson & Messier 2000, DeGiudice et al. 2002, Tveraa et al. 2003). Interestingly, interactions between population density and late winter environmental conditions indicate that harsh winters affect individuals more at high than at low population densities (e.g. Portier et al. 1998, Coulson et al. 2000, Coulson et al. 2001). Both density-dependence and climatic conditions, especially during the later period of gestation, have negative effects at the individual level as they affect birth date, birth body mass, juvenile survival and future reproductive success (Albon, Clutton-Brock & Guinness 1987, Clutton-Brock et al. 1987, 1992, Rose, Clutton-Brock & Guinness 1998, Forchhammer et al. 2001).

The weather in Rum is variable and this has important consequences on the growth, survival, recruitment and reproduction of deer (Albon & Clutton-Brock 1988, Clutton-Brock & Albon 1989, Albon et al. 1992). The lives of red deer are dictated by the seasons. To better understand how the timing of climate variability affects red deer performance and grassland productivity in Rum, I applied a combination of the critical climate window approach and growing degree day (GDD) models (e.g. Roy & Sparks 2000, van de Pol & Cockburn 2011) to long-term longitudinal data on red deer and monthly measurements of grass biomass on the Isle of Rum, Scotland. The main motivation was to explore the multiple pathways by which environmental variation can impact herbivore ecology, and identify the environmental drivers shaping different red deer demographic processes and vegetation productivity. In practice, there has been little effort to develop methods to evaluate the influence of weather using finer scale temporal intervals. Yet, these methods would highlight the periods when the relationship between the demographic processes and weather are strongest. Understanding how changes in the timing of climate forcing will affect herbivores relies not only on understanding the quantity of food available to them, but also the quality of the available forage on offer. More specifically, do they operate directly on the animal by imposing energetic stresses, or indirectly by influencing food supply? I shall demonstrate the usefulness of these methods, by providing an estimate of the contribution of each environmental variable to the temporal variation in traits related to survival and recruitment in the red deer population in
Rum. What time of the year is likely to be most important climatically? How will such complexities, if they are important, impact in our ability to make generalisations about the role of climate across species, or even across population of the same species in different places?

5.2. Methods

5.2.1. Red deer demographics and phenological traits

The wild population of red deer in the North Block of the Isle of Rum, Scotland, has been under intensive study since the early 1970s. Culling of the population in the 12 km² North Block study area ceased in 1972. Individual deer are recognized as a result of artificial markings and natural variation, and are closely monitored throughout their lifetimes (Clutton-Brock et al. 1982).

Population density

The deer year runs from June through the following May. Three censuses are carried out every year: June-August, September-December and January-May.

The criteria for establishing residency in the study area follow stringent rules: the minimum number of sightings to be included in the annual total needs to be 50; the minimum proportion of censuses in which a deer is seen must be 0.1. All three censuses can be used in the calculations.

During the calving season, pregnant hinds are closely watched for behaviour indicating possible parturition, in order to obtain accurate times of birth. Newborn calves are captured and weighed, measured, blood sampled and uniquely marked (see Clutton-Brock et al. 1982 for further details).

During the autumn rut, daily censuses of the entire study area are carried out. The identity and location of all males holding a harem are noted, as are the identities of all females within each male's harem. Females are watched intently for signs of oestrus such as being mounted and intense attention from males (Guinness et al. 1971). Most mortality in the study population occurs during winter, and regular censuses and searches of the study area at this time allow us to locate the majority of carcasses and keep track of over-winter mortality (Clutton-Brock et al. 1982). The first decade of the long-term study of deer in the
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

North Block of Rum was characterized by a pronounced increase in female population size, following the cessation of culling in 1972 (Clutton-Brock et al. 1982, 2002, Coulson et al. 2004). Over the first 10–15 years of the study period, the number of resident adult females in the study increased while the number of males declined (Coulson et al. 2004). Early in the 1980s, the population is thought to have reached carrying capacity, there is a protracted increase in 1993-1998, and the number of resident adult females using the study area has fluctuated around 200 individuals ever since (Coulson et al. 2004). The apparent density-dependence of phenological traits across the entire study period seems more likely to be driven by the pronounced changes in population size over the first decade of the study, rather than by subsequent fluctuations around carrying capacity. To avoid potentially confounding effects of the increase in density across the first decade of the study on breeding phenology, I have restricted my analyses to the period during which the population has been at or around carrying capacity. I therefore used phenological and life history data collected on Rum between 1980 and 2009. For the purposes of the analysis in this chapter, I do not include calves in the population estimate. Estimates including females only and estimates including both sexes were calculated.

**Average birth date phenology**

I examine trends in birth date across the years from 1980 to 2007. I investigated birth date correlation with mothers’ age and with weather in the autumn preceding birth. Birth date phenology was expressed in Julian days since the 1st of January. The vast majority of parturition dates were known with certainty as a result of close monitoring of maternal behaviour during the calving season and any uncertain dates were excluded. The data for parturition contained a very small number of extremely early or late events, which skewed the distributions of these traits. To ensure assumptions of normality were met, I excluded these extreme outliers from the analyses, removing parturition dates outside of the range 1st May – 31st July (one observation before May and 32 observations after July: <2% of data).

**Mean birth weight trends**

I examined trends in mean birth weight across the years from 1980 to 2008. Because young calves gain weigh rapidly after birth, the estimated birth weight
had to be calculated as by regressing the weigh of the calves against days after parturition. Analysis was carried out separately for the two sexes.

**Female reproduction allocation (proportion of females breeding)**

Density-dependence in the probability of a female becoming pregnant may be difficult to detect if the probability is also affected by density-independent factors. I investigated the relationships among weather parameters, population density, and number of females with calves. In red deer, only the mature females (aged 3 or more) may be pregnant, with a single calf. Females with a calf may be less likely to conceive in a given year. Analysis was carried out for the period of 1980 till 2010.

**Offspring survival through first year (to 1st of May of the following year)**

Density-dependence in juvenile survival may be difficult to detect if survival is also affected by density-independent factors. Most natural deaths occur in late winter (February to April). Calves are the most likely to succumb to the lack of food and harsh weather as are males which fail to recover condition from the rut, particularly in wet and windy colder years. As spring approaches, weather conditions improve and the grass begins to grow again. Many deer calves will die in their first or second winter of life: only 45% of male calves and 50% of female calves make it to their second birthday. Analysis was carried out for calves born in the period of 1980 till 2008.

### 5.2.2. The vegetation community

The Isle of Rum is a 10 684-ha nature reserve situated in the Inner Hebrides off the northwest coast of Scotland (57°0'N, 6°20'W). Rum has an oceanic climate with mild, wet and windy weather for much of the year. It is a mountainous island, with the highest peak, Askival, rising over 800 m. The productive grasslands characterize valleys near seashores; heaths and bogs prevail on elevated terrain (Ball 1987). The distribution of main vegetation types has been mapped by Ferreira (1970). Clutton-Brock, Guinness & Albon (1982) and Clutton-Brock & Ball (1987) give a description of the fauna on Rum, and the flora is detailed by Pearman et al. (2008)
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

Sampling and sorting
In order to estimate primary productivity of vegetation and grazing offtake by the red deer, short-term grazing exclosures were set up. 60x60x20 cm steel exclosures were placed at 7 sites throughout the North Block.

Nine sites are situated on “greens” around the coast from Kilmory to Shamhnan Insir. Vegetation samples are picked every month from March until November inclusive. For the purpose of the analysis in this chapter, I restrict the analysis to aggregations of live and dead biomass inside and outside the exclosures. Vegetation samples were subsampled and approximately 20% of each was sorted into live and dead grasses and forbs and bryophytes. All vegetation was over dried at 40°C for 24 hours and weighed.

Plant productivity
Productivity is a function of leaf area. Climate variable associated with the history of leaf area development, temperature, day length and resource supply. If there were no deer in the island productivity inside the exclosures should be the same as outside the exclosures (I=O). For the purpose of the analysis, the sites are averaged out so I look at a single measure of productivity per month. For more details for the vegetation collection methodology see Iason, Duck & Clutton-Brock (1986).

This analysis was performed on the data from 1990 onwards, for each month separately and then for the two seasons April-June and July-September.

Vegetation Trends
This analysis was performed on the data from 1990 onwards.

a) Live biomass inside the exclosures
This represents the grass sward ungrazed for the previous 30 days. I used linear regression to assess whether there were trends in monthly productivity across the years.

b) Live biomass outside the exclosures
This represents the standing crop of the grazed sward. The motivation for also estimating outside productivity is to control for history. I tested for serial autocorrelation between months within each year, hypothesizing a 12 month lag
in maximum acf. I then used linear regression to assess whether there were trends in productivity.

c) Offtake

Offtake is a measure of consumed plant productivity that is closely related to deer numbers. I calculated the difference between live biomass inside and outside the exclosures for every month and every year. I then averaged each offtake measure for all plots so as to have one value per month. Offtake per capita should be the most likely determinant of deer performance.

**Actual evapotranspiration**

Rosenzweig’s rule (1968) predicts a close linear relationship between log primary productivity and log actual evapotranspiration. Evapotranspiration is a function of weather data, mostly, with some assumptions made about the crop. There is some uncertainty due to variations in plant density, leaf area and water availability. We may need to fill in gaps in time series where the parameters for the Penman equation are not available, or for areas not covered by remote sensing.

This method only requires daily measurements of maximum and minimum temperature (°C) and wind speed (m/s) to estimate the parameters in the Penman equation to calculate evapotranspiration. The Penman equation is:

\[
ET_{sz} = \frac{0.408 \Delta (R_n - G) + \gamma \frac{C_n}{T + 273.15} u_z (e_s - e_a)}{\Delta + \gamma (1 + C_d u_z)}
\]

where:

- \( ET_{sz} \) = standardized reference crop evapotranspiration for short crop (mm/day),
- \( R_n \) = calculated net radiation at the crop surface (MJ/m²/day for daily time steps),
- \( G \) = soil heat flux density at the soil surface (MJ/m²/day),
- \( T \) = mean daily or hourly air temperature at 1.5 height (°C),
$u_2$ = mean daily or hourly wind speed at 2-m height (m s$^{-1}$),

$e_s$ = saturation vapor pressure at 1.5 m height (kPa), calculated for daily time steps as the average of saturation vapour pressure at maximum and minimum air temperature,

$e_a$ = mean actual vapor pressure at 1.5 m height (kPa),

$\Delta$ = slope of the saturation vapour pressure-temperature curve (kPa/$\degree$C),

$\gamma$ = psychrometric constant (kPa/$\degree$C),

$C_N$ = numerator constant that changes with reference type (K mm s$^3$/ Mg/ day)

$C_d$ = denominator constant that changes with reference type

Units for the 0.408 coefficient are m$^2$ mm/ MJ.

Soil and plant parameters were taken from general tables provided in FAO-56 (Allen et al. 2005), specifically for Rum’s geographic location and with the following approximations:

The albedo, $\alpha \approx 0.23$;

The mean actual vapour pressure, $e_a \approx 0.6108 \exp \left( \frac{17.27 T_{\text{min}} + 237.3}{T_{\text{min}} + 273.15} \right)$ kPa;

Soil heat flux density $G \approx 0$ MJ/m$^2$/day;

The numerator constant $C_N \approx 37$ Kmm s$^3$/Mg/day, since we assume short reference vegetation height crop 0.12m.

The denominator constant $C_d \approx \begin{cases} 0.24 \text{ Kmm s}^3/\text{Mg/day}, & R_n > 0 \\ 0.96 \text{ Kmm s}^3/\text{Mg/day}, & R_n \leq 0 \end{cases}$
The incoming solar radiation $R_S \approx k_{RS} \sqrt{(T_{max} - T_{min})} R_a \, \text{MJ/m}^2/\text{day}$, where $R_a$ is the extra-terrestrial ET radiation.

The calculated evapotranspiration follows the expected annual cycle. The procedure was tested in chapter 3 where the data are available for the use of the full Penman equation. For the details of the calculation see Appendix A.

![Evapotranspiration](image)

**Figure 5-1** Evapotranspiration calculated using only wind and temperature time series. Six years are shown here for illustration only.

### 5.2.3. Rum weather time series

In this chapter, I use the reconstructed weather time series (see chapter 2 for details) that includes daily minimum and maximum temperature ($^\circ$C), total precipitation (mm) and average wind speed (ms$^{-1}$) from 1965 till 2009. The 4 explanatory variables show differing degrees of correlation with each other (table 5-1). There is no significant change in precipitation regimes Rum over the 47 years; however, the island is becoming warmer and less windy, with an increase in temperature by at least 1.5$^\circ$C and a decrease in wind speed by at least 1.88 ms$^{-1}$ over that same period.
Table 5-1 Cross-correlation of the local weather variables on Rum (1965-2009).

