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DAVIS, MIRANDA,LYNN

How to cite:

DAVIS, MIRANDA,LYNN (2013) *Projecting the impact of climate change on ungulate population dynamics: the importance of trophic interactions*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/8513/

Projecting the impact of climate change on ungulate population dynamics: the importance of trophic interactions

By

Miranda Lynn Davis

School of Biological and Biomedical Sciences

Durham University

2013

Submitted for the degree of Doctor of Philosophy

Abstract

Many projections of climate change impacts on ecological communities do not consider population dynamics or trophic interactions in species responses to climate. Therefore, they do not produce the estimates of population growth needed by wildlife managers. As herbivores, roe deer (*Capreolus capreolus*) are clearly affected by climate and by interactions with other trophic levels. They are dependent on vegetation for food and subject to predation by multiple species. Consequently, long-term datasets on this ungulate provide the opportunity to explore the importance of trophic interactions while estimating how population dynamics respond to changing climatic conditions.

I used the relationship between temporal variation in climate and an index of net primary productivity to project increases in vegetation production for three study sites under future climate scenarios. Analyses of annual variation in the survival and reproductive rates of roe deer at two sites in Sweden demonstrated the importance of indirect effects of climate via changes in vegetation, in addition to the effects of predation and harvest on roe deer demography. Roe deer population growth in response to climate change was estimated using models incorporating both vegetation changes and vital rates into mechanistic simulations. These simulations highlighted the potential for climate change to increase deer population growth and for an increase in harvest and predation to reduce that growth. However, the uncertainty surrounding each level of these analyses was high. Additionally, an investigation of the factors affecting predation of roe deer by the wolf (*Canis lupus*) identified additional ecological complexities and sources of uncertainty that warrant consideration. This pervasive uncertainty indicates a need for cautious interpretation of results in this thesis, but also provides insight into priorities for future research. Collectively, these analyses demonstrate the theoretical and management value of taking a holistic and demographically explicit approach to estimating species responses to climate change.

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Acknowledgements

Many thanks to my supervisors, Phil Stephens and Steve Willis, for discussions and feedback on analyses and chapter drafts throughout this process. Special thanks to my external supervisor, Petter Kjellander, for allowing me to work with hard-won data, providing insights in roe deer ecology, and for being a wonderful mentor. Similarly, I am very grateful to Marco Apollonio and to Henrik Andrén for welcoming me into their research groups. I would like to thank everyone who has worked so hard over the years collecting the data used in this study. I am grateful to the many people who have provided advice which ultimately made this project possible: Ralf Ohlemuller, Shane Richards, Bob Baxter, Steve Hancock, Elena Bassi, Andrea Marcon, Nathalie Pettorelli, Stefan Fronzek, Martin DeKauwe, Mat Williams, Richard Essery, and Andrew Challinor. Thanks to the Durham University Doctoral Fellowship for financial support.

Thanks to the all the past and present members of the Durham University Adaptation and Environment Group for providing insightful discussions on many topics both in and out of the office (did someone say “Vic-at-Six”?)! In particular, I would like to thank Tom Mason, George Palmer, Naiara O’Mahoney, Christine Howard, Andy Lloyd, Ellie Devenish-Nelsen, Steve Hancock, Chantelle Kerr, and Julia Birchall for countless coffee breaks, late nights, weekend walks, and home-cooked meals; our friendships made me at home throughout my time in Durham. To the newest members of Lab 13, thank you for sharing in laughs and chocolate binges when I needed them most.

Thanks to all my family and friends for shaping my life in so many ways. To my friends, thanks for reminding me of life outside of work and for letting me know that I can be at home wherever I go. I am infinitely grateful to Mom and Dad, for their unwavering encouragement, patience and understanding. To Julia and Ganesh, thanks for offering me a home away from home. To my grandparents, thanks for being there and for consistently reminding me of all that I have to be thankful for. To my sister, Mary, thanks for never letting the distance get in the way. Finally, to my husband, Robi, thank you for so much, but most of all for sticking by me through everything and for giving me the strength to see it all through. Without you this would not have been possible!

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Chapter 1 – General introduction

Introduction

This thesis focuses on describing the role of climate and trophic interactions in the population dynamics of a widespread European ungulate, the roe deer (*Capreolus capreolus*). In this introductory chapter, I begin by explaining the need for models of wildlife population dynamics in response to climate change. I also briefly introduce the European ungulate community, including roe deer, as a relatively well-monitored ecological system that is well-suited to studies of trophic interactions and their role in population dynamics. I then describe global climate change and the expected consequences for ecological communities. This section focuses on the utility and limitations of the species distributions models often used to project species range shifts. I also describe the uncertainties involved in all climate impact research and discuss how they can be considered in statistical analyses. I move on to discuss the need for predictive models of population growth for use in wildlife management. In particular, this section highlights why many current studies of climate and population dynamics do not provide the information needed by wildlife managers. Next, I summarise the potential drivers of population dynamics, and consider the importance of the interactions which take place across trophic levels. I explain the potential effects of climate on populations and how these effects may interact with both bottom-up and top-down trophic interactions to determine the response of wildlife populations to climate change. Following these more general sections, I introduce the European ungulate community and my focal species, the roe deer. I discuss the status of ungulate populations in Europe and briefly review current knowledge of their ecology as it relates to the scope of this thesis. I summarise the relevant aspects of roe deer population dynamics with a focus on research to date regarding the role of climate and trophic interactions in roe deer ecology. The penultimate section introduces the three study sites that I focus on in this thesis. Finally, I provide a general thesis outline with a brief description of each chapter’s contents.

Background

The impacts of global climate change are difficult to overestimate. Recent climatic changes have been associated with a range of ecological changes including, but not limited to, geographic range shifts (Parmesan and Yohe 2003), global increases in primary production (Nemani et al. 2003) and phenological mismatches between consumers and their resources (Carey 2009). Climate change impacts are expected to permeate all levels of ecological organization (e.g. individual – population – community – ecosystem) with potentially devastating effects for global biodiversity (Bellard et al. 2012). One of the best-studied consequences of climate change is its potential to cause shifts in the geographic range of species, thereby placing some species at risk of extinction and altering the composition of ecological communities (Hill et al. 2002, Thomas et al. 2004, Huntley et al. 2008, Willis et al. 2009a). While a very valuable first step, these studies provide an incomplete picture of how wildlife distributions will be affected by changes in climate. A number of authors (Barnard and Thuiller 2008, Van der Putten et al. 2010, Walther 2010, Pagel and Schurr 2012) have pointed out that the species distribution models used to create projections of responses to climate change usually assume that species are in equilibrium with their environment, thus overlooking the role of population dynamics and trophic interactions (but see Parmesan 2006, Huntley et al. 2010, Traill et al. 2010 for reviews and exceptions).

Because wildlife managers rely on estimates of population abundance and growth to make adaptive management decisions (Walters 1986, Mills 2007), the omission of population dynamics and non-climatic factors from many studies of climate impacts can limit the practical utility of their results. So, why have the responses of population growth to climate change not been addressed more thoroughly? There are at least two inter-related answers to this question.