<table>
<thead>
<tr>
<th>Weather variables</th>
<th>Min. Temp</th>
<th>Max Temp</th>
<th>Precipitation</th>
<th>Wind speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Min. Temp</td>
<td>1.00</td>
<td>0.80</td>
<td>0.10</td>
<td>-0.12</td>
</tr>
<tr>
<td>Max. Temp</td>
<td></td>
<td>1.00</td>
<td>-0.06</td>
<td>-0.33</td>
</tr>
<tr>
<td>Precipitation</td>
<td></td>
<td></td>
<td>1.00</td>
<td>0.32</td>
</tr>
<tr>
<td>Wind speed</td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
</tr>
</tbody>
</table>

Weather variables and aggregations
I mostly used the daily values but also aggregates of these values, either as monthly means, windows (explained below) or season-long aggregates.

Growing day degrees
As in chapters 3 and 4, I used measures of growing day degrees (GDD) to provide an estimate of local climatic conditions in relation to vegetation growth, GDD is a proxy for vegetation growth. (Grant et al. 1986, Snyder et al. 1999, Bonhomme, 2000). GDD is estimated as the cumulative sum of the daily mean temperatures above a threshold over a set period (Barnett et al., 2006), Both, the threshold and the period, are adjusted to optimize the explanatory power of the variable.

Critical Windows
I used linear regression to estimate the each red deer demographics and phenological traits, as well as plant phenology (biomass inside and outside the cages) on the average temperature, total precipitation, and average wind, as well as accumulated growing day degrees over a specified time-window. I compared the predictive power of each variable in different time-windows using a proxy for $r^2$: (null deviance-deviance)/null deviance. In addition to using the best combinations according to $r^2$, windows were further selected according to the following rules: the combination of window start and length could not exceed the 1st of May of the birth year, and also the minimum p value of the considered weather variables (linear or quadratic form) needed to be 0.05. The linear regressions used for the search for the
best windows included deer density as measured in the January-May census of the
deer year, along with linear and quadratic terms for the weather variable in question.

All critical windows that reflect time lags were ran with different rates of decay
(from $\alpha = 0$ to $\alpha = 0.2$) to test for the potential importance of the weather from the
farthest to the closest date prior to the event, thus allowing windows with different
statistical weight. I only show results of the models with no decay ($\alpha = 0$) since there
was no significant different between the different rates. The relative importance
of different dates is captured in the width of the window.

a) **Average birth date windows** - I varied both the starting date of the sliding
window starting in on the 1\textsuperscript{st} of July in seven day intervals up the 15\textsuperscript{th} of November of
the previous year (days given in ordinal dates, i.e. 1 for 1\textsuperscript{st} January and 365 or 366
for 31\textsuperscript{st} December, depending on leap years) and the duration of the window with
lengths varying from 7 to 112 days in 7-day intervals. The rational for this, was to
capture the weather affecting mothers’ condition during oestrus.

b) **Offspring mean birth weight windows** - Same procedure as above, with starting
date on the 1\textsuperscript{st} of September of the previous year up the 1\textsuperscript{st} of May of the year of
birth.

c) **Female reproduction allocation windows** - Same procedure as above, with
windows starting in on the 1\textsuperscript{st} of July of the year before birth up the 1\textsuperscript{st} of May of the
year of birth.

d) **Calf survival windows** - Same procedure as above, with windows starting on
the 1\textsuperscript{st} of March of the year of birth till 1\textsuperscript{st} of May of the following year depicting
approximately the first year of the calves.

e) **Plant productivity windows** - Same procedure as above, to estimate the biomass
in each month for both inside and outside the cages, on the average temperature,
total precipitation, average wind speed, accumulated growing day degrees and
evapotranspiration over a specified time-window. For each month, I varied both the
starting date of the sliding window starting in on the first of January in seven-day
intervals up the 15\textsuperscript{th} of the month in question of the year of collection. The linear
regressions used for the search of the best windows included deer density; when
possible, plant biomass of the previous month, along with linear and quadratic terms
for the weather variable in question. The rationale for this, is that deer population is
also an important driver for biomass on the island, so the weather variables that remain in models explain biomass variation controlled for deer numbers.

5.2.4. Statistical models

I use the following response variables: average birth weight, plant biomass, female reproduction allocation and calf survival.

**Linear models**

Stepwise deletion was performed, where the least significant terms were removed sequentially until all remaining terms were significant at $P < 0.05$ to produce the minimal adequate model (MAM). All MAM’s were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors.

**Generalised linear models (GLM)**

- **a) Female reproduction allocation** - I used generalised linear regression with a quasi-binomial error structure (to correct for overdispersion) to estimate the proportion of females having calves on the average temperature, total precipitation, and average wind, as well as accumulated growing day degrees over a specified time-window. From the stepwise deletion, where the least significant terms were removed sequentially until all remaining terms were significant at $P < 0.05$ to produce the minimal adequate model (MAM). All MAM’s were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors. Models were compared using ANOVA to justify retaining or excluding variables, and Akaike’s information criterion (AIC) used to compare model fit. Where the ANOVA indicated no significant difference between the models ($P > 0.05$) the model with the highest degrees of freedom was retained. Where a significant difference occurred the model with the lowest residual deviance was retained.

- **b) Calf survival** - Same procedure as above.
5.3. Results

5.3.1. Population density

For the purpose of the analysis in this chapter, I will consider the female population density and grazing pressure, as recorded in the January-May census, as proxy for deer density in the Kilmory study area. In some analysis I also use the September-December census of females. Population time series is shown in figure 5-3. There is a sharp decline in 1992, followed by 5 consecutive years of increase after which the population fluctuates around 200.

![Population Time Series](image)

Figure 5-2 Female population density in the Kilmory study-area (Rum) at the time of the January-May census. The asymptotic, food-limited female density increased more than two-fold after shooting stop in 1972.

5.3.2. Calves birth date

Mean birth date has been advancing by approximately one day each two years (p=7.01e-7) over the period 1980-2007 (figure 5-4).
Critical windows

Temperature’s best window, in the form of day degrees was between mid August and Mid September, with a threshold of 4°C. Precipitation’s best window was at a similar period. Wind’s window was longer starting in mid July going up to end of October (table 5-2 and 5-3).

Table 5-2 Critical windows of the weather variables that remained in the MAM for estimating mean birth date. GDD means growing degree-days. These windows are of the year before birth.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Best Window</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>18.08-15.09, threshold: 4°C</td>
</tr>
<tr>
<td>Precipitation</td>
<td>29.08-11.09</td>
</tr>
<tr>
<td>Wind speed</td>
<td>11.07-31.10</td>
</tr>
</tbody>
</table>
The linear model

Table 5-3 Weather critical windows for mean birth date estimation. Only the significant terms are shown ($r^2 = 0.71$, 24 df).

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>-0.081</td>
<td>9.55</td>
<td>16.36</td>
<td>1.62e-14***</td>
</tr>
<tr>
<td>Precipitation</td>
<td>0.016</td>
<td>0.01</td>
<td>2.41</td>
<td>0.024*</td>
</tr>
<tr>
<td>Wind speed</td>
<td>0.036</td>
<td>0.011</td>
<td>3.285</td>
<td>0.00312**</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = ^*$, $P < 0.01 = ^{**}$, $P < 0.001 = ^{***}$. Non-significant effects are not shown. $P$ values for significant effects are taken from the model output of the MAM.

If we assume that gestation period is constant, we can infer that conception date in Rum is occurring earlier.

This particular wind window is the weather variable that remains in the model that is trended. Average wind speed for this critical window has decreased by 0.56 m/s for the period 1980-2007 ($F_{1,26}=6.2$, $p=0.01$).

Figure 5-4 Mean birth date varying with average wind speed (critical window 11.07-31.10 of the year previous to birth year). Average wind speed for this critical window has decreased by 0.56 m/s for the period 1980-2007 ($F_{1,26}=6.2$, $p=0.01$).
**Maternal age effects**

Here I fitted a non-parametric curve and we can see that birthdate is earlier with younger and older mothers (figure 5-5).

![Figure 5-5 Mother’s age effects on parturition date. The line is a non-parametric curve.](image)

This is a good example of the difference between statistically significant and biologically important. These effects are very small. Because the effect is so small, I have not included this or other demographic parameter (other than deer density) in the weather models.

**5.3.3. Offspring mean birth weight**

In both female and males calves, the weight is highly variable between years, with no significant trend across the years. The candidate critical windows for the weather variables differ slightly for the two sexes. Birth weight is not correlated with deer density; nevertheless deer density has a negative effect on male birth weight (figure 5-6 and 5-7).
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

The best weather critical windows for the two sexes are fairly similar. For females, temperature’s best window, in the form of day degrees, was between mid February and March, with a threshold of 7°C. Average temperate best window runs from end of February to end of April. Both windows for precipitation and wind did not stay the MAM. (table 5-4).

**Figure 5-6** Female birth weight varying with female deer density (census Jan-May 1980-2011).

**Figure 5-7** Male birth weight varying with female deer density (census Jan-May 1980-2011).
Table 5-4 Best candidate critical windows that explain female calf birth weight. Windows in bold are those that remain in the MAM. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>16.02-02.03, threshold 7°C</td>
<td>19.01-09.03, threshold 4°C</td>
</tr>
<tr>
<td>Average Temperature</td>
<td>23.02-27.04</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>08.09-06.10</td>
<td>17.11-05.01</td>
</tr>
<tr>
<td>Wind speed</td>
<td>08.09-06.10</td>
<td></td>
</tr>
</tbody>
</table>

For males, temperature’s best window, in the form of day degrees was between mid February and March, with a threshold of 4°C. Windows for average temperate precipitation and wind did not stay the MAM. (table 5-5).

Table 5-5 Best candidate critical windows that explain male birth weight. Windows in bold are those that remain in the MAM. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>09.02-20.04, threshold 4°C</td>
</tr>
<tr>
<td>Average Temperature</td>
<td>09.02-20.04</td>
</tr>
<tr>
<td>Precipitation</td>
<td>29.12-05.01</td>
</tr>
<tr>
<td>Wind speed</td>
<td>08.09-03.11</td>
</tr>
</tbody>
</table>
The linear models

Warm late winters have a positive effect on mean birth weight for both sexes. Deer density seems to be only important for male calf birth weight; it is possible that there is a bigger energetic investment on the part of mothers (tables 5-6 and 5-7).

Table 5-6 Minimum adequate model (MAM) where only the significant terms that explain female birth weight are shown ($r^2 = 0.4$)

<table>
<thead>
<tr>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female birth weight</td>
<td>GDD w.1</td>
<td>0.03</td>
<td>0.01</td>
<td>3.01</td>
</tr>
<tr>
<td></td>
<td>Average Temperature w.1</td>
<td>0.16</td>
<td>0.05</td>
<td>2.8</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***$. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

Table 5-7 Minimum adequate model (MAM) where only the significant terms that explain male birth weight are shown ($r^2 = 0.4$).

<table>
<thead>
<tr>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male birth weight</td>
<td>Deer density</td>
<td>-0.005</td>
<td>0.001</td>
<td>-2.6</td>
</tr>
<tr>
<td></td>
<td>GDD w.1</td>
<td>0.005</td>
<td>0.001</td>
<td>4.5</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***$. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

5.3.4. Female reproduction allocation (proportion of females breeding)

The proportion of females breeding varies widely across the years. There was a slight but non significant negative trend (figure 5-8).

I tested for serial autocorrelations, which could have been caused by age groups having particularly high calf incidence in one year and low in another. Again, this was not significant (max partial acf=0.24, p>0.05). Because it is not trended and there was no serial autocorrelation, I can do a regression of proportion female deer
with calves against female deer density of the year before (September-December census) against proportion of mothers \( (F_{1,29} = 5.6, p < 0.05) \).

![Figure 5-8 Proportion of mothers varying with female deer density, \( (F_{1,29} = 5.6, p < 0.05) \). (September through November census of the year before).](image)

### The Critical Windows

Temperature’s best window, in the form of day degrees was for the month of June, with a threshold of 7°C. Precipitation best window was from mid July to mid September. Windows for average temperature and wind did not stay the MAM. (table 5-8).

**Table 5-8 Best candidate critical windows that explain whether females reproduction allocation. Windows in bold are those that remain in the MAM. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.**

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>06.06-20.06, threshold 7°C</td>
<td>15.08-10.10, threshold 4°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>06.06-20.06</td>
<td>15.08-10.10</td>
</tr>
<tr>
<td>Precipitation</td>
<td>11.07-19.09</td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>19.12-26.12</td>
<td>20.03-01.05</td>
</tr>
</tbody>
</table>
The GLM

Warm Junes increase female allocation, but wet summers have a negative effect (table 5-9).

Table 5-9 GLM with quasibinomial error distribution. Only the significant predictors of females’ reproduction allocation are shown. Residual deviance 50.5, 31 df.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Std. Error</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deer density</td>
<td>-0.006</td>
<td>0.001</td>
<td>-2.8</td>
</tr>
<tr>
<td>GDD w.1</td>
<td>0.006</td>
<td>0.001</td>
<td>3.3</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-0.001</td>
<td>0.0002</td>
<td>-4.7</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = ^*$, $P < 0.01 = ^{**}$, $P < 0.001 = ^{***}$. Non-significant effects are not shown. $P$ values for significant effects are taken from the model output of the MAM.

5.3.5. Offspring survival through 1st year (to the 1st of May following year)

The Critical windows

Precipitation best window was from mid August to mid September. Windows for GDD, average temperature and wind did not stay the MAM. (table 5-10).