Firstly, the dynamics of wildlife populations are complicated, and, therefore, it is a substantial challenge to build accurate models of population growth in response to climate. Population growth is an amalgamation of many non-independent processes including those associated with survival and reproduction (Caswell 2001). Variation in the vital rates that determine population growth can be driven by environmental factors including climatic conditions and interactions among trophic levels, which may be influenced by climate in turn (Gaillard et al. 2000b, Pettorelli et al. 2007, Grande et al. 2009, Owen-Smith 2010, Webb et al. 2012). These effects could be direct; for example, increased heat stress could drive high mortality (Roth et al. 2012, Sherley et al. 2012). However, many of the impacts of climate change on vital rates are likely to be indirect, through changes in food availability or through interactions with other species which have been affected (Zarnetske et al. 2012). For example, the observed increases in the productivity of vegetation (Nemani et al. 2003, Slayback et al. 2003, Boisvenue and Running 2006) could have extensive knock-on effects for herbivores and their predators because plants provide habitat and food resources for so many animals (Martin and Maron 2012). Additionally, several non-climatic factors (e.g. predation and hunting by humans) influence population dynamics and these factors are changing at the same time as climate. The effects of climate change might be mitigated by mortality due to these other climate-independent factors which could stabilise population dynamics (Wilmers et al. 2007a, Zarnetske et al. 2012). For models of population dynamics to be realistic, provide accurate estimates of population growth under a changing climate and inform mitigation plans, they will need to encompass this complexity and incorporate a wide range of climatic and non-climatic drivers.

Secondly, a thorough understanding of population dynamics requires a large volume of high quality data (Caswell 2001, Dinsmore and Johnson 2005, Purves et al. 2013). The limited data available for many species have likely inhibited the development of complex population models. To estimate the temporal relationships between vital rates and their drivers, the datasets analysed must encompass variation in both. In the past, the use of large herbivore populations in demographic studies was limited by a need for data spanning many years (Gaillard et al. 1998a); today, there are numerous long-term studies of herbivore populations which have made large contributions to the field of population dynamics (Gaillard et al. 1998a, Owen-Smith 2010). However, to incorporate the variety of factors needed to produce accurate estimates of population growth, long-term data is needed across multiple trophic levels (Berteaux et al. 2006). In many systems, the data available are insufficient and this has meant that management decisions are based on an incomplete understanding of wildlife populations (Dinsmore and Johnson 2005).

In light of these challenges, temperate ungulate populations have several attributes that make them well-suited to studies of population growth in response to climate change. Large ungulates are widespread throughout much of the northern hemisphere where their populations are monitored due to societal interest in their management. Many are economically valuable game animals yet are considered pests in areas where they are especially abundant (McShea et al. 1997, Cederlund et al. 1998, Gordon et al. 2004, Apollonio et al. 2010). As a result, some temperate ungulate populations have been monitored for decades; their dynamics have been the subject of much study and are relatively well understood (Gaillard et al. 2000b, Owen-Smith 2010). Because they are primarily herbivores, they are directly dependent on vegetation with the result that their populations are likely to show an indirect response to climate change through climate-driven changes in vegetation. Additionally, ungulates are affected by top-down sources of mortality including harvest by humans (one of the primary methods of ungulate management; Apollonio 2010) and natural predation, where predators are present. This is especially pertinent in areas of Eurasia and North America where large predator populations have begun to recover after centuries of persecution (Swenson et al. 1995, Mech and Boitani 2003, Linnell et al. 2005, Beschta and Ripple 2009). Because temperate herbivore populations are generally well-monitored and their populations are clearly impacted by climate and trophic interactions, they present good model systems with which to investigate the direct and indirect effects of climate change on population dynamics.

In this thesis, I investigate the potential consequences of climate change for the population dynamics of a temperate ungulate, the roe deer (*Capreolus capreolus*), using data from three European study sites. The roe deer is the most numerous of European ungulates (Apollonio et al. 2010). The development of management plans for roe deer populations is of current interest due to its importance as a harvested species (according to one estimate there are over 2.5 million roe deer shot annually in Europe; Burbaite and Csanyi 2010) and due to uncertainty regarding the impacts of climate change and recovering predator populations (primarily those of the grey wolf, *Canis lupus*, and Eurasian lynx, *Lynx lynx*) (Aanes et al. 1998, Melis et al. 2009, Apollonio et al. 2010). By studying the effects of climate change on roe deer population dynamics, I aim to aid the future management of this ungulate and to gain insight into the interplay between climatic factors and trophic interactions in population ecology.

Global climate change and its ecological ramifications

Global climate change is likely to be an important driver of ecological change over this century. An increase in the atmospheric concentration of greenhouse gases (GHG; including CO_2 and CH_4 among others) that trap heat in the Earth's atmosphere appears to be driving global climatic changes, which are altering environmental conditions on the Earth's surface (Forster et al. 2007). Global mean temperatures rose by approximately 0.74 °C between 1900 and 2000 (Trenberth et al. 2007) and are likely to increase 2-6 °C further by 2100, as GHG concentrations continue to rise (Meehl et al. 2007). The pattern of warming varies spatially and seasonally and the greatest increases in temperature are expected at northern latitudes during the winter months (Fig. 1.1) (Meehl et al. 2007). Patterns of expected precipitation changes are more variable; in general, precipitation is expected to increase over much of the globe (by > 20% at most latitudes), but decreases in precipitation (by up to ~20%) are considered likely in Mediterranean and subtropical areas (Fig. 1.1) (Meehl et al. 2007). Along with these changes in temperature and precipitation, many other climatic changes are expected including alterations in patterns of air pressure (Gillett 2005), wind (Qiu 2012), cloud cover (Clement et al. 2009) and snow cover (Cess et al. 1991). Additionally, heightened climatic variability is expected to increase the frequency of extreme events, including heat waves (Meehl and Tebaldi 2004, Schar et al. 2004), heavy precipitation (Palmer and Ralsanen 2002), and strong winds (Young et al. 2011).

The potential impacts of expected climatic changes for the natural world are enormous (IPCC 2007a). It has been suggested that by 2050, under some scenarios of global climate change, extinction of 18-35% of species could occur (Thomas et al. 2004). However, there are many other ways that climate change will impact ecological systems. Shifts in spatial distributions have been documented or projected for a variety of taxa including plants (Keith et al. 2008), insects (Hill et al. 2002), reptiles and amphibians (Raxworthy et al. 2008), birds (Huntley et al. 2008), and mammals (Hughes et al. 2012). Increased drought frequency is expected to change the structure of avian communities in North America (Albright et al. 2010). Phenological mismatches between annual breeding cycles and the timing of food availability (usually the spring flush of vegetation) have been linked to declines in the reproductive performance of many species including birds (Both et al. 2006, Carey 2009) and ungulates

(Post and Forchhammer 2008, Gaillard et al. 2013). Animal behaviour could also be affected; for example, climate-driven changes in the primary productivity of aquatic systems are expected to reduce up-river migrations in Arctic Char (*Salvelinus alpinus*) populations (Finstad and Hein 2012). Nemani et al. (2003) estimate that global terrestrial primary productivity increased by 6% between 1982 and 1999 in response to climate change; a continued increase in vegetation productivity could have innumerable consequences for the animal communities which depend on vegetation for food. These examples outline a few of the ways that global climate change may influence ecological systems. It is important to consider that these effects are not independent. There is an urgent need for holistic approaches that consider the simultaneous effects of climate change on multiple aspects of ecological communities (Purves et al. 2013).