Table 5-10 Best candidate critical windows that explain whether calves’ survival through their first year. Windows in bold are those that remain in the MAM. Windows are labeled 1 through 3, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>01.03-29.03 threshold 4°C</td>
<td>30.08-06.09, threshold 4°C</td>
<td>18.10-31.01, threshold 7°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>24.05-21.06</td>
<td>30.08-06.09</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>19.04-10.05</td>
<td>23.08-13.09</td>
<td>20.09-01.22</td>
</tr>
<tr>
<td>Wind speed</td>
<td>26.04-17.05</td>
<td>26.07-09.08</td>
<td>10.01-24.01</td>
</tr>
</tbody>
</table>
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

The GLM

High density and wet Septembers have a negative effect on calf survival (table 5-11).

Table 5-11 GLM with quasibinomial error distribution. Only the significant predictors of calf survival to first year are shown. Residual deviance 187, 31 df.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Std. Error</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calf survival</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deer density</td>
<td>-0.009</td>
<td>0.003</td>
<td>-2.8</td>
</tr>
<tr>
<td>Precipitation w.2</td>
<td>-0.003</td>
<td>0.0008</td>
<td>-3.4</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

5.3.6. Plant biomass

Trends in live plant biomass inside the exclosures

There has been increase in productivity in most months between April and November for the period 1990 to 2009. In all months, we observe a great interannual variability. The months that are trended show a regression line in the figure (figures 5-9 to 5-12).

Figure 5-9 Live plant biomass collected from inside the cages. Left shows April productivity where no trend is observed for the period 1990-2009 (p=0.464, 18 df) Right shows May productivity where the dashed line represents the regression of in Live productive against year (p=0.0416, 18 df).
Figure 5-10 Live plant biomass collected from inside the cages. Left shows June productivity, where the dashed line represents the regression of in Live productive against year \((p=0.0415)\). Right shows July productivity, where no trend is observed for the period 1990-2009 \((p=0.333)\).

Figure 5-11 Live plant biomass collected from inside the cages. Left shows August productivity, where the dashed line represents the regression of in Live productive against year \((p=0.00424)\). Right shows September productivity, where the dashed line represents the regression of in Live productive against year \((p=0.0473)\).
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

Figure 5-12 Live plant biomass collected from inside the cages. Left shows October productivity, where no trend is observed for the period 1990-2009 (p=0.927). Right shows November productivity, where no trend is observed for the period 1990-2009 (p=0.236).

Seasonal Productivity

There is again an observed large interannual variability in total early season growth (figure 5-13). 1994 and 2006 are the years with the lowest productivity. 1997, 2003 and 2007 are the years with the highest productivity (see discussion).

Figure 5-13 Total live plant biomass collected from inside the cages for the early season growth averaged across April-June. The dashed line shows the positive trend in biomass between 1990 and 2009 (p = 0.036).
In the late growing season, we still observe a large interannual variability in productivity (figure 5-14). 1991 is the year with the lowest productivity. 1995, 1997 and 2006 are the years with the highest productivity (see discussion).

![Figure 5-14: Live plant biomass collected from inside the cages for the late growing season averaged across July-September. The dashed line shows the positive trend in biomass between 1990 and 2009 (p= 0.004).](figure)

**Trends in live plant biomass outside the exclosures**

There has been increase in productivity in most months between April and November for the period 1990 to 2009. In all months, we observe a great interannual variability (figures 5-16-5-19).
Figure 5-15 Live plant biomass collected from outside the cages. Left shows April productivity, where no trend is observed for the period 1990-2009 (p=0.821). Right shows May productivity where the dashed line represents the regression of in Live productive against year (p=0.0437).

Figure 5-16 Live plant biomass collected from outside the cages. Left shows June productivity, where the dashed line represents the regression of in Live productive against year (p=0.0183). Right shows July productivity where the dashed line represents the regression of in Live productive against year (p=0.0057).
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

Figure 5-17 Live plant biomass collected from outside the cages. Left shows August productivity, where the dashed line represents the regression of in Live productive against year (p=0.0033). Right shows July productivity where the dashed line represents the regression of in Live productive against year (p=0.0167).

Figure 5-18 Live plant biomass collected from outside the cages. Left shows October productivity, where no trend is observed for the period 1990-2009 (p=0.625). Right shows November productivity, where no trend is observed for the period 1990-2009 (p=0.236).
There is an approximate 4-fold increase in average biomass outside the exclosures from April (the beginning of the growing season) to July. Offtake average biomass ranges from, approximately, 0.5g per 10cm² quadrat in April up to 3.5 g in June-July (figure 5-19).

5.3.7. Vegetation productivity critical windows

For the months from April to November the critical windows for each of the weather variables (Growing day degrees (GDD), average temperature, precipitation, wind speed and evapotranspiration), were fit and the best windows chosen to then enter the linear model to explain monthly productivity. Not surprisingly, for the different months, optimal GDD thresholds vary.

Live biomass inside the cages monthly productivity

Precipitation best window was from February to March for April biomass. Windows for GDD, average temperature and wind did not stay the MAM (table 5-12).
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

Table 5-12 Best candidate critical windows for each of the weather variables to explain April productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 4, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>20.10-10.11</td>
<td>22.12-23.03</td>
<td>Threshold 4 °C</td>
<td>Threshold 6.5 °C</td>
</tr>
<tr>
<td>Average temp</td>
<td>26.01-13.04</td>
<td>16.02-16.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>03.11-01.12</td>
<td>01.12-28.12</td>
<td><strong>02.02-09.03</strong></td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>22.12-30.03</td>
<td>22.12-06.04</td>
<td>05.01-23.03</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>08.09-22.09</td>
<td>08.08-29.09</td>
<td>02.02-29.02</td>
<td>23.02-02.03</td>
</tr>
</tbody>
</table>

For May, temperature’s best window, in the form of day degrees was for end of June to mid April, with a threshold of 5.5°C. Precipitation best window was for the same period. Windows for average temperature and wind did not stay the MAM (table 5-13).

Table 5-13 Best candidate critical windows for each of the weather variables to explain May productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 4, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td><strong>26.03-16.04</strong></td>
<td>09.04-14.04</td>
<td>Threshold 5.5 °C</td>
<td>4 °C</td>
</tr>
<tr>
<td>Average temp</td>
<td>22.01-14.05</td>
<td>05.02-14.05</td>
<td>26.03-16.04</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>26.03-30.04</td>
<td><strong>19.03-23.04</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>26.03-23.04</td>
<td>19.03-23.04</td>
<td>02.04-16.04</td>
<td>26.03-07.05</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>15.01-05.02</td>
<td>05.02-23.04</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
For June, none of the best windows remained in the MAM (table 5-14).

Table 5-14 Best candidate critical windows for each of the weather variables to explain June productivity (live biomass inside the cages). GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>GDD</em></td>
<td>09.04-23.04 Threshold 4 °C</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Precipitation</em></td>
<td>19.02-26.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Evapotranspiration</em></td>
<td>12.03-02.04</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For July, only evapotranspiration window from February tend of March stated in the MAM (table 5-15).

Table 5-15 Best candidate critical windows for each of the weather variables to explain July productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 3, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>GDD</em></td>
<td>05.02-19.02</td>
<td>29.01-19.02</td>
<td>04.06-02.07</td>
</tr>
<tr>
<td></td>
<td>Threshold 4 °C</td>
<td>Threshold 4.5 °C</td>
<td>Threshold 4 °C</td>
</tr>
<tr>
<td><em>Average temperature</em></td>
<td>05.02-19.02</td>
<td>05.02-05.03</td>
<td>08.01-26.02</td>
</tr>
<tr>
<td><em>Precipitation</em></td>
<td>29.01-19.02</td>
<td>05.02-19.02</td>
<td>16.04-04.06</td>
</tr>
<tr>
<td><em>Wind speed</em></td>
<td>05.03-26.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Evapotranspiration</em></td>
<td><strong>05.02-26.03</strong></td>
<td>19.03-26.03</td>
<td>02.07-09.07</td>
</tr>
</tbody>
</table>

For August, average temperature’s best window was for mid May to end of May GDD. Precipitation best window was from mid July to mid September. Windows for average temperature, evapotranspiration and wind did not stay the MAM (table 5-16).
Table 5-16 Best candidate critical windows for each of the weather variables to explain August productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 4, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>14.05-28.05</td>
<td>01.01-12.03</td>
<td>28.05-11.06</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Threshold 4°C</td>
<td>Threshold 4°C</td>
<td>Threshold 4°C</td>
<td></td>
</tr>
<tr>
<td><strong>Average temperature</strong></td>
<td><strong>14.05-28.05</strong></td>
<td>28.05-11.06</td>
<td>08.01-12.03</td>
<td></td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td>12.02-28.05</td>
<td>14.05-25.06</td>
<td>14.05-09.07</td>
<td></td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td>01.01-29.01</td>
<td>01.01-12.02</td>
<td>16.04-21.05</td>
<td>09.07-30.07</td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>14.05-16.07</td>
<td>14.05-23.07</td>
<td>23.04-06.08</td>
<td></td>
</tr>
</tbody>
</table>

For September, average temperature’s best window was for the month of July. GDD, evapotranspiration, precipitation best window was from mid July to mid September. Windows for average temperature and wind did not stay the MAM (table 5-17).

Table 5-17 Best candidate critical windows for each of the weather variables to explain September productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 3, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>08.01-22.01</td>
<td>02.07-09.07</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Threshold 5°C</td>
<td>Threshold 4°C</td>
<td></td>
</tr>
<tr>
<td><strong>Average temperature</strong></td>
<td>08.01-22.01</td>
<td>25.06-09.07</td>
<td><strong>02.07-29.07</strong></td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td>26.03-23.04</td>
<td>19.01-12.02</td>
<td></td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td>22.01-19.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>15.01-19.03</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For October, average temperature’s best window was from first week of September to the beginning of October.. Windows for GDD, precipitation, evapotranspiration and wind did not stay the MAM (table 5-18).
Table 5-18 Best candidate critical windows for each of the weather variables to explain October productivity (live biomass inside the cages). Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>08.09-01.10 Threshold 5.5°C</td>
<td></td>
</tr>
<tr>
<td><strong>Average temperature</strong></td>
<td>08.09-01.10</td>
<td></td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td>06.08-01.10</td>
<td></td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td>14.05-02.07</td>
<td>09.07-23.07</td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>02.04-16.04</td>
<td></td>
</tr>
</tbody>
</table>

For November, temperature’s best window, in the form of GDD with threshold of 4°C was from end of January to mid April. Precipitation best window was from end of May to beginning of July. Windows for average temperature evapotranspiration wind did not stay the MAM. (table 5-19).

Table 5-19 Best candidate critical windows for each of the weather variables to explain November productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 3, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>22.01-05.02</td>
<td><strong>22.01-16.04</strong></td>
<td>05.03-09.04</td>
</tr>
<tr>
<td></td>
<td>Threshold 5°C</td>
<td><strong>Threshold 4°C</strong></td>
<td>Threshold 4°C</td>
</tr>
<tr>
<td><strong>Average temperature</strong></td>
<td>29.01-16.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td><strong>28.05-02.07</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>01.01-29.01</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Live biomass inside the exclosures - Seasonal productivity

a) Early season growth (corresponds to the months of April through June)

For the early season, none of the weather windows remained in the MAM (table 5-20).

Table 5-20 Best candidate critical windows for each of the weather variables to explain the early season growth (April-June) productivity (live biomass inside the cages). Windows are labeled 1 through 4, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>23.02-25.05</td>
<td>23.02-08.06</td>
<td>Threshold: 4°C</td>
<td>Threshold: 4°C</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>02.02-25.05</td>
<td>26.01-18.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>temperature</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td>23.02-02.03</td>
<td>29.12-05.01</td>
<td>24.11-19.01</td>
<td></td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td>27.10-17.11</td>
<td>01.12-12.01</td>
<td>13.10-17.11</td>
<td>26.01-16.02</td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>12.01-02.02</td>
<td>05.01.20.04</td>
<td>09.02-20.04</td>
<td>23.02-20.04</td>
</tr>
</tbody>
</table>

b) Late season growth (corresponds to the months from June through September)

For the late season, temperature’s best window, in the form of GDD with threshold of 5°C was from end of January to end of March. Average temperature’s best window was between end of August and the first week of September. Wind’s best window was from May to end of June. Windows for precipitation and evapotranspiration did not stay the MAM. (table 5-21).
Table 5-21 Best candidate critical windows for each of the weather variables to explain late season growth (July-September) productivity (live biomass inside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 3, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
<th>Window 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>22.01-22.03</td>
<td>15.02-22.03</td>
<td>08.02-22.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Threshold: 5° C</td>
<td></td>
<td>4.5° C</td>
<td></td>
<td>Threshold: 5° C</td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td>15.02-22.03</td>
<td>23.08-06.09</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>01.02-15.02</td>
<td>01.03-15.03</td>
<td>30.08-06.09</td>
<td>09.08-23.08</td>
<td>02.08-23.08</td>
</tr>
<tr>
<td>Wind speed</td>
<td>03.05-28.06</td>
<td>03.05-26.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>01.02-26.04</td>
<td>05.07-12.07</td>
<td>09.08-23.08</td>
<td>02.08-23.08</td>
<td></td>
</tr>
</tbody>
</table>
Live biomass outside the cages monthly productivity

The best candidate weather windows for the outside biomass were much clearer to choose from than the ones for the inside.