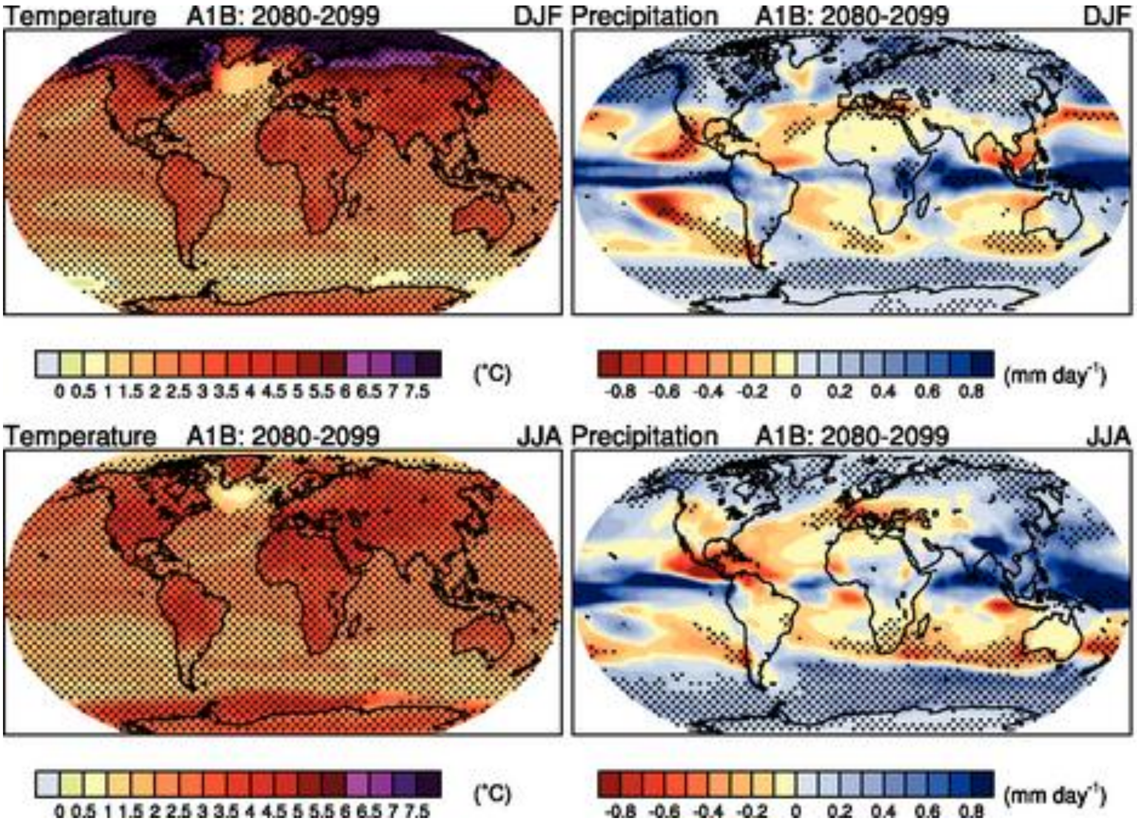

Fig. 1.1: The projected mean change in surface air temperature (°C, left) and precipitation (mm per day, right) are shown for the 2080-2099 period based on the SRES A1B scenario. The temperature and precipitation changes projected for boreal winter (including the December, January and February months, DJF) are shown in the top row while the changes projected for summer (including June, July, and August, JJA) are shown in the bottom row. Mean changes are calculated relative to the 1980-1990 period and represent multi-model averages (based on multiple atmospheric-oceanic global circulation models; see IPCC 2007b for more detail). Stippling marks areas where the inter-model standard deviation is smaller than the multi-model mean change. (Source: IPCC 2007b, Fig. 10.9).

Species distribution models

To date, bioclimatic envelope models have been the primary tool used to document and project the responses of species to climate change (Hill et al. 2002, Midgley et al. 2002, Huntley et al. 2004, Thomas et al. 2004, Thuiller et al. 2006, Hole et al. 2009, Thuiller et al. 2009). Knowledge of a species' current range is modelled as a direct response to current climate conditions and then used to project the potential future distribution of suitable habitat for that species given altered climatic conditions. Range projections based on this method have allowed not only the description of potential climate impacts for given species, but have also provided estimates of the future distributions of biological diversity (Jetz et al. 2007), the future effectiveness of protected area networks (Hole et al. 2009, Araujo et al. 2011, Bagchi et al. 2013) and identified key areas for future conservation (Carroll et al. 2010). However, the usefulness of bioclimatic envelope models has been debated for many reasons including their omission of interactions among trophic levels and population dynamics (Davis et al. 1998, Pearson and Dawson 2003, Beale et al. 2008).

Traditionally, the effects of intervening trophic levels (e.g. the distribution of biotic food resources) are not considered in species distribution models; however, the incorporation of land-use and vegetation distributions into such analyses is becoming more common (see Thuiller et al. 2006, Moore et al. 2007, Preston et al. 2008, Hughes et al. 2012 for some examples). This progress has been facilitated by the availability of land cover datasets (e.g. GlobCorine 2009 land cover dataset; © ESA 2010 and Université Catholique de Louvain) and of remotely-sensed global vegetation data such as the Normalized Difference Vegetation Index (NDVI). NDVI is a satellite-detected measure of the greenness of the Earth's surface, which is correlated with vegetation production (Tucker 1980, Running 1990, Field et al. 1995). NDVI has been successfully used to describe relationships between climate, vegetation, and animals in a variety of ecological systems (Pettorelli et al. 2005c). Additionally, dynamic global vegetation models (Foley et al. 1998, Bonan et al. 2003) have been developed which can be coupled to global climate models to simulate the responses of plants to climate changes in a more mechanistic manner (addressing processes such as plant growth, mortality and dispersal explicitly). Technological advances such as these make it easier for researchers studying the geographic distribution of consumer species to account for primary production as well as climate in their models. Nevertheless, as discussed further below, obtaining the data necessary to model multi-trophic responses to climate represents a substantial challenge for ecological researchers and has limited research in this area (Berteaux et al. 2006, Purves et al. 2013).

Historically, species distribution models have commonly made use of occupancy data (based on presence-absence records) and have not incorporated relative abundance, population trends, or dispersal ability of species (Shoo et al. 2005, Jarema et al. 2009, Huntley et al. 2010). Changes in range extent might be a conservative measure of climate change impacts because changes in abundance within that range are likely to take place at a faster rate (Shoo et al. 2005). Awareness of this issue is growing and a number of studies have modelled dispersal (Willis et al. 2009b, Anderson et al. 2012) or spatial variation in abundance or population growth (Shoo et al. 2005, Gregory et al. 2009, Jarema et al. 2009); however, these studies have stopped short of modelling population dynamics explicitly in response to climate (c.f. Jenouvrier et al. 2012). One of the current challenges for species distribution modelling is to integrate mechanistic models of temporal population dynamics into the geographic framework commonly used to examine species responses to environmental change (Huntley et al. 2010). A rapidly growing number of studies use such integrated models but the majority focus on plants (7 out of 9 known studies; c.f Anderson et al. 2009 on lagomorphs, and Fordham et al. 2012b on lizards) and they generally assume that the importance of drivers and the strength of the relationships with vital rates are the same across sites (Keith et al. 2008, Anderson et al. 2009, Lawson et al. 2010, Conlisk et al. 2012, Dullinger et al. 2012, Fordham et al. 2012a, Fordham et al. 2012b, Regan et al. 2012, Conlisk et al. 2013). Because the factors regulating populations can vary from one site to the next, often in response to environmental gradients (Melis et al. 2006, Hopcraft et al. 2010, Melis et al. 2010), it is useful to build models of population dynamics at varying sites. Such site-specific studies provide insight into where and when different drivers of population dynamics are most important for a given species.

Uncertainty in projections of climate change and its impacts

Modelling future climate change, and species responses to it, is fraught with uncertainty (Giorgi 2005). This uncertainty is, in part, due to the need to extrapolate beyond the range of observed climate conditions and to the inaccuracies in data on species’ distributions, abundances and their drivers. Projections of future climate are also based on assumptions about physical and chemical processes in the Earth's climate system, the future growth of human populations and the trajectory of technological development. Minimizing the uncertainty in projections, through the collection and use of high quality data, is instrumental to estimating species responses accurately. However, because removing all uncertainty from projections is impossible, it is important to recognise and account for existing sources wherever possible (Langford et al. 2011, Evans 2012).

One step towards accounting for uncertainty in projections of species responses to climate change is to consider different GHG emission scenarios. The IPCC Special Report on Emission Scenarios (SRES; Nakicenovic et al. 2000) outlined forty emissions scenarios (classed within four scenario families: A1, A2, B1, and B2) for use in modelling future climate changes (Figure 1.2) which provide a basis for comparison widely used in climate impact research (Ewert et al. 2005, Metzger et al. 2005, Scholze et al. 2006, IPCC 2007a, Ravenscroft et al. 2010). These "SRES" describe potential trajectories for future emissions of GHG and aerosols depending on the route of demographic, economic, social, environmental, and technological development of human society through 2100. Four of these scenarios (A1FI, A2, B1, and B2) encompass 68% of the total uncertainty in future GHG emissions as estimated by the SRES (Fig. 1.2; Nakicenovic et al. 2000, Mitchell et al. 2004). The B1 and B2 scenarios describe futures in which there is a reduction in the use of material resources and a focus on cleaner and more efficient energy production; they are generally associated with lower concentrations of CO_2 emissions and climate change than the A1 and A2 scenario families. The A2 scenario describes an alternate future in which continued economic development and ever increasing human population size results in high GHG emissions, which drive climate change. In the A1FI scenario future development depends heavily on the use of fossil fuels, thus, GHG emissions and climate change are generally very high (Nakicenovic et al. 2000).

Another way to account for uncertainty in projections of climate impacts is to use multiple general circulation models (GCMs) simultaneously. GCMs simulate the dynamics driving the Earth's climate. There are many different GCMs, which differ in their assumptions about the physical and chemical processes that drive climate. Ensembles of predictions, based on multiple GCMs, provide one approach to quantifying the uncertainty surrounding these assumptions (Araujo and New 2007, Thuiller et al. 2009); ensemble predictions are now used routinely in impact studies (e.g. Buisson et al. 2010, Garcia et al. 2012, Bagchi et al. 2013).

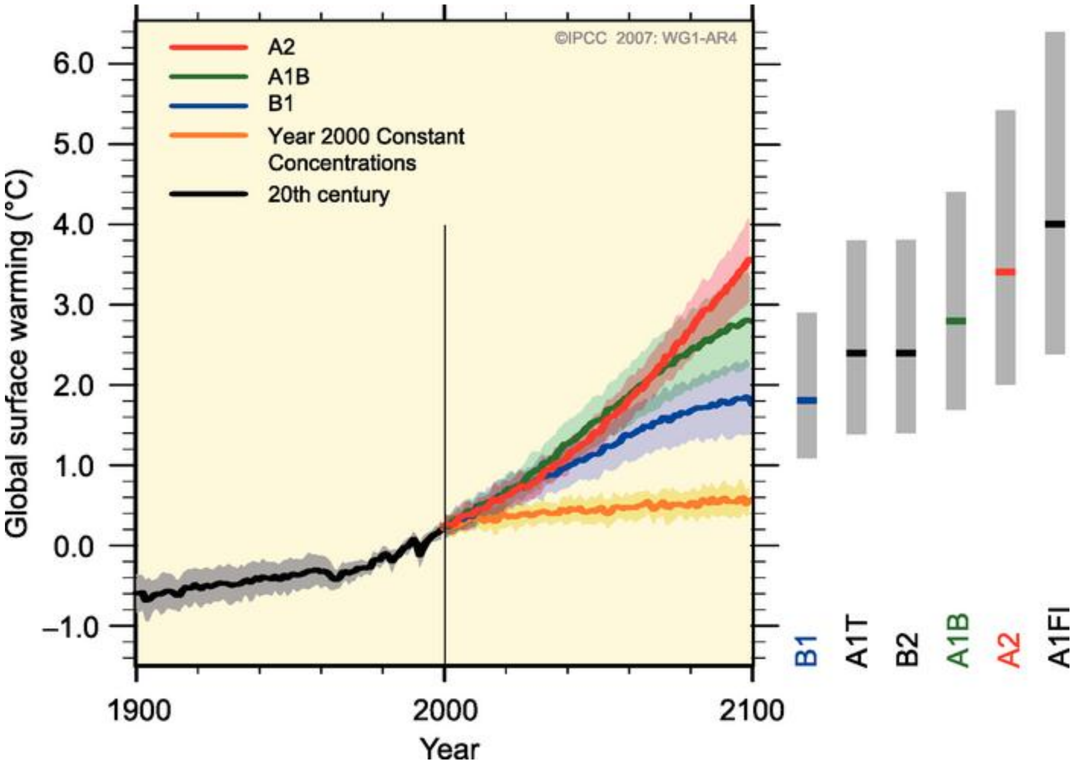

Figure 1.2: The observed global mean temperature for 1900-2000 and the projected global mean temperature associated with six SRES scenarios for 2000-2100. Values displayed as the estimated difference relative to the temperatures for the 1980-1999 period. Solid lines represent the multi-model average warming (based on multiple atmospheric-oceanic general circulation models, a.k.a. AOGCMs; see IPCC 2007b for more detail) while the shading represents the ±1 standard deviation range of annual averages from individual models. The orange line is not a scenario; it represents a continuation of the observed atmospheric concentration of greenhouse gases from the year 2000. The bars at the right illustrate the best estimate (solid line within each bar) and the likely (> 66% probability) range of temperature change by 2090-2099 for each scenario (assessed using multi-model averages of AOGCMs; see IPPC 2007b for more detail). (Source: IPCC 2007b, Fig. SPM.5)

The addition of population models to species distribution models is likely to introduce additional uncertainty, compounding the uncertainty in projections resulting from such integrated dynamic distribution models (McLoughlin and Messier 2004, Conlisk et al. 2013). The parameters in ecological models are estimated with error. This error can come from stochasticity in measures resulting from samples (sampling error) or from true underlying variation in the process(es) being modelled (process error); both sampling and process error will be incorporated into projections generated using these models (Dinsmore and Johnson 2005). A further source of uncertainty stems from the choice of predictors in the models, and this could potentially be quantified by using model averaging techniques (Whittingham et al. 2006). While individual studies will often address only a subset of these sources of variation, it is important to acknowledge the presence of additional uncertainties and interpret any projections of future population dynamics accordingly.