For April, average temperature’s best window, was from mid of January to mid April. Evapotranspiration best window was from February to mid April. Windows for GDD, precipitation and wind did not stay the MAM. (table 5-22).

Table 5-22 Best candidate critical windows for each of the weather variables to explain April productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2 from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>5.12-09.03 Threshold 6.5°C</td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td>19.01-13.04</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>27.10-12.01</td>
<td>29.09-19.01</td>
</tr>
<tr>
<td>Wind speed</td>
<td>05.01-23.03</td>
<td>22.12-30.03</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>08.09-22.09</td>
<td>09.02-13.04</td>
</tr>
</tbody>
</table>

For May, temperature’s best window, in the form of GDD with a threshold of 5°C was the month of April. Windows for average temperature, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-23).

Table 5-23 Best candidate critical windows for each of the weather variables to explain May productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>26.02-05-03 Threshold 5.5°C</td>
<td>02.04-30.04 Threshold 5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>26.02-05.03</td>
<td>22.01-14.05</td>
</tr>
<tr>
<td>Precipitation</td>
<td>19.03-23.04</td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>19.03-23</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>05.02-23.04</td>
<td>12.03-23.04</td>
</tr>
</tbody>
</table>
For June, precipitation best window was from end of March to mid April. Windows for GDD, average temperature, evapotranspiration and wind did not stay the MAM. (table 5-24).

Table 5-24 Best candidate critical windows for each of the weather variables to explain June productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Only one window is shown, as the choice was very clear. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>02.04-23-04 Threshold 5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>05.02-26.02</td>
</tr>
<tr>
<td>Precipitation</td>
<td><strong>26.03-16.04</strong></td>
</tr>
<tr>
<td>Wind speed</td>
<td>15.01-02.04</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>05.03-02.04</td>
</tr>
</tbody>
</table>

For July, best precipitation window was in May. Windows GDD, for average temperature, evapotranspiration and wind did not stay the MAM. (table 5-25).

Table 5-25 Best candidate critical windows for each of the weather variables to explain July productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>05.02-19.02 Threshold 4°C</td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td>29.01-05.03</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td><strong>01.05-28.05</strong></td>
<td>25.06-02.07</td>
</tr>
<tr>
<td>Wind speed</td>
<td>05.03-26.04</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>14.05-21.05</td>
<td>02.07-29.07</td>
</tr>
</tbody>
</table>

For August, wind best window was from mid March to second week of April. Windows for GDD, average temperature, evapotranspiration and precipitation did not stay the MAM. (table 5-26).
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

Table 5-26 Best candidate critical windows for each of the weather variables to explain August productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>19.03-26.03 Threshold 4°C</td>
<td>22.01-14.05</td>
</tr>
<tr>
<td>Average temperature</td>
<td>19.03-26.03</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>12.02-28.05</td>
<td>14.05-02.07</td>
</tr>
<tr>
<td>Wind speed</td>
<td>19.03-09.04</td>
<td>09.07-30.07</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>14.05-16.07</td>
<td>09.05-06.08</td>
</tr>
</tbody>
</table>

For September, none of the windows stayed the MAM. (table 5-27).

Table 5-27 Best candidate critical windows for each of the weather variables to explain September productivity (live biomass outside the cages). Only one window is shown, as the choice was very clear. There were no candidate wind critical windows for this month. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>01.01-22.01 Threshold 5.5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>08.01-22.01</td>
</tr>
<tr>
<td>Precipitation</td>
<td>16.04-23.04</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>12.02-19.03</td>
</tr>
</tbody>
</table>

For October, temperature’s best window, in the form of GDD with a threshold of 5°C was between first week of January and beginning of February. Evapotranspiration best window was between February and March. Windows for average temperature, precipitation and wind did not stay the MAM. (table 5-28).

Table 5-28 Best candidate critical windows for each of the weather variables to explain October productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>08.01-05.02 Threshold 5°C</td>
<td>10.09-15.10 Threshold 6.5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>10.09-15.10</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>14.05-28.05</td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>10.09-01.10</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>12.02-12.03</td>
<td></td>
</tr>
</tbody>
</table>
For November, evapotranspiration best window was from the month of January. Windows for GDD, average temperature, precipitation and wind did not stay the MAM. (table 5-29).

Table 5-29 Best candidate critical windows for each of the weather variables to explain November productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>05.03-09.04 Threshold 4°C</td>
<td>05.10-29.10</td>
</tr>
<tr>
<td>Average temperature</td>
<td>22.01-16.04</td>
<td>05.10-29.05</td>
</tr>
<tr>
<td>Precipitation</td>
<td>05.10-29.05</td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>09.04-23.04</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>01.01-29.01</td>
<td></td>
</tr>
</tbody>
</table>

Seasonal productivity - Live biomass outside the exclosures

a) Early season growth (corresponds to the months of April through June)

For the early season, evapotranspiration best window was from the first week of February to third week of April. Windows for average temperature, evapotranspiration, precipitation and wind did not stay the MAM (table 5-30).

Table 5-30 Best candidate critical windows for each of the weather variables to explain the early season growth (April-June) productivity (live biomass outside the cages). Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>23.02-25.05 Threshold 4.5°C</td>
<td>23.03-08.06 Threshold 4.5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>02.02-25.05</td>
<td>16.02-08.06</td>
</tr>
<tr>
<td>Precipitation</td>
<td>23.02-02.03</td>
<td>29.04-05.06</td>
</tr>
<tr>
<td>Wind speed</td>
<td>12.01-30.03</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>09.02-20.04</td>
<td></td>
</tr>
</tbody>
</table>
b) Late season growth (corresponds to the months from June through September)

For the late season, average temperature’s best window between third week of August and first week of September. Wind best window was between mid August and mid September. Windows for GDD, evapotranspiration and precipitation did not stay the MAM. (table 5-31).

Table 5-31 Best candidate critical windows for each of the weather variables to explain late season growth (July-September) productivity (live biomass outside the cages). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>22.02-08.03 Threshold 4°C</td>
<td>23.08-06.09 Threshold 5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>15.02-08.03</td>
<td>23.08-06.09</td>
</tr>
<tr>
<td>Precipitation</td>
<td>01.02-25.02</td>
<td>12.07-23.08</td>
</tr>
<tr>
<td>Wind speed</td>
<td>16.08-13.09</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>05.07-12.07</td>
<td>02.08-23.08</td>
</tr>
</tbody>
</table>

Offtake monthly productivity critical windows

Like for biomass outside the exclosures, the best candidate weather windows for offtake were much clearer to choose from than the ones for the inside.

For April, precipitation best windows was between late September and mid October of the previous year. Evapotranspiration was in February. Windows for GDD, average temperature and wind did not stay the MAM. (table 5-32).

Table 5-32 Best candidate critical windows for each of the weather variables to explain April productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. There wer clear best critical windows. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>13.10-27.11 Threshold 4°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>05.01-31.01</td>
</tr>
<tr>
<td>Precipitation</td>
<td>29.09-13.10</td>
</tr>
<tr>
<td>Wind speed</td>
<td>08.09-13.10</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>02.02-16.02</td>
</tr>
</tbody>
</table>
For May, average temperature’s best window was the month of April. Windows for GDD, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-33).

Table 5-33 Best candidate critical windows for each of the weather variables to explain May productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. There were no good critical windows for wind. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>03.04-30.04 Threshold 4°C</td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td><strong>03.04-30.04</strong></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>19.03-23.04</td>
<td>26.03-30.04</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>26.02-05.03</td>
<td>12.02-12.03</td>
</tr>
</tbody>
</table>

For June, temperature’s best window, in the form of GDD with a threshold of 5.5°C was between mid March and third week of of April. Windows for average temperature, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-34).

Table 5-34 Best candidate critical windows for each of the weather variables to explain June productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. There were clear best critical windows. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td><strong>12.03-19.04 Threshold 5.5°C</strong></td>
</tr>
<tr>
<td>Average temperature</td>
<td>12.03-19.04</td>
</tr>
<tr>
<td>Precipitation</td>
<td>05.03-29.05</td>
</tr>
<tr>
<td>Wind speed</td>
<td>29.01-12.03</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>12.05-02.06</td>
</tr>
</tbody>
</table>
For July, average temperature’s best window was between mid April and third week of June. Windows for GDD, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-35).

Table 5-35 Best candidate critical windows for each of the weather variables to explain July productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. There were clear best critical windows. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>02.04-23.06 Threshold 7°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>16.04-23.06</td>
</tr>
<tr>
<td>Precipitation</td>
<td>30.04-04.04</td>
</tr>
<tr>
<td>Wind speed</td>
<td>04.06-09.07</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>30.04-21.05</td>
</tr>
</tbody>
</table>

For August, precipitation’s best window was in July. Wind best window was between third week of May to mid August. Windows for GDD, average temperature and evapotranspiration did not stay the MAM. (table 5-36).

Table 5-36 Best candidate critical windows for each of the weather variables to explain August productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>04.06-21.06 Threshold 4°C</td>
<td>28.05-25.07 Threshold 5°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>04.06-21.06</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>03.07-30.07</td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>21.05-13.08</td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>30.04-21.05</td>
<td>14.05-16.07</td>
</tr>
</tbody>
</table>
For September, average temperature’s best window was between mid June and first week of July. Windows for GDD, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-37).

Table 5-37 Best candidate critical windows for each of the weather variables to explain September productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. There were clear best candidate critical windows. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>11.06-09.07 Threshold 5.5°C</td>
</tr>
<tr>
<td><strong>Average temperature</strong></td>
<td>11.06-09.07</td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td>14.05-20.08</td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td>14.05-18.06</td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>21.05-27.08</td>
</tr>
</tbody>
</table>

For October, precipitations best window was between mid August and mid October. Windows for GDD, average temperature, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-38).

Table 5-38 Best candidate critical windows for each of the weather variables to explain October productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GDD</strong></td>
<td>19.03-02.04 Threshold 6.5°C</td>
<td></td>
</tr>
<tr>
<td><strong>Average temperature</strong></td>
<td>19.03-02.04</td>
<td></td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td>10.08-15.10</td>
<td>09.04-16.07</td>
</tr>
<tr>
<td><strong>Wind speed</strong></td>
<td>28.05-11.06</td>
<td></td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong></td>
<td>26.03-16.07</td>
<td></td>
</tr>
</tbody>
</table>
For November, average temperature best window was between mid May and first week of July. Windows for GDD, evapotranspiration, precipitation and wind did not stay the MAM. (table 5-39).

Table 5-39 Best candidate critical windows for each of the weather variables to explain November productivity (offtake). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 and 2, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>22.01-05.02 Threshold 7°C</td>
</tr>
<tr>
<td>Average temperature</td>
<td>14.05-09.07</td>
</tr>
<tr>
<td>Precipitation</td>
<td>28.05-23.07</td>
</tr>
<tr>
<td>Wind speed</td>
<td>28.05-13.08</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>26.03-09.04</td>
</tr>
</tbody>
</table>

**Seasonal productivity - offtake**

a) Early season growth (corresponds to the months of April through June)

For early season, none of the windows stayed the MAM (table 5-40).

Table 5-40 Best candidate critical windows for each of the weather variables to explain the early season growth (April-June) productivity (offtake). Windows are labeled 1 through 3, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>23.02-25.05 Threshold 4°C</td>
<td>23.02-08.06 Threshold 4°C</td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td>02.02-25.05</td>
<td>26.01-18.05</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>24.11-19.01</td>
<td>29.12-15.01</td>
<td>23.02-27.03</td>
</tr>
<tr>
<td>Wind speed</td>
<td>27.10-17.11</td>
<td>01.12-12.01</td>
<td>26.01-16-02</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>12.01-02.01</td>
<td>09.02-20.04</td>
<td></td>
</tr>
</tbody>
</table>
b) Late season growth (corresponds to the months from June through September)

For the late season, Wind speed best window was between beginning of May and end of June. Evapotranspiration best window is in August. Windows for GDD, average temperature and precipitation did not stay the MAM. (table 5-41).

Table 5-41 Best candidate critical windows for each of the weather variables to explain late season growth (July-September) productivity (offatke). The windows in bold are the significant windows after fitting a linear regression model to explain productivity. The windows in bold are the significant windows after fitting a linear regression model to explain productivity. Windows are labeled 1 through 4, from the farthest to the closest to the event in time. GDD means growing degree-days.