The management of wildlife populations for the future: predicting population growth

Wildlife populations are managed all over the world. The three most obvious reasons for management are: to increase population sizes, to decrease population sizes, and to maintain a stable population (Dinsmore and Johnson 2005). In all of these cases, managers generally want to know how large populations are, how populations are changing (whether they are currently increasing, decreasing or stable) and, perhaps most importantly, how the future size of populations can be manipulated. In order to manage wildlife populations to minimise the effects of climate change on ecological systems, managers need to be able to predict how climate and other expected environmental changes will impact the growth of their populations of interest (Boyce et al. 2006, Evans 2012). A great deal of research has investigated the role of climate in wildlife population dynamics, but at least three considerations can limit its utility for management targeted at dealing with the impacts of climate change; they are discussed in the three paragraphs that follow.

The first consideration pertains to the scale at which current projections of species distributions operate, regardless of whether they incorporate population dynamics explicitly. Projections of species responses to climate change are generally presented in the form of range shifts at relatively large geographic scales (i.e. continental or global). Given the global extent of expected changes this broad focus is necessary in order to coordinate global management responses. However, management decisions are often made by regional or local managers with respect to particular habitat patches (e.g. a stretch of forest or a lake) or wildlife populations (Mills 2007). To make these decisions managers need to anticipate changes at the spatial scales they work with and therefore large-scale projections might be of limited use without some indication of whether projected species' responses will apply in their sites of interest (Evans 2012). That the responses of populations to climate fluctuations can vary across populations even among areas with similar climates (Grotan 2007), challenges the small-scale relevance of distribution projections which assume relationships between vital rates and their drivers to be consistent among sites. To assess whether general projections are relevant for site-specific management, a better understanding of spatial variation in how populations respond to changes in climate is necessary.

The second consideration is the need for a thorough understanding of the mechanistic relationships between vital rates and their drivers in order to estimate and manipulate population growth in response to environmental variation (Gordon et al. 2004, Boyce et al. 2006). Many demographic studies model population growth as a function of observed stochastic variation in vital rates without including environmental drivers (Tuljapurkar 2010). For predictions to be accurate, models of climatic effects on vital rates must include all important variables and must realistically describe the relationships amongst those variables (Berteaux et al. 2006, Evans 2012). Omitting non-climatic effects or misrepresenting climatic effects as direct when they are not (thus omitting intermediate variables) can decrease model accuracy and utility. For example, the omission of the effect of management activities from a model, can limit the researcher’s ability to a) accurately measure the effect of climate across areas where variation in management confounds climatic effects and b) gain insight into how management might be used to mitigate climate impacts. As already discussed, most species distribution models used to project species’ range shifts omit trophic interactions and the effects of non-climatic variables; it has been demonstrated that these omissions can have a substantial effect on modelled outcomes (Conlisk et al. 2012, Conlisk et al. 2013). Similarly, many studies that model the effects of climate on population growth or vital rates at a smaller spatial scale use climate metrics directly (Forchhammer et al. 1998, Forchhammer et al. 2002, Wang et al. 2002, Grotan et al. 2008, Griffin et al. 2011) and infer indirect effects via vegetation without including vegetation data (see Post and Stenseth 1999 for an earlier discussion of this issue). In many cases, these omissions are likely due to lack of data on one or more important drivers and, therefore, may be difficult to rectify.

The third consideration pertains to how models are used and examined once they have been developed. Once an understanding of a vital rate’s drivers has been achieved, and a model has been developed, it must be used predictively for managers to be able to anticipate the effects of environmental changes (Boyce et al. 2006, Evans 2012); this is rarely attempted outside of large-scale spatial distribution modelling. For example, of the 396 studies producing matrix models of plant populations reviewed by Crone (2011), 85% calculated deterministic growth rates assuming that vital rates remained constant over time. Demographic studies often concentrate on identifying the key drivers of population dynamics using observed time-series from sites of interest without thoroughly examining or discussing the predictive ability of the models which were constructed (see Rasmussen et al. 2006 for an example of an exception to this). It is very rare for these studies to use developed models to project dynamics given climate change. For example, while ungulates are common subjects for studies of climate and population dynamics (Gaillard et al. 2000b, Owen-Smith 2010, Mysterud and Saether 2011), to my knowledge only one study has used models of vital rates to project the dynamics of an ungulate population given climate change (Wang et al. 2002). This gap can often be corrected through further analyses of existing data. One way to quantify the ability of models to estimate vital rates under a given set of driving conditions is to use cross-validation procedures that test if the models can accurately estimate the vital rates for subsets of the data that are left out of the model fitting process (Mac Nally 2000, Olden and Jackson 2000, Olden et al. 2002). Models which perform well can then be used to forecast future changes in vital rates, while also presenting measures of the uncertainty surrounding estimates.

The drivers of population dynamics

Within a species, population growth rates vary over space and time due to intrinsic density dependence (Nicholson 1954) and due to extrinsic “environmental” factors (Andrewartha and Birch 1954, Tuljapurkar 1990). The extrinsic impact of environmental variability is the primary focus of this thesis; however, environmental factors often interact with density to influence population growth, thus a consideration of density dependence is essential. The importance of density dependence is well documented, particularly for large mammalian herbivore populations (Fowler 1987, Bonenfant et al. 2009). Density often interacts with environmental factors (such as resource availability) to drive changes in herbivore body mass which affect vital rates such as fecundity, survival, and dispersal (Bonenfant et al. 2009, Owen-Smith 2010). There is a substantial literature describing the mathematical formulation of density dependence in animal population dynamics, including non-linear dynamics (Dennis and Taper 1994, McCullough 1999, Owen-Smith 2006, Coulson et al. 2008). However, estimating density dependence, especially in its more complex nonlinear forms, can be very difficult; this is especially the case with observational datasets that incorporate a large amount of sampling error (particularly in estimates of abundance) (Hassell 1986, Shenk and White 1995, Shenk et al. 1998, Fowler et al. 2006, Freckleton et al. 2006). While models of population dynamics would ideally consider multiple functional forms of density dependence, these difficulties often preclude such a thorough examination of its role in the case of small, observational datasets.

Extrinsic environmental drivers of population dynamics include direct effects of abiotic conditions and the effects of biotic interactions among species. Abiotic factors can include, but are not limited to, the influence of climate (Wang et al. 2002), pollution (Fischer et al. 2013), chemical nutrients (Binzer et al. 2012), or other types of disturbance such as fire (Lawson et al. 2010). Biotic interactions can take place within or across trophic levels and can be influenced by abiotic conditions. Interactions across trophic levels, or simply "trophic interactions", have long interested ecologists because of their importance in driving population dynamics and determining the structure of ecological communities (Power 1992; further discussion below). Interactions within a trophic level typically take the form of inter-species competition for shared resources (Lotka 1925, Volterra 1926, Gause 1934, Tilman 1982, Oksanen 1987) or apparent competition in which one prey species can influence another by affecting the response of a shared predator (Holt 1977, Chaneton and Bonsall 2000, Morris et al. 2004). In this thesis, I focus primarily on trophic interactions and I consider competitive interactions within a trophic level as secondary. There are two main reasons for this. Firstly, as just described, competitive interactions usually exert their influence on populations via the modification of trophic interactions (e.g. by limiting access to food); therefore, it seems necessary to describe interactions across trophic levels, before addressing inter-species competition. Secondly, it seems likely that many of the early effects of climate change on population dynamics will take place via bottom-up trophic interactions (described below).