<table>
<thead>
<tr>
<th>Weather variable</th>
<th>Window 1</th>
<th>Window 2</th>
<th>Window 3</th>
<th>Window 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD</td>
<td>22.02-22.03</td>
<td>08.02-22.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Threshold 5°C</td>
<td>Threshold 5.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average temperature</td>
<td>15.02-23.02</td>
<td>23.08-06.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>01.02-15.02</td>
<td>01.03-15.04</td>
<td>02.08-23.08</td>
<td>09.08-06.09</td>
</tr>
<tr>
<td>Wind speed</td>
<td>03.05-28.06</td>
<td>03.05-26.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>01.02-26.04</td>
<td></td>
<td>02.08-23.08</td>
<td></td>
</tr>
</tbody>
</table>

5.3.8. Vegetation productivity linear models

Live biomass inside the cages monthly productivity linear models

As in chapter 3, the models fitted with weather variables outperformed the models using evapotranspiration as an explanatory variable.
a) Linear models with weather variables as predictors

Deer density is only important at the beginning of the growing season. Weather variables vary in their timing and effects depending of the month (table 5.42).

**Table 5-42** Mean monthly in live productivity linear models. Maximum models also include female deer density and live biomass outside the cages. Minimum adequate model (MAM) where only the significant terms.

<table>
<thead>
<tr>
<th>Month</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>April in live biomass</td>
<td>April out live biomass</td>
<td>1.06</td>
<td>0.12</td>
<td>8.8</td>
<td>1.6e07 ***</td>
<td>0.92</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Precipitation w.3</td>
<td>0.006</td>
<td>0.002</td>
<td>2.8</td>
<td>0.01</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Deer density</td>
<td>-0.02</td>
<td>0.007</td>
<td>-2.81</td>
<td>0.04</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>May in live biomass</td>
<td>May out live biomass</td>
<td>0.97</td>
<td>0.10</td>
<td>9.5</td>
<td>7.2e-08 ***</td>
<td>0.83</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>GDD w.1</td>
<td>0.1</td>
<td>0.04</td>
<td>2.6</td>
<td>0.002</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Precipitation w.2</td>
<td>0.01</td>
<td>0.004</td>
<td>2.8</td>
<td>0.01</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>June in live biomass</td>
<td>June out live biomass</td>
<td>0.94</td>
<td>0.18</td>
<td>5.12</td>
<td>7.13e-5 ***</td>
<td>0.58</td>
<td>18</td>
</tr>
<tr>
<td>July in live biomass</td>
<td>July out live biomass</td>
<td>0.94</td>
<td>0.17</td>
<td>5.6</td>
<td>2.33e-5 ***</td>
<td>0.62</td>
<td>18</td>
</tr>
</tbody>
</table>
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

<table>
<thead>
<tr>
<th></th>
<th>August in live biomass</th>
<th>September in live biomass</th>
<th>October in live biomass</th>
<th>November in live biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>August out live biomass</td>
<td>1.09</td>
<td>0.88</td>
<td>0.53</td>
<td>1.2</td>
</tr>
<tr>
<td>August out live biomass</td>
<td>0.1</td>
<td>0.17</td>
<td>0.19</td>
<td>0.11</td>
</tr>
<tr>
<td>Average temp. w1</td>
<td>-0.42</td>
<td>-0.4</td>
<td>0.33</td>
<td>-0.008</td>
</tr>
<tr>
<td>Average temp. w1</td>
<td>0.16</td>
<td>0.15</td>
<td>0.16</td>
<td>0.002</td>
</tr>
<tr>
<td>Average temp. w1</td>
<td>-2.5</td>
<td>-2.46</td>
<td>2.1</td>
<td>-3.4</td>
</tr>
<tr>
<td>GDD w.2</td>
<td>10.5</td>
<td>5.1</td>
<td>2.8</td>
<td>10.6</td>
</tr>
<tr>
<td>Precipitation w.1</td>
<td>1.49e-8</td>
<td>8.17e-5</td>
<td>0.001</td>
<td>2.07e-8</td>
</tr>
<tr>
<td>GDD w.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation w.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: $P < 0.05 = \ast, P < 0.01 = \ast\ast, P < 0.001 = \ast\ast\ast$. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

b) Linear models with evapotranspiration windows as predictors

Off all the months, only in July evapotranspiration windows remain in the model, the biomass outside the exclosures is highly correlated with the biomass inside in all months (table 5-43).
Table 5.43 Mean monthly in live productivity linear models. Maximum models also include female deer density and live biomass outside the cages. Minimum adequate model (MAM) where only the significant terms.

<table>
<thead>
<tr>
<th>Month</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>April in live biomass</td>
<td>April out live biomass</td>
<td>0.97</td>
<td>0.1</td>
<td>8.9</td>
<td>4.56e-08***</td>
<td>0.8</td>
<td>18</td>
</tr>
<tr>
<td>May in live biomass</td>
<td>May out live biomass</td>
<td>0.97</td>
<td>0.10</td>
<td>9.5</td>
<td>1.72e-08***</td>
<td>0.8</td>
<td>18</td>
</tr>
<tr>
<td>June in live biomass</td>
<td>June out live biomass</td>
<td>0.94</td>
<td>0.18</td>
<td>5.12</td>
<td>7.13e-5***</td>
<td>0.58</td>
<td>18</td>
</tr>
<tr>
<td>July in live biomass</td>
<td>July out live biomass</td>
<td>0.91</td>
<td>0.15</td>
<td>5.97</td>
<td>1.53e-05***</td>
<td>0.70</td>
<td>17</td>
</tr>
<tr>
<td>Evapotranspiration w.1</td>
<td></td>
<td>-0.93</td>
<td>0.41</td>
<td>2.3</td>
<td>0.04</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>August in live biomass</td>
<td>August out live biomass</td>
<td>1.0</td>
<td>0.11</td>
<td>10.6</td>
<td>5.98e-09***</td>
<td>0.87</td>
<td>17</td>
</tr>
<tr>
<td>September in live biomass</td>
<td>September out live biomass</td>
<td>1.0</td>
<td>0.17</td>
<td>6.1</td>
<td>1.01e-05***</td>
<td>0.67</td>
<td>18</td>
</tr>
<tr>
<td>October in live biomass</td>
<td>October out live biomass</td>
<td>0.72</td>
<td>0.18</td>
<td>3.9</td>
<td>0.001</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>November in live biomass</td>
<td>November in live biomass</td>
<td>1.1</td>
<td>0.15</td>
<td>7.5</td>
<td>8.05e-07***</td>
<td>0.55</td>
<td>17</td>
</tr>
</tbody>
</table>

Note: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

Live biomass inside the cages seasonal productivity linear models

All the maximum models include live biomass outside the cages as well as deer density. For the early season growth model, it appears weather is not a good predictor, only the outside live biomass. This could just be a consequence of
aggregation, as we would be summing the effects of independent weather variables (central limit theory). This is not so much the case for the late season, where some weather effects remain the model (table 5-44).

a) Linear models with weather variables as predictors

The early season growth model didn’t retain any of the weather variables, in the late season model; we can see an integration of the different weather variables working in tandem through the season (table 5-44 and 4-45)

Table 5-44 Seasonal Plant productivity. Early season growth corresponds to the live biomass productivity inside cages for the months of April-June. Late season growth corresponds to the live biomass productivity inside cages for the months of June-September.

<table>
<thead>
<tr>
<th>Season Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early growth season</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outside live biomass</td>
<td>0.91</td>
<td>0.11</td>
<td>8.59</td>
<td>8.75 e-08</td>
<td>***</td>
<td>18</td>
</tr>
<tr>
<td>GDD w.1</td>
<td>-0.061</td>
<td>0.01</td>
<td>-3.7</td>
<td>0.002</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>Average temperature w.2</td>
<td>-0.92</td>
<td>0.37</td>
<td>-2.4</td>
<td>0.02</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Wind w.1</td>
<td>1.87</td>
<td>0.71</td>
<td>2.6</td>
<td>0.02</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Late season growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outside live biomass</td>
<td>0.95</td>
<td>0.09</td>
<td>10.5</td>
<td>9.13e-8</td>
<td>***</td>
<td>13</td>
</tr>
<tr>
<td>Early season live biomass</td>
<td>0.46</td>
<td>0.1</td>
<td>4.5</td>
<td>0.0005</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>GDD w.1</td>
<td>-0.061</td>
<td>0.01</td>
<td>-3.7</td>
<td>0.002</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>Average temperature w.2</td>
<td>-0.92</td>
<td>0.37</td>
<td>-2.4</td>
<td>0.02</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Wind w.1</td>
<td>1.87</td>
<td>0.71</td>
<td>2.6</td>
<td>0.02</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.
b) Linear models with evapotranspiration windows as predictors

Table 5-45 Seasonal Plant productivity. Early season growth corresponds to the live biomass productivity inside cages for the months of April-June. Late season growth corresponds to the live biomass productivity inside cages for the months of June-September.

<table>
<thead>
<tr>
<th>Season</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early season</td>
<td>Out live biomass</td>
<td>0.91</td>
<td>0.11</td>
<td>8.59</td>
<td>8.75 e-08</td>
<td>0.7</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late season</td>
<td>Out live biomass</td>
<td>1.1</td>
<td>0.14</td>
<td>8.5</td>
<td>1.58e-07</td>
<td>0.8</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

Live biomass outside the cages monthly productivity linear models

a) Linear models with weather variables as predictors

Overall, again the weather variables models preform better, however for the months of October and November, evapotranspiration models performed much better. Note the negative effects of evapotranspiration, in those months (figures 5-46 and 5-47).

Table 5-46 Mean monthly outside live productivity linear models. Maximum models also include female deer density. Minimum adequate model (MAM) where only the significant terms.

<table>
<thead>
<tr>
<th>Month</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>April outside biomass</td>
<td>Deer density</td>
<td>-0.024</td>
<td>0.011</td>
<td>-2.22</td>
<td>0.04</td>
<td>*</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Average temp.</td>
<td>0.859</td>
<td>0.33</td>
<td>2.5</td>
<td>0.02</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>w.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May outside biomass</td>
<td>GDD w.2</td>
<td>0.051</td>
<td>0.012</td>
<td>4.18</td>
<td>0.0006</td>
<td>***</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Precipitation</td>
<td>0.01</td>
<td>0.003</td>
<td>3.5</td>
<td>0.0027</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>w.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June outside biomass</td>
<td>Precipitation</td>
<td>-0.017</td>
<td>0.005</td>
<td>-3.8</td>
<td>0.001</td>
<td>**</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>w.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July outside biomass</td>
<td>Precipitations</td>
<td>0.05</td>
<td>0.02</td>
<td>2.4</td>
<td>0.03</td>
<td>*</td>
<td>18</td>
</tr>
</tbody>
</table>
Chapter 5 Identifying the critical climatic time windows that affect plant productivity and red deer performance in the Isle of Rum.

b) Linear models with evapotranspiration windows as predictors

Table 5-47 Mean monthly outside live productivity linear models. Maximum models also include female deer density. Minimum adequate model (MAM) where only the significant terms.

<table>
<thead>
<tr>
<th>Month</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>April Biomass outside</td>
<td>Evapotranspiration w.2</td>
<td>0.5752</td>
<td>0.15</td>
<td>3.8</td>
<td>0.001</td>
<td>**</td>
<td>18</td>
</tr>
<tr>
<td>May Biomass outside</td>
<td>Evapotranspiration w.2</td>
<td>0.436</td>
<td>0.13</td>
<td>3.4</td>
<td>0.003</td>
<td>**</td>
<td>18</td>
</tr>
<tr>
<td>October Biomass outside</td>
<td>Evapotranspiration w.1</td>
<td>-1.85</td>
<td>0.271</td>
<td>-6.81</td>
<td>5.87e-06</td>
<td>***</td>
<td>15</td>
</tr>
<tr>
<td>November Biomass outside</td>
<td>Evapotranspiration w.1</td>
<td>-1.1</td>
<td>0.45</td>
<td>-2.42</td>
<td>0.0271</td>
<td>*</td>
<td>17</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: $P < 0.05 = ^*$, $P < 0.01 = ^{**}$, $P < 0.001 = ^{***}$. Non-significant effects are not shown. $P$ values for significant effects are taken from the model output of the MAM.
Live biomass outside the cages seasonal productivity linear models

All the maximum models include deer density. For the late season, the early season biomass is included in the model (figures 5-48 and 5-49).

a) Linear models with weather variables as predictors

Table 5-48 Seasonal Plant productivity. Early season growth corresponds to the live biomass productivity outside cages for the months of April-June. Late season growth corresponds to the live biomass productivity outside cages for the months of June-September.

<table>
<thead>
<tr>
<th>Season</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early season</td>
<td>Deer density</td>
<td>-0.07</td>
<td>0.03</td>
<td>2.4</td>
<td>0.02</td>
<td>*</td>
<td>17</td>
</tr>
<tr>
<td>growth</td>
<td>GDD w.2</td>
<td>0.04</td>
<td>0.01</td>
<td>3.3</td>
<td>0.003**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Deer density</td>
<td>-0.2</td>
<td>0.03</td>
<td>5.3</td>
<td>0.0001***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late season</td>
<td>Average temp. w.2</td>
<td>-2.21</td>
<td>0.82</td>
<td>-2.6</td>
<td>0.01</td>
<td>*</td>
<td>14</td>
</tr>
<tr>
<td>growth</td>
<td>Precipitation w.2</td>
<td>-0.03</td>
<td>0.01</td>
<td>-2.3</td>
<td>0.03</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wind w.1</td>
<td>-1.97</td>
<td>0.68</td>
<td>-2.9</td>
<td>0.011</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

b) Linear models with evapotranspiration windows as predictors

Table 5-49 Seasonal Plant productivity. Early season growth corresponds to the live biomass productivity inside cages for the months of April-June. Late season growth corresponds to the live biomass productivity inside cages for the months of June-September.

<table>
<thead>
<tr>
<th>Season</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early season</td>
<td>Evapotranspiration w.1</td>
<td>1.2</td>
<td>0.22</td>
<td>5.47</td>
<td>3.34e-05***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late season</td>
<td>Early season growth</td>
<td>0.64</td>
<td>0.25</td>
<td>2.5</td>
<td>0.02</td>
<td>*</td>
<td>17</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.
Offtake biomass monthly productivity linear models

As the other biomass models, the models fitted with weather variables outperformed the models using evapotranspiration as an explanatory variable (5-50 and 5-51).

a) Linear models with weather variables as predictors

Table 5-50 Mean monthly offtake productivity linear models. Minimum adequate model (MAM) where only the significant terms.

<table>
<thead>
<tr>
<th>Month</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>April offtake biomass</td>
<td>Precipitation w.1</td>
<td>0.004</td>
<td>0.001</td>
<td>4.4</td>
<td>0.0003</td>
<td>***</td>
<td>18</td>
</tr>
<tr>
<td>May offtake biomass</td>
<td>Average temp. w.1</td>
<td>0.09</td>
<td>0.15</td>
<td>0.62</td>
<td>0.04</td>
<td>*</td>
<td>18</td>
</tr>
<tr>
<td>June offtake biomass</td>
<td>GDD w.1</td>
<td>0.061</td>
<td>0.03</td>
<td>2.21</td>
<td>0.04</td>
<td>*</td>
<td>18</td>
</tr>
<tr>
<td>July offtake biomass</td>
<td>Average temp. w.1</td>
<td>-0.16</td>
<td>0.15</td>
<td>-1.1</td>
<td>0.03</td>
<td>*</td>
<td>18</td>
</tr>
<tr>
<td>August offtake biomass</td>
<td>Precipitation w.1</td>
<td>-0.02</td>
<td>0.005</td>
<td>-4.5</td>
<td>0.0004</td>
<td>***</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Wind w.1</td>
<td>1.6</td>
<td>0.48</td>
<td>3.4</td>
<td>0.004</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>September offtake biomass</td>
<td>Average temp. w.1</td>
<td>-0.61</td>
<td>0.24</td>
<td>-2.5</td>
<td>0.02</td>
<td>*</td>
<td>18</td>
</tr>
<tr>
<td>October offtake biomass</td>
<td>Precipitation w.1</td>
<td>0.02</td>
<td>0.005</td>
<td>2.7</td>
<td>0.01</td>
<td>*</td>
<td>16</td>
</tr>
<tr>
<td>November offtake biomass</td>
<td>Average temp. w.1</td>
<td>0.36</td>
<td>0.13</td>
<td>-2.7</td>
<td>0.01</td>
<td>*</td>
<td>17</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: * P < 0.05, ** P < 0.01, *** P < 0.001. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.

b) Linear models with evapotranspiration windows as predictors

Table 5-51 Mean monthly offtake productivity linear models. Minimum adequate model (MAM) where only the significant terms.

<table>
<thead>
<tr>
<th>Month</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>April offtake biomass</td>
<td>Evapotranspiration w.1</td>
<td>-0.9</td>
<td>0.34</td>
<td>-2.6</td>
<td>0.01</td>
<td>*</td>
<td>18</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: * P < 0.05, ** P < 0.01, *** P < 0.001. Non-significant effects are not shown. P values for significant effects are taken from the model output of the MAM.
Live biomass outside the cages seasonal productivity linear models

For the early season growth model, it appears weather is not a good predictor. This could just be a consequence of aggregation, as we would be summing the effects of independent weather variables. This is not so much the case for the late season, where wind and evapotranspiration effects remain the models (tables 5-52 and 5-53).

a) Linear models with weather variables as predictors

Table 5-52 Seasonal Plant productivity. Early season growth corresponds to the live biomass productivity outside cages for the months of April-June. Late season growth corresponds to the live biomass productivity outside cages for the months of June-September.

<table>
<thead>
<tr>
<th>Season</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late season growth</td>
<td>Wind w.1</td>
<td>2.1</td>
<td>0.91</td>
<td>2.2</td>
<td>0.03*</td>
<td>0.24</td>
<td>17</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: $P < 0.05 = \ast$, $P < 0.01 = \ast\ast$, $P < 0.001 = \ast\ast\ast$. Non-significant effects are not shown. $P$ values for significant effects are taken from the model output of the MAM.

b) Linear models with evapotranspiration windows as predictors

Table 5-53 Seasonal Plant productivity. Early season growth corresponds to the live biomass productivity outside cages for the months of April-June. Late season growth corresponds to the live biomass productivity outside cages for the months of June-September.

<table>
<thead>
<tr>
<th>Season</th>
<th>Window</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t value</th>
<th>P</th>
<th>R²</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late season growth</td>
<td>Evapotranspiration w.2</td>
<td>0.2</td>
<td>0.1</td>
<td>21.9</td>
<td>0.03*</td>
<td>0.17</td>
<td>17</td>
</tr>
</tbody>
</table>

Notes: Asterisks indicate the level of significance: $P < 0.05 = \ast$, $P < 0.01 = \ast\ast$, $P < 0.001 = \ast\ast\ast$. Non-significant effects are not shown. $P$ values for significant effects are taken from the model output of the MAM.

5.4. Discussion

Both climate and food availability affected deer performance. The analysis in this chapter reinforces the conclusions of previous studies of the red deer in Rum (Albon & Clutton-Brock 1988, Post & Stenseth 1999, Mysterud et al. 2008b, Moyes et al. 2011). I too found both direct (i.e. thermoregulation) and indirect (i.e. plant growth and food availability) effects of temperature and precipitation influence herbivore phenology and demography.
Although the direct effect of climate particularly the influence of winter weather have been documented previously (e.g. Clutton-Brock & Albon 1986, Martinez-Jauregui et al. 2009), this chapter begins to identify the nature and magnitude of some of the direct effects of local weather on demographic processes but most importantly, the indirect effects of climate operating through the the grass sward (food supply).

**Average birth date phenology**

The breeding phenology of both female and male red deer in the North Block study area of Rum has advanced significantly over the last 28 years (Moyes et al. 2011). The red deer in Rum have experienced an increase in summer temperature and a decrease in summer rain (see chapter 2 for details) over the last decades. This is consistent with the wider patterns of climate warming and plant growth season lengthening observed in temperate regions of the world (Menzel & Fabian 1999, IPCC 2007).

Mean birth date is advancing by half a day per year (figure 5-4). I confined the critical period search to the summer autumn before birth. Because the question lies in by how many there is a shift, the hypothesis was that birth date would be dependent on relationship of the weather experienced by deer during the time of rut and conception, assuming that length of gestation remains fairly constant. The critical periods show that warm days, in the form of GDD (threshold 4°C) in the summer prior to birth, before conception (August-September) advances parturition date, most likely through indirect effects on food supply. Whereas precipitation (August) and wind exposure (July-October) had the opposite effect, delaying parturition date (tables 5-2 and 5-3). These effects are either behavioural (constraining rut) or physiological by delaying female entering oestrus. The observed relationships between birth date and measure of growing day degrees (proxy for temperature), precipitation and wind exposure in my analysis are broadly consistent with the idea that climate effects on phenology represent a condition dependent response to an increase in food availability at key junctures in the annual breeding cycle (Mysterud et al. 2008b).

Intuitively, mothers’ age (figure 5-6) should also have an effect on parturition date, since associations between mean offspring phenotype and maternal age have been extensively documented in free-living ungulate populations. A common observation is that maternal performance shows an initial increase with after
primiparity. For example offspring weight and survival traits tend to increase with maternal age (Wilson & Festa-Bianchet 2009), while the reverse may be the case for birth date (since in temperate environments earlier birth allows a longer period for offspring growth prior to winter; Rutberg1987).

In my analysis I see birth date is earlier when very young or very old mothers. This is slightly different from previously documented by Clutton-Brock et al. (1982), who showed in the same population of red deer an initial decrease in birth date with maternal age and an increase for the oldest mothers.

Fitting a non-parametric curve shows that there is indeed an effect, albeit small. This is a good example of the difference between statistically significance and biological importance. Because of this, I have not included this or other demographic parameter other than deer density in the weather models.

**Offspring birth weight**

I analysed males and females body mass at birth separately (figures 5-7 and 5-8). Both showed large interannual variability. The rationale for this was that the mother’s investment depends on the sex of the offspring, so possibly there are different weather variables at different times during gestation. My results agree with Coulson et al. 2003, where birth weight is better correlated with temperature from February to April.

Female birth weight is positively affected by mild winters (February-March, here in the form of GDD with a threshold of 7°C). This is effect is reinforced by the also positive effect of average temperature between March and April (tables 5-4 and 5-6). This possibly has both an effect on thermoregulation of the mothers, as well as possibly not preventing foraging due to need for sheltering. In females, increasing density was not related to changes in average birth weight, probably because by the later stages in of gestation in early spring, all hinds are in relatively poor condition whether population density is high or low (Mitchell, McGowan & Nicholson 1976). Any effects of competition on foetal growth were likely to be obscured by the substantial effects of variation in spring climate on primary productivity. More likely the decision to become (or stay) pregnant is density dependent (figure 5-9). The lack of clear negative density dependence and the interaction with environmental conditions on offspring body mass fit well with the hypothesis cast for reindeer which
states that females have adopted a risk averse reproductive allocation (Bardsen et al. 2008, 2009, 2011, Bardsen 2009).

Male’s birth weight is, also positively affected by warm temperatures between February and April (here in the form of GDD, like before for females, same threshold tables 5-5 and 5-7). In addition, density has a negative effect, thus supporting the hypothesis that mothers invest more energetic efforts in male offspring. It was reassuring to find that the critical periods for both females and males were almost identical. These intervals are better correlated with birth body mass rather than the April- May interval previously used in previous analyses of birth weight in the same population (Albon, Guinness & Clutton-Brock 1983, Albon et al. 1987, Kruuk et al. 1999). My results suggest these estimates encapsulated much of the period when temperature most strongly influence birth weight, nevertheless, the best window seems to be between mid February to end of April (tables 4.3-4.6). Moreover, unlike in previous analysis, (Simms et al. 2007), precipitation does not appear to affect birth weight, at least not directly.

My results confirm that higher temperatures during late pregnancy have a positive effect on birth weight in red deer, presumably because warm spring temperature advance the onset of grass growth and increased the mothers’ plane of nutrition (Albon et al. 1992).

Recruitment and survival
For populations living in a fluctuating environment, the relative importance of survival and recruitment for population growth can vary among demographic classes (Coulson, Gaillard & Festa-Bianchet 2005, Ezard et al. 2006, Morris et al. 2008). For this chapter I investigated two particular examples:

a) Female reproduction allocation
The proportion of females pregnant (figure 5-9) is positively affected by warm Junes (in the form of GDD, June is also when the longest days of the year occur). Wet summers (July- September) and deer density have a negative effect on calf having (tables 5-7 and 4.8).

These results support the idea that female deer increase their reproductive allocation during improved environmental conditions. This result is supported by other studies where females seemed thus to experience a reduced cost in reproduction when the preceding winter was advantageous (e.g. Festa-Bianchet, Gaillard & Jorgenson
1998, Tveraa et al. 2003). These relationships may also represent an example of the effects of climate operating through variation in food supply. In mammalian herbivores, with long life spans, individuals favour their own survival over reproduction. The balance between reproduction and survival should depend on environmental conditions affecting the two traits (e.g. Saether 1997, Gaillard & Yoccoz 2003). This trade off is especially important in northern temperate environments where reproduction takes place during the favourable season, whereas survival is constrained in the unfavourable season (Saether 1997). This is not surprising, as reproductive allocation is predicted to reduce the probability of surviving to the next year (Weladji et al. 2008). This reproduction vs. survival trade-off is one of the most studied in ecology (e.g. Reznick 1985, Clutton-Brock 1991, Clutton-Brock et al. 1996, Tavechia et al. 2005).

b) Calf survival through the first winter
The strongest declines in red deer offspring survival in Rum are not driven directly by bad winter weather (e.g. through the increased costs of thermoregulation, or indirectly because of dieback of forage, as suggested, previously, by Albon & Clutton-Brock 1983). Tables 5-10 and 5-11 show that, deer density and midsummer (mid August to mid September) have a negative effect on calf survival through first birthday. So it is the condition they are in as they enter winter that defines their probability of survival. This is supported by studies on reindeer, which indicate that reduced survival during harsh winters may be linked to reproductive decisions during the previous summer (Bardsen et al. 2011).