That the importance of trophic interactions in ecological systems is widely acknowledged is demonstrated by the debate over the relative importance of "top-down" and "bottom-up" factors in population control (McNamara and Houston 1987, Wilson 1987, Terborgh 1988). Proponents of the "bottom-up" school of thought argue that populations and communities are regulated by the production of primary producers or the overall input of nutrients at the lowest trophic level (Wilson 1987). The top-down school of thought asserts that community dynamics are largely controlled by the upper trophic levels through "trophic cascades". In the most basic three-level trophic cascade, predators control prey populations (i.e. middle-level consumers) and, thus, allow the lowest trophic levels to exist without being completely exploited by middle-level consumers (Hairston et al. 1960, Terborgh 1988). While the relative importance of top-down vs. bottom-up forces remains a topic of much discussion (Bonsall et al. 1998, Miller et al. 2001, Ray et al. 2005, Terborgh et al. 2005, Estes et al. 2011), there is a general consensus that these forces act simultaneously to control populations (Hunter and Price 1992, Power 1992, Elmhagen and Rushton 2007). There has also been an assertion that bottom-up effects, namely effects of food resources, are commonly the primary factor regulating the growth of animal populations (Power 1992, Sinclair and Krebs 2002); top-down factors (e.g. predation), and social interactions within a species (e.g. territoriality which can lead to density dependence) can be thought of as secondary processes that override or modify bottom-up effects (Sinclair and Krebs 2002). This assertion is supported by an abundance of studies, which have found that the influence of predation on populations is dependent on the favourability of climate and vegetation conditions (Pace et al. 1999, Jedrzejewska et al. 2005, Melis et al. 2006, Elmhagen and Rushton 2007, Hopcraft et al. 2010).

The role of climate and trophic interactions in population dynamics

Direct effects of climate

Climate change has the potential to affect the demography of animal populations directly. It seems likely that many of the direct effects of climate will be related to thermoregulation. Extreme temperatures are likely to increase the costs of thermoregulation (Shrestha et al. 2012), which could have implications for mortality and reproductive rates. Some populations might experience heightened mortality due to rising temperatures, especially when there is a simultaneous decrease in precipitation, which could lead to water limitation (Wallach et al. 2007, Welbergen et al. 2008, du Plessis et al. 2012, Krockenberger et al. 2012). For species in northern areas, climate can also directly affect mortality rates, when increased snowfall increases the energy cost of mobility in winter (Parker et al. 1984). However, many of the impacts of climate on animal populations are likely to be indirect and be mediated via biotic interactions among species or trophic levels (McCarty 2001, Traill et al. 2010, Van der Putten et al. 2010, Mysterud and Saether 2011). A recent study of beaver (*Castor canadensis*) distributions found that most of the variation explained by climate could alternatively be attributed to “non-climatic variables” such as landscape and vegetation characteristics (Jarema et al. 2009). While this finding does not challenge the importance of climate, it does highlight the extent to which climatic effects may be indirect.

Effects of climate and bottom-up trophic interactions

One of the most obvious ways that climate is likely to impact animal populations indirectly is through bottom-up trophic interactions. Climate-driven changes at the level of the primary producer could have a strong influence on the first-order consumers that depend on them. Likewise, any changes in first-order consumers will probably have ramifications for second-order consumers. With respect to the dynamics of terrestrial wildlife populations, this means that climate-driven changes in vegetation are likely to influence the dynamics of herbivores and their predators.

Plant growth is directly related to climate; indeed, either temperature or water availability is the primary factor limiting vegetation growth over an estimated 73% of the Earth’s vegetative surface (the other 27% is thought to be limited by solar radiation; Nemani et al. 2003). Climate-driven changes in plant chemistry and plant community composition could affect the quality of forage available to herbivores (Kaarlejarvi et al. 2012). More broadly, changes in the timing and spatial distribution of vegetation production are particularly likely to have wide-ranging impacts on herbivore communities. The timing of the spring flush of vegetation is advancing throughout much of the Northern hemisphere (Zhang et al. 2004, Schwartz et al. 2006). Studies have documented both positive and negative effects of earlier spring onset on animal performance (measured in terms of body condition, vital rates, or abundance; e.g. Pettorelli et al. 2005b, Carey 2009, Gaillard et al. 2013). Changes in the amount of forage available to consumers seem particularly likely to have strong effects on herbivores and their predators. The geographic distributions of insects, birds, and mammals have all been related to net primary productivity (Bailey et al. 2004, Despland et al. 2004, Melis et al. 2006, Melis et al. 2009, St-Louis et al. 2009). While, Nemani et al. (2003) estimated an overall increase in net primary productivity (NPP), they also found that NPP decreased in some areas (approximately 7% of the global vegetated area, as opposed to 25% in which an upward trend was observed). It seems likely that continued increases in vegetation production could positively affect the vital rates and population growth of many consumers (and potentially their predators); simultaneously, animal populations could be negatively affected in areas where NPP declines.

Already, studies have implicated such bottom-up effects of climate on wildlife population dynamics (Forchhammer et al. 2002, Wang et al. 2002, Grotan et al. 2008, Gilg et al. 2009), but, as already discussed, few explicitly link climate to changes in vegetation and relate these effects on vegetation to changes in population growth. With the widespread availability of remotely-sensed vegetation metrics such as NDVI, it should now be possible to incorporate vegetation effects in analyses at many sites where long-term monitoring programs have not included vegetation. A number of demographic studies have already used NDVI successfully to explain variation in the performance of large herbivores in terms of vital rates, population growth or numbers (e. g. Melis et al. 2006, Rasmussen et al. 2006, Pettorelli et al. 2007). Other studies have investigated links between NDVI and variation in body mass (Pettorelli et al. 2006, Mysterud et al. 2007, Martinez-Jauregui et al. 2009). In large herbivore populations, body mass is often closely related to measures of survival and fecundity (Gaillard et al. 2000b); thus, variation in body mass can provide a great deal of insight into how herbivore populations are likely to respond to environmental conditions. However, without knowing the ultimate effect of changes in body mass on vital rates, it is not possible to use body mass to estimate changes in population growth. Therefore, I do not include these analyses when I refer to studies of demography or population dynamics in this thesis.

Effects of climate and top-down trophic interactions

Climatic variation can influence the effects of upper trophic levels on population dynamics; however, because top predators are absent from many systems and because of the complex feedback loops that develop among trophic levels, the effects of climate on top-down processes appear to be less well documented and less well understood. Shifts in the geographic range of predators could release prey species from predation pressure or expose them to additional sources of predation. For example, it has been suggested that rising temperatures might be causing red foxes (*Vulpes vulpes*) to spread northward and displace arctic foxes (*Alopex lagopus*)

(Hersteinsson and Macdonald 1992, Herfindal et al. 2010); the implications of these changes for prey species are unknown. Additionally, impacts of predators on prey can be modified by climate in ways that are not directly related to changes in predator abundance. The extent of snow cover can affect predator behaviour (e.g. snow depth is related to pack size in wolves; Post et al. 1999) and prey mobility (deep snow can impede ungulate escapes; Cederlund 1982, Cederlund and Lindström 1983) and, thus, influence predation rates (Hebblewhite 2005, Hegel et al. 2010a, Hegel et al. 2010b). It is also notable that herbivory rates can be affected by climatic conditions including temperature and snow cover (Roy et al. 2004, Torp et al. 2010). Changes in herbivore distributions caused by climate-related changes in predation could have important knock-on implications for primary producers because of the extensive impacts of herbivory on recruitment within plant populations (McShea et al. 1997, Partl et al. 2002, McShea et al. 2005, Beschta and Ripple 2009). Of course, changing climatic conditions might also have simultaneous and direct effects on primary producers (as described earlier). The potential for feedback loops to develop between top-down and bottom-up processes, which can both be affected by climate simultaneously, makes it challenging to tease apart the mechanisms behind climatic impacts on communities. While top-down processes are likely to be affected by climate change, describing such effects can be difficult in light of the more noticeable bottom-up effects of climate.