Consequently in red deer, in young growing animals, climatic stress may inhibit rapid weight gain immediately prior to winter and therefore the probability of surviving the winter. Additionally, another reason could be due to the fact that nutritional quality might decline in years with greater midsummer precipitation, or low deer numbers, as this leads to an increase in flowering stem production. Stems have lower protein and digestible organic matter, and a relative increase in stem production lowers the nutritional value of the grass (Illius & Gordon 2000, Craine et al. 2009). So we could argue that in Rum red deer are mostly limited by the quality (but I have no measures of this) of the food rather than the quantity. Reductions in precipitation that increase overall diet quality could increase red deer performance even when total forage biomass decreases (Breman & de Wit 1995, Sheaffer et al. 1992, Ellery et al. 1995, Sanderson et al. 1997, Craine et al. 2009), so calves enter
the winter in poorer condition. My analysis suggests that summer weight gain period is key (mother’s condition, and hay crop size). This fits well with the theory that juveniles are generally more sensitive to environmental conditions than prime aged individuals (Gaillard et al. 2000). This happens indirectly through changes in maternal reproductive allocation, e.g. decreased birth body mass in response to harsh in utero environmental conditions (Forchhammer et al. 2001, Adams 2005).

Vegetation productivity

This analysis addresses the issue of understanding the temporal dynamics of productivity in grasslands and the responses to climate change. I investigated the interannual variation in vegetation production for individual seasons or months by analysing the growing season (divided in to two periods: early and late), as well as at the individual months, as this variation in production is more sensitive and complex than response at an annual scale. I found that grassland productivity was poorly explained by variability in precipitation on its own.

Vegetation productivity was analysed separately into ungrazed (inside exclosures), grazed (outside exclosures) and offtake (difference between inside and out). In both the grazed and ungrazed grass sward, productivity is increasing in most months for the past 20 years; nevertheless the interannual variability is very large (5-10 to 5-15 and 5-16 to 5-20). The different swards (grazed, ungrazed) had relatively the same critical periods affecting productivity for the different months varying in length mostly. That influence of weather on vegetation activity varied between months though. Regulation of vegetation productivity was closely coupled with warming, where there was an optimum of temperature that increased production, at the beginning of spring, but too much warmth in the summer months negatively affects productivity. High temperatures (in the form if GDD with the threshold of 5.5°C) between March and April have a positive effect in productivity, most likely by having an effect on how early spring starts. In contrast, relatively, warm weather has a low negative effect on productivity in the summer months, presumably because of drought stress on the plant. This idea of an optimum could potential have implications with future climate change scenarios. Outside the exclosures, there was a 4-fold increase in biomass from April to July (figure 5-20). It has been reported that the effects of climatic variables on grassland biomass varied among the different season (Jobbagy & Sala 2000, Fabricante et al. 2009, Ma et al. 2010). The analysis
in this chapter supports this, it also indicates that various patterns and different controls by climatic variables.

For the ungrazed and ungrazed plots, as well as for offtake, as observed in St. Kilda (Chapter 4), GDD thresholds vary depending on the season, again depicting the balance of investment in growth, protection and reproduction (tables 5-12 to 5-21, 5-22 to 5-31, 5-32 to 5.42). Deer density only has a negative effect on plant biomass in April, this is not surprising, as this is the beginning of the growing season, where vegetation is at its lowest. This also shows that productivity in Rum is less affected by deer density during the leaf area main growing season, unless offtake is 0, which only occurs at the beginning of the season. Precipitation has a positive effect at the beginning of the growing season (April and May), after which it has no significant effects on plant production.

What is most interesting is that the critical periods are not necessarily immediately before the event, but an integration of weather in the months before (tables 5-12 to 5-21 and 5-26 and 5-46). For example, in November, productivity is affected by how warm the previous winter was and on how much rain fell in May July.

In the ungrazed plots, during late season growth (figure 5-15) years with low productivity (e.g. 1991) were years in which August temperature was 2°C higher than the long-term mean. Years with high productivity (e.g. 1995, 1997, 2006) were years that had an average August temperature followed by a cooler than average September.

Aboveground outside biomass in early growing season (May-June) showed an increasing trend over the past decades, is probably associated with advanced spring phenology. This has been observed in other temperate areas (e.g. Menzel et al. 2001, Lee et al 2002). Therefore, warmer springs are probably a major driver in increase in aboveground biomass and initial leaf area for that period. Increasing temperatures in early spring may stimulate plant growth directly by promoting plant metabolism or indirectly by enhancing water absorption and nutrient supply (Mckenna & Houle 2000). The fact that precipitation, in the summer months is not a major driver of plant production suggests that water availability might be sufficient for plant growth during the growing season in most years, thus the sensitivity of the whole community to climate change may be eliminated or dampened by complex species interactions (i.e. complementary effect, Cleland et al. 2006).
All previous studies attempting to investigate the weather effects on vegetation productivity in Rum, have not addressed the importance of evapotranspiration in plant biomass production. I calculated evapotranspiration for all months and growing seasons, using the only temperature, precipitation and wind variables. Details of the calculations are in the methods and in appendix A. This is a very important variable to consider since high soil moisture deficits are not uncommon in the Inner Hebrides (Green & Harding 1983) and can retard plant growth (Munro & Davies 1973). Remarkably though, for the most part, however, models using weather variables performed better than models using evapotranspiration. Evapotranspiration actually had a significant negative effect on plant production in April, May July, October, and November. The windows for evapotranspiration for these months were not immediately preceding the monthly production. In fact, most of the evapotranspiration critical periods were from January till April. Another unexpected result was the negative effect of evapotranspiration (tables 5-44, 5-48, 5-50). Rosenzweig (1968) showed that across ecosystems there was a positive relationship between the log of actual evapotranspiration and log productivity (both averaged across years). This does not seem to apply within a year. The negative effects of evapotranspiration here could be symptomatic of sink-limited growth conditions, in which plants have to compensate for water loss, where net photosynthesis is lower than transpiration.

Increased spring temperatures and earlier cumulative precipitation contributed to the increase in April May production while increased temperature may have caused decreased biomass in the late growing season (September and November).

During the summer, food is apparently abundant, with primary production exceeding offtake on all but the most preferred vegetation communities (Albon & Clutton-Brock 1986). However, seasonal variation in production may have important consequence for winter-feeding. Year to year variation in monthly plant biomass is closely related not only to the weather experienced in the months immediately before but on the weather experienced up to 9 months before. This is the stock of food that is depleted by growing over the winter months. Variation in size of this crop in late summer could easily have consequences that were felt in late winter (e.g. Festa-Bianchet et al. 2001).

Albon & Clutton-Brock (1988) argued that low rainfall at the time of early primary production between May and July (the driest months of the year) may
depress deer performance through retarded grass production, while low rainfall in the autumn may enhance deer performance because it is associated with a large late season growth in grass production. My results somewhat support these hypothesis, however, my analysis has a more holistic approach of the island’s climate, as it fine tunes the relationship of month-by-month plant production looking at several weather variables and their interaction with each other and plant production. Specifically, in the month of June production isn’t really affected by the weather conditions (figure 4.18 and table 4.12). Also in the months corresponding to the secondary peak growth (July-September), although moisture deficit is a limiting factor through increased evapotranspiration, temperature seems to be the main factor limiting plant growth rather than transpiration associated with primary production (through evaporation).

These results indicate that the responses of plant growth to climate change vary among the growing seasons. Thus, this is important theme in predicting the feedbacks of grassland ecosystems to future climate change.

Conclusion

Populations are limited by both environmental conditions and population density (e.g. Sinclair & Pech 1996). Nevertheless, neither density dependence, nor climate, act directly on population abundance, but through demographic processes operating at the individual level, affecting population vital rates (e.g. survival Caswell 2001).

In this chapter, the results indicate that changes in the timing of precipitation and warming are important drivers in the grassland community in Rum for both plants and red deer. This evidence suggests that climate variation play an important role in the population dynamics of red deer in Rum through food availability and their condition entering winter.

Coulson et al. (2004) have argued that, because the red deer population fluctuates around carrying capacity, and has done so for most of the study period (after 1980), the detection of density dependence is now difficult. My results, for the most part support this view. However in male birth body mass, female breeding probability and calf survival there is a significant negative effect of population density, albeit weak.

This analysis provides new insights into the actual contributions of critical periods for local weather induced changes at different times throughout the red deer life cycle. The results suggest that most of the weather effects discussed above on
male and female phenology traits and condition are strongly felt indirectly through variation in plant growth conditions in different seasons, reflecting differences in the period in which physiological constraints limit the onset of the breeding cycle between the sexes. Determining these critical periods affecting the population dynamics is of large interest as this could help gaining a better understanding of the relative influences of recruitment and adult survival and to what extent the population dynamics are affected by environmental conditions during breeding or survival seasons. Moreover, subtle shifts in the timing of the critical periods could have large effects in the future. The main results, also contribute to the large body of literature that shows that population dynamics of ungulates are determined by a combination of stochastic and density dependent factors, their magnitude and timing.

**Future work**

It would be very interesting to investigate further the possible critical periods for conception. Also, to investigate if body weight is positively correlated with summer May-July rainfall since it may increase the feeding on the most preferred nutritious swards? Is rate of weight loss greater in years that biomass of new heather is low? With this explore the possible effects of diet quality

Improved winter or spring conditions may lead to increased foetal growth rates and previous studies have suggested parturition dates are partly under offspring control and ay be triggered upon attaining a target size (Asher 2007). So in addition to what I have looked at, it will be interesting to explore a wider critical to include overwinter and spring prior to birth weather periods. It would have been incredibly interesting to analyse the weather effects at the red deer individual level, rather than population means. It would have been interesting to explore variations in individual quality, since high quality individuals may better cope with the costs of reproduction.

With all the critical periods for productivity established it would be interesting to investigate the plant productivity dynamics in the context of different climate change scenarios.

Finally, it would be interesting to further test Rosenzweig’s findings with more data and see the degree of scatter.
Chapter 6 Discussion

How does one establish cause and effect from observational studies? This is one of oldest and most difficult questions in field ecology. In one sense, the answer is “you can’t”: the best you can do is correlation, and correlation of course does not imply causation. Some sceptics go so far as to label any attempt at discovering cause and effect in observation studies as “data dredging”. Their view is that if you look hard enough and long enough you will eventually find something statistically significant and then you can publish and move on.

Few ecologists doubt the importance of weather differences from one year to the next, but until recently, very little effort was expended in trying to find robust protocols for asking the important questions:

• which weather variables are most important?
• when do they have their most important effects?
• what effect sizes do they generate?
• what is the shape of the relationship between the weather variable and the ecological response variable?

This thesis uses three classic long-term studies to address these questions. The Park Grass Experiment at Rothamsted provides an unrivalled source of data on primary production in the absence of herbivory: we have quantitative evidence of the size of the first and second hay crops for every year since 1880, along with locally measured daily data on temperature and precipitation. I use this dataset to understand the determinants of grass yield across the growing season. The results of this analysis are then used to inform our understanding of weather effects in two food-limited plant-herbivore systems: the Red Deer of Rum and the Soay Sheep of St Kilda. The key
point is that in food-limited plant-herbivore systems there is no necessary relationship between plant productivity and plant biomass: increases in plant production may simply lead to increase in consumption by the animals, with no net change in plant biomass. This is very important in studies of weather impacts because plant biomass data are often the only plant data available, and there is no guarantee that weather leading to increased productivity would have any measurable effect on plant biomass. If we could measure herbivore productivity, then good weather for plant productivity might be detectable in terms of improved animal productivity.

For hardy species like Red Deer and Soay Sheep we would not necessarily expect any direct negative impacts of “bad weather” on animal performance. Extreme heat loss during winter, and protracted periods during which shelter takes precedence over foraging, would be taken in their stride by animals in good condition. In a food-limited system, however, there are likely to be years in which the unfavourable season leads to more or less severe starvation and loss of body condition (e.g. in years when high population density coincides with low food availability). Under these circumstances, direct weather effects may increase the death rate of the oldest and the youngest animals; the animals cannot forage effectively enough to prevent a chronic loss of body condition and eventual death.

In most years, however, these direct negative effects of weather on animal performance are likely to be less important than indirect effects of weather acting on the animals’ food supply. The most important components of this are likely to be the date of the onset of grass growth in spring, the availability of heat and water during the rapid growth phase, and the date of the end of grass growth in autumn. The regular seasonal ups and downs of plant biomass will be tuned by weather conditions, such that the size of the standing crop biomass at the onset of winter and the quality of that forage (particularly its nitrogen-content and digestibility) will determine the likely fate of the herbivores over the next 6 months. Whether or not this food supply will be sufficient is dependent largely on the number of animals at the start of winter: the negative impacts of food shortage on herbivore demography are almost certain to be density-dependent (essentially scramble competition for a diminishing stock of forage until grass growth starts again in spring). Because
plant physiological processes are all strongly temperature dependent, we can be confident that temperature will have important effects on food production. Even in environments where rainfall is as high as it is in the Outer Hebrides and Inner Hebrides, soil moisture levels in summer can be low enough to restrict primary productivity.