It is also possible that top-down forces could act independently of climate and either exacerbate or ameliorate the effects of climate change on ecological systems. Mortality due to predation can limit prey abundance (Paine 1966, Mech et al. 2003, Kalka et al. 2008) and, in some cases, increase the probability that prey become extinct (Schoener et al. 2001). Additionally, predator activities can create a “landscape of fear” and affect prey behaviour (Brown et al. 1999, Laundre 2010). Efforts to avoid predation risk may limit prey’s use of optimal habitat (Fortin et al. 2005, Crosmary et al. 2012, Vijayan et al. 2012), which could negatively affect individual fitness and population growth (Nelson et al. 2004). If consumer populations are negatively affected by climate, then predators could be yet one more factor placing stress on their populations. For example, the combination of harsh winters (characterized by heavy snowfall), low primary productivity, human harvest and lynx predation has been associated with declining roe deer populations in Norway (Melis et al. 2009). Alternatively, if climate-driven increases in vegetation lead to increases in consumer populations, predation could help mitigate that effect. Using theoretical models of prey dynamics, Wilmers et al. (2007a, 2007b) showed that fluctuations in prey populations resulting from climate-driven changes in productivity patterns can be dampened by predation. Similarly, a study from Isle Royale (Lake Superior, USA) found that the effect of climate on moose population growth was weaker when wolves were abundant (Wilmers et al. 2006).

Harvest by humans is a top-down source of mortality and could control consumer populations in response to climate change. Hunting is a common form of wildlife management, especially when populations of mammals or birds are considered overly abundant (Ankney 1996, Gordon et al. 2004, Rushton et al. 2006, Toigo et al. 2008, Miller et al. 2011). Harvests could be a particularly important way of mitigating climate change effects in areas where large predators are absent. However, harvests are not necessarily a substitute for the ecological effects of predation. Typically, the areas and times of year when humans hunt are regulated; therefore, the changes in prey behaviour that are caused by human hunting activities are unlikely to the same as those caused by natural predation (Kuijper 2011).

Identifying the role of predation in prey population dynamics can be difficult for two main reasons. Firstly, while predators are recovering in some areas of the world, top predators are still absent from many systems (Steneck et al. 2005). Secondly, the ultimate impact of predation on prey is influenced by many interrelated processes. For example, if predator numbers and the rate of capture per predator increase quickly as a function of prey abundance (i.e. predators show a strong numerical and functional response to prey), predation can have a much stronger negative effect on prey populations (see Messier 1994, Messier 1995 for field applications, and Gotelli 2001 for description of theoretical concepts). Prey selection can also be important. For example, cursorial predators, which prey disproportionately on the young, old, or sick individuals within a population, may have relatively low potential to limit population growth because they kill individuals likely to die anyway. Ambush predators are more likely to attack prime-age individuals and, therefore, are more likely to control fluctuations in prey abundance (Sinclair et al. 2003, Wilmers et al. 2007a). Predators may also select one prey species over others (e.g. Okarma 1995, Garrott et al. 2007); as a result, the variety of prey species available and their relative abundance can impact predation patterns. This complexity, in combination with the low densities at which large predators often exist, means that analyses of predation often involve small and noisy datasets. As such, analyses which simultaneously aim to address the effects of predation and climate change on ecological communities are likely to incorporate a large amount of uncertainty and must be approached with caution.

Ungulate populations in Europe

Throughout much of Europe, ungulates are widespread and abundant. Ungulates play a central role in European forests and, as such, there is a need to manage their populations in the face of environmental changes. Approximately 20 species of wild ungulates inhabit the continent and the geographic ranges of most of these species are expanding (Apollonio et al. 2010). Management of these populations is motivated by their economic value as game species and a desire to minimise their negative impacts on the environment (e.g. the inhibition of forest regeneration) and human society (e.g. crop damage and traffic accidents) (Groot Bruinderink and Hazebroek 1996, Cederlund et al. 1998, Geisser and Reyer 2004, Apollonio et al. 2010).

Recent rises in ungulate abundance have been attributed to a combination of factors including shifting human demography (from rural to urban areas) and a lack of natural predators (Saezroyuela and Telleria 1986, Harmer 1994, Rounsevell et al. 2006, Bolte et al. 2009, Apollonio et al. 2010). It is unknown whether these ungulate populations will continue to increase with climate change and the recovery of large predator populations. While many studies document climatic effects on European ungulates (discussed further below), there is a paucity of publications which project changes in these species' distributions with climate change (Mysterud and Saether 2011). The simultaneous recovery of European carnivore populations (grey wolf, *Canis lupus*, Eurasian lynx, *Lynx lynx*, and brown bear, *Ursus arctos*), after centuries of persecution (Swenson et al. 1995, Mech and Boitani 2003, Linnell et al. 2005, Breitenmoser et al. 2008, Basille et al. 2009), adds another, poorly-understood factor that will help to shape this rapidly changing system. Research to date suggests that both bottom-up (including effects of climate and vegetation-related food resources) and top-down forces (including effects of predation and human harvest) play important roles in the dynamics of European ungulate populations (Jedrzejewska et al. 2005, Melis et al. 2006, Melis et al. 2009). A thorough understanding of the response of ungulate populations to the expected changes in climatic, vegetation, and predation conditions is needed to underpin the future management of ungulates in Europe.

Bottom-up effects on European ungulates: climate and vegetation

Because European ungulates are primarily herbivorous, one of the most obvious ways in which climatic change is likely to impact their populations is through changes in vegetation-related food resources. Over the next century, temperatures in Europe are expected to rise more steeply than global temperatures, increasing by up to 5 °C under some scenarios (Christensen et al. 2007). The magnitude of temperature increases is expected to be greatest during the winter in north-eastern Europe (Fig. 1.3). Projections of precipitation changes are more variable across regions and seasons; in general, northern Europe is projected to experience increased precipitation while southern areas are likely to experience decreases (especially during the summer months; Fig. 1.3) (Giorgi et al. 2004, Raisanen et al. 2004, Rowell 2005). In northern Europe, these