The principal method adopted in this thesis involves “critical windows”. The question is when a particular weather variable has its principal effects: when does the effect begin and how long does it last. This involves simple, but computationally intensive statistical analysis. I take a variety of temperature thresholds, and for each one, try a wide range of start dates and end dates, computing the explanatory power of each combination of parameters. I take the combination that maximizes the explanatory power of the variable in question. These thresholds and windows are then used in models combining multiple weather variables; these models are then simplified to discover the minimal adequate model for each response variable (be this animal demography, plant biomass or plant productivity).

In order to use the full span of data available from Rum and St Kilda, it was necessary to reconstruct daily weather data using the nearest suitable surrogate station for which daily data were available. For Rum, this turned out to be Tiree and for St Kilda, Stornoway. I used Generalized Additive Models to predict daily maximum and minimum temperatures, daily rainfall and daily run of wind. Weather data from St Kilda since 1999 were available for calibration, and these regression models were used to predict daily weather from 1954 onwards. A single data set containing the reconstructed and actual weather data was then used in statistical modeling to discover the relationship between weather and demography for the Soay Sheep on St Kilda and between weather and plant production in temporary herbivore exclosures on Rum.

6.1. Reconstructing weather data

A new approach to interpolating weather data from local weather stations and gridded observations is introduced and evaluated. I describe the interpolation
procedure used for reconstructing the daily weather time series for the islands of St. Kilda and Rum, Scotland. For each of the climatic variables, the choice of model is based on verification statistics and by comparing the observed values with the estimated values at each point. This gives a measure of fit of the method at predicting values when using a proxy station for calibration. The resulting time series provide estimates of seasonal variability as well as year-to-year variability. In both islands, the weather trends observed were in the same direction. There is no significant change in precipitation regimes for either island; however, both Rum and St. Kilda are becoming warmer and less windy, with stronger trends occurring in Rum, with an increase in temperature by at least 1.5°C and a decrease in wind speed by at least 1.88 ms⁻¹ over 47 years. In St. Kilda there was an increase in temperature by at least 0.9°C and a decrease in wind speed by at least 1.65 ms⁻¹ over 55 years. With this knowledge, we might be able to pinpoint the specific drivers for the observed changes in the dynamics and performance of animal populations and plant communities on both islands.

6.2. Weather and grass growth at Park Grass Rothamsted

Future climate is forecasted to include greater precipitation variability and more frequent heat waves, but the degree to which the timing of climate variability impacts ecosystems is uncertain. I examined the seasonal impacts of climate variability on 130 years of grass productivity at the Park Grass Experiment, in the South of England, focusing on the question of when precisely is weather most critical for yield. First, I estimate the relationship between weather and yields over a period of 130 years by splitting this period into sub periods and found that weather impacts change over time. I found that spring rainfall affects the sward productivity throughout the growing season, with a carry-over effect on to autumn yield. For both yields, spring rain and temperature are critical. Second, I explore both linear and non-linear impacts of weather on yield, finding non-linear relationships of temperature and rainfall on yield. The slope of the decline above an optimum is
significantly steeper than the incline below it. If these patterns are general across ecosystems, predictions of ecosystem response to climate change will have to account not only the magnitude of climate variability but also for its timing.

### 6.3. Weather and Soay Sheep on St Kilda

Weather can influence animal herbivore population performance and dynamics directly via effects on organism vital rates and mortality through energetic costs on thermoregulation, and indirectly via effects on interaction with resources’ quantity and quality. This potential complexity is rendered more tractable for Soay sheep (*Ovis aries*) on St. Kilda, where predators and obvious competitors are absent and disease is seldom detected as a cause of mortality.

The results suggest that most of the weather effects on male and female condition are strongly felt indirectly through variation in plant growth conditions in different seasons. At age 2, a sheep’s weight is affected only by density dependence (most likely availability of food) and not directly by weather at all. For the most part, mild winter weather seems to increase August weight, most likely through early onset of vegetation growth. Individuals of different age will exhibit differing performance due to differing ability to cope with environmental stochasticity; amount of variation in demography and how the environment changes over time. Summer temperature and precipitation affect vegetation quality and quantity, which in turn affect the amount of reserves accumulated by lambs during summer, and their ability to survive the winter.

I conclude that density-dependent processes and density-independent climatic variables work in tandem to drive the dynamics of fluctuating populations. My findings also support the growing realization that the interaction between climatic variables and density-dependent factors may be a widespread phenomenon.
6.4. Weather and plant production on Rum

Identifying the critical time window during which climatic drivers affect the expression of phenological, behavioural, and demographic traits is crucial for predicting the impact of climate change on trait and population dynamics. Using long-term data sets for both red deer (*Cervus elaphus*) and vegetation in Rum, I illustrate that the climatic window identified by the sliding window method explains most of the phenological variation in deer traits and vegetation productivity. The results suggest that most of the weather effects on male and female phenology traits and condition are strongly felt indirectly through variation in plant growth conditions in different seasons, reflecting differences in the period in which physiological constraints limit the onset of the breeding cycle between the sexes. My findings suggest that the deer condition in the summer prior and autumn of conception have significant effects on parturition date.

Deer density and mid August to mid September precipitation, have a negative effect on calf survival through first birthday. So it is the condition they are in as they enter winter that defines their probability of survival (rather than the severity of the winter itself).

What is most interesting is that the critical periods affecting plant growth are not necessarily those acting immediately before the event, but rather an integration of weather conditions over the months before. For example, in November, productivity is affected by how warm the previous winter was and on how much rain fell in May July. This idea of an optimum could potential have implications with future climate change scenarios.

My results indicate that changes in the timing of precipitation and warming are important drivers in the grassland community in Rum for both plants and red deer. This evidence suggests that climate variation play an important role in the population dynamics of red deer in Rum through food availability and their condition entering winter, but red deer are not affecting plant productivity in the island.
6.5. Caveats and implications for future work

Overall, my results show that the statistical signatures of weather effects on herbivore performance and sward production are strong but different. There is statistical evidence that weather plays a role in explaining the different demographic processes and the timing of life-cycle components.

The hazards of over-fitting when using many weather variables and many time windows is arguable (Knape & de Valpine 2010), but increasing the number of covariates increases the chance of including the relevant variables. My ruthless model simplification means that marginally significant parameters are left out and I am acutely aware of the possibility of over-interpretation in observational studies such as these.

All three-population chapters have revealed that species and populations react to fluctuations of climate and weather through an intricate interplay between demographic traits and combinations of environmental factors. So predicting the response of a population to weather change requires detailed data on population structure or individual based data. This has generated the idea that “the devil is in the details” for understanding populations change (Coulson & Clutton-Brock 2002, Benton Plaistow & Coulson 2006), implying that extensive data and background knowledge is necessary to resolve the mechanisms by which changes in weather and climate lead to changes in population size.

Populations strongly affected by weather are less accurately forecast (Hastings et al. 1993) and less manageable from the standpoints of conservation biology (Ginzburg et al. 1990, Stacey & Taper 1992, Allen et al. 1993) and pest management (Berryman 1991a, Turchin 1991).

Winter is considered the energetic bottleneck for many ungulates in northern latitudes and studies of climate related effects on ungulate demography have frequently emphasized the importance of severity of winter (Post & Stenseth 1998, Coulson et al. 2001, Garrot et al. 2003). What I did find though was that summer weather was the main contributor for lamb/calf survival.

Evidence from these chapters suggests that variation in summer climate, hypothesized to operate through its effects on plant phenology and
summer nutrition, have demographic consequences. During summer, female ungulates in northern climates have high daily metabolisable energy requirements in relation to lactation and recovering from previous winter weight loss (Cook et al. 2004).

In short, the work presented here reinforces the view that direct weather effects on wild, food-limited ungulates are likely to be less prevalent, and probably less important, than indirect effects of weather acting on the food supply. From Park Grass we learn the weather that maximises grass growth (wet spring following an early start to the growing season) and that early season productivity can have carry-over effects on late season growth. From Rum and St Kilda we learn that “killing weather” in winter is not the principal driving force of fluctuations in animal populations, but more likely a subtle interplay of animal population density, age and size structure, interacting with weather effects on plant growth and the duration of the growing season. It looks as though dry summer weather can reduce food production in some years, despite the very high total average annual rainfall typically experienced in these Hebridean Islands.
Appendix A Evapotranspiration calculations

This approach for calculating evapotranspiration is a function of weather data, mostly, with some assumptions made about the crop. There is some uncertainty due to variations in plant density, leaf area and water availability. This method may prove to be valuable for filling in gaps in time series where the parameters for the Penman equation are not available, or for areas not covered by remote sensing.

This method only requires daily measurements of maximum and minimum temperature (°C) and wind speed (m/s) to estimate the parameters in the Penman equation to calculate evapotranspiration. This is the Penman equation:

\[
ET_{sz} = \frac{0.408 \Delta (R_n - G) + \gamma \frac{C_n}{T + 273.15} u_z (e_s - e_a)}{\Delta + \gamma (1 + C_a u_z)}
\]

where:
- \( ET_{sz} \) = standardized reference crop evapotranspiration for short crop (mm/day),
- \( R_n \) = calculated net radiation at the crop surface (MJ/m²/day for daily time steps),
- \( G \) = soil heat flux density at the soil surface (MJ/m²/day),
- \( T \) = mean daily or hourly air temperature at 1.5 height (°C),
- \( \Delta \) = psychrometric constant (kPa/°C),
- \( e_s \) = saturated vapor pressure (kPa),
- \( e_a \) = actual vapor pressure (kPa),
- \( C_n \) = constant (kPa/°C),
- \( C_a \) = constant (kPa/°C),
- \( u_z \) = wind speed at a reference height (m/s)
\( u_z \) = mean daily or hourly wind speed at 2-m height (m s\(^{-1}\)),

\( e_s \) = saturation vapor pressure at 1.5 m height (kPa), calculated for daily time steps as the average of saturation vapour pressure at maximum and minimum air temperature,

\( e_a \) = mean actual vapor pressure at 1.5 m height (kPa),

\( \Delta \) = slope of the saturation vapour pressure-temperature curve (kPa/°C),

\( \gamma \) = psychrometric constant (kPa/°C),

\( C_N \) = numerator constant that changes with reference type (K mm s\(^3\)/Mg/day)

\( C_d \) = denominator constant that changes with reference type

Units for the 0.408 coefficient are m\(^2\) mm/MJ.

Soil and plant parameters were taken from general tables provided in FAO-56 (Allen et al. 2005), specifically for Rum’s geographic location and with the following approximations:

The albedo, \( \alpha \approx 0.23 \);

The mean actual vapour pressure, \( e_a \approx 0.6108 \exp\left( \frac{17.27 T_{\text{min}}}{T_{\text{min}}+257.3} \right) \) kPa;

Soil heat flux density \( G \approx 0 \) MJ/m\(^2\)/day;

The numerator constant \( C_N \approx 37 \) Kmm s\(^3\)/Mg/day, since we assume short reference vegetation height crop 0.12m.

The denominator constant \( C_d \approx \begin{cases} 0.24 \text{ Kmm s}^3/\text{Mg/day}, & R_N > 0 \ , \\ 0.96 \text{ Kmm s}^3/\text{Mg/day}, & R_N \leq 0 \end{cases} \)
The incoming solar radiation \( R_S \approx k_{RS} \sqrt{(T_{\text{max}} - T_{\text{min}})} R_e \) MJ/m\(^2\)/day, where \( R_e \) is the extraterrestrial ET radiation.

The calculated evapotranspiration follows the expected annual cycle. The procedure has been validated in chapter 3 where the data are available for the use of the full Penman equation. Because this method is based on certain assumptions the data are less scattered than in reality.

Details of the calculations:
\[ C_N = 37 \]
\[ C_d = 0.24 \text{ if } R_{\text{d}} > 0, \text{ else } 0.96 \]
G = 0 for daily time-steps
\[ e_a = \frac{e^a(T_{\text{max}}) + e^a(T_{\text{min}})}{2} \]
\[ \Delta = \frac{2503 \exp \left( \frac{17.27 T}{T + 237.3} \right)}{(T + 237.3)^2} \]
\[ \gamma = 0.00065P \]
\[ P = 101.3 \left( \frac{293 - 0.00065Z}{293} \right)^{5.26}, \text{ where } Z \text{ is elevation} \]
\[ R_N = R_{NS} - \alpha R_{NL} \]
\[ R_{NL} = \delta fcd(0.34 - 0.14 \sqrt{e_a \left[ \frac{T_{\text{max}} + T_{\text{min}}}{2} \right]}) \]
\[ \delta = \text{Stefan – Boltzman} = 4.901 \times 10^{-8} \text{MJK}^{-4} \text{m}^{-2} \text{d}^{-1} \]
\[ fcd = 1.35 \frac{R_s}{R_{so}} - 0.35, \text{ where } fcd \text{ is cloudiness function } 0.05 < fcd < 1 \]
\[ R_{se} = (0.75 + 2.10^{-5}Z)R_e \]
\[ R_e = \frac{24}{\pi} G_{sc} + \sin \rho + \cos \rho, \text{ where } \rho \text{ is latitude radian} \]
\[ G_{sc} = 4.92 \text{ MJm}^{-2} \text{h}^{-1} \]
References


Coulson T, Hudson E.J. (2003) When is the birth rate the key factor associated with population dynamics? In: Reproductive Science and
References