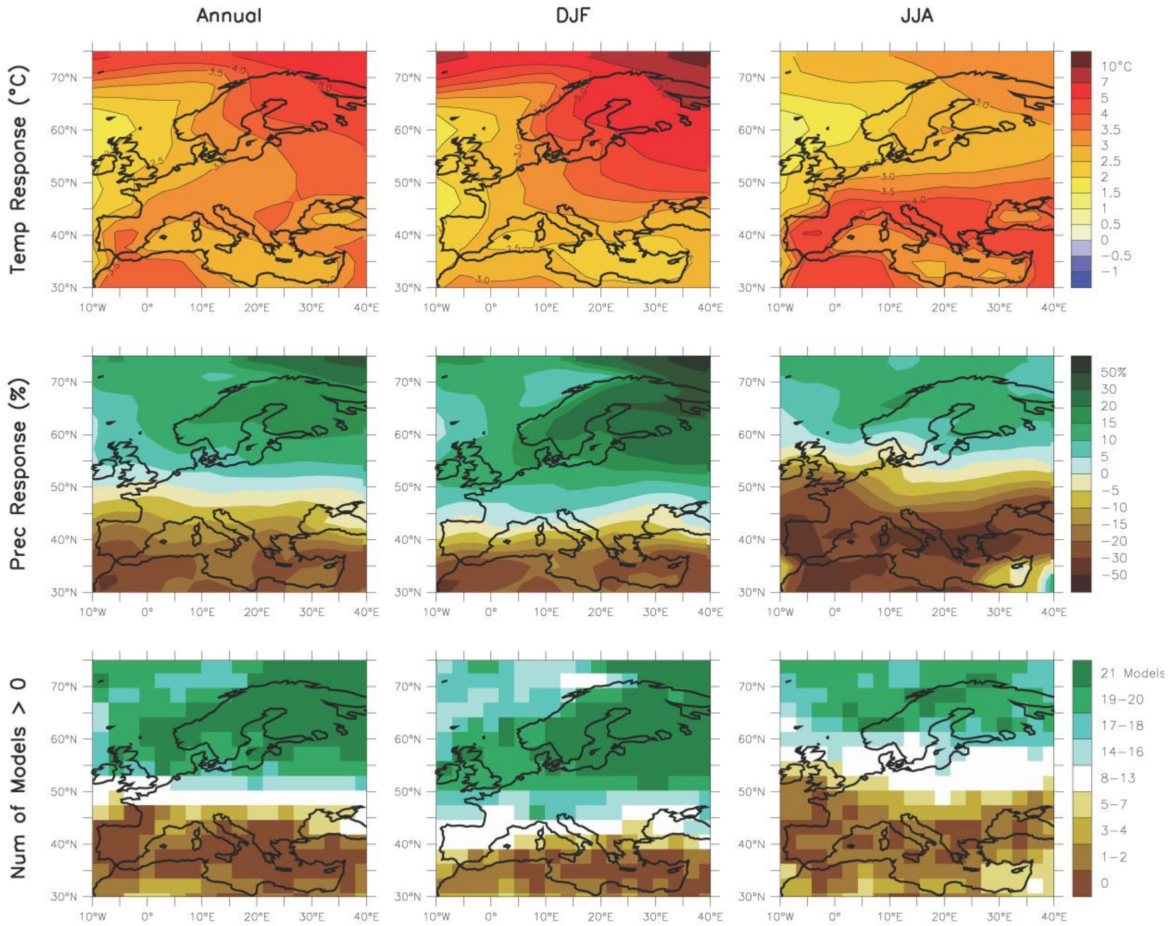

Figure 1.3: Simulated temperature and precipitation changes based on 21 climate models under the A1B SRES scenario. The top row shows the annual mean, December-January-February (DJF), and June-July-August (JJA), change in temperature between the 1980-1999 and 2080-2099 periods. The middle row shows the annual, DJF, and JJA mean percentage change in precipitation. The final row shows the number of models that predict precipitation increases for the indicated area and period. (Source: IPCC 2007b, Fig. 11.5)

changes are likely to translate into longer growing seasons and increased productivity, while in some areas of southern Europe, vegetation may be negatively affected by the increased heat and aridity (Boisvenue and Running 2006, Parmiggiani et al. 2006, Fronzek and Carter 2007, Penuelas et al. 2007). There is already evidence of an increase in vegetation production in northern Europe from 1982 to 1999 (based on NDVI; Slayback et al. 2003). The expected increase in productivity has led to suggestions that climate change will positively affect many already widespread ungulate populations (Melis et al. 2006, Melis et al. 2009, Apollonio et al. 2010). However, other populations, particularly those in water-limited areas or endemic to alpine habitats, seem likely to be negatively affected by warmer conditions (Apollonio et al. 2010, Mysterud and Saether 2011).

A substantial literature documents climatic and vegetation-related effects on a variety of ungulate species in European sites. This research has drawn attention to the importance of a detailed understanding of the system being studied (Clutton-Brock and Coulson 2002, Månsson and Lundberg 2006) due to differences among age groups (Coulson et al. 2001, Festa-Bianchet et al. 2003), sites (Grotan et al. 2008, Martinez-Jauregui et al. 2009), and species (Putnam et al. 1996, Post and Stenseth 1999, Pettorelli et al. 2007). Despite this variation, there are some effects of climate and vegetation that have been repeatedly identified as important. There has been an emphasis on the mixed effects of winter precipitation which operate indirectly by influencing the timing of the spring vegetation flush (e.g. Post and Stenseth 1999) or by reducing access to ground vegetation (e.g. Hansen et al. 2011). Winter precipitation has been associated with variation in the population size, home range size, body mass, and vital rates of numerous European ungulates including roe deer, wild boar (*Sus scrofa*), moose (*Alces alces*), ibex (*Capra ibex*), red deer (*Cervus elaphus*), soay sheep (*Ovis aries*), and reindeer (*Rangifer tarandus*) (Cederlund and Lindström 1983, Cederlund et al. 1991b, Okarma et al. 1995, Post and Stenseth 1999, Coulson et al. 2001, Mysterud and Ostbye 2006, Grotan et al. 2008, Mysterud et al. 2008, Hansen et al. 2011). A growing number of studies document direct (positive) relationships between vegetation production (often indexed using remotely-sensed measures such as NDVI) and ungulate population density (Melis et al. 2006, Melis et al. 2009), body mass (Pettorelli et al. 2006, Mysterud et al. 2008, Martinez-Jauregui et al. 2009) and vital rates (Pettorelli et al. 2007). Several analyses have highlighted potential mismatches between the timing of ungulate reproductive cycles (with births taking place in spring) and spring vegetation flushes (Post and Stenseth 1999, Loe et al. 2005, Pettorelli et al. 2007, Gaillard et al. 2013). Such analyses highlight the potential for climate change to have extensive bottom-up effects on European ungulates.

Top-down effects on European ungulates: predation and harvest

Seasonal harvests are the primary tool used to control ungulate abundance in Europe (Apollonio et al. 2010) and, as such, hunting is an important source of top-down mortality in many populations. However, in some cases hunting is no longer sufficient to control population growth. For example, the harvest necessary to prevent population growth of wild boar is often very large, sometimes greater than the pre-reproduction population size (Csanyi 1995, McIlroy 1995). In the population studied by Toigo et al. (2008), approximately 50% of the population was harvested annually and yet boar abundance continued to increase.

Wild carnivores could contribute to ungulate population control by providing an additional year-round source of top-down mortality. Predation, particularly by recovering populations of wolves and lynx, is an important cause of natural mortality in European ungulate communities (Okarma 1995, Okarma et al. 1997, Aanes et al. 1998). Many populations of these predators are relatively new and exist at low densities in a human dominated landscape. Predation on livestock and game species makes their abundance a controversial issue, yet there is also a desire to conserve these species and allow them to fulfil their ecological roles as top predators. Balancing these two concerns has led to active management of predators through culling or recreational hunting in some areas (Swenson et al. 1995, Chapron et al. 2003, Herfindal et al. 2005a, Andrén et al. 2006). A firm understanding of predation in Europe could support ungulate management and predator conservation efforts by identifying predator abundances that maintain ecological function and minimise conflict with humans.

In spite of the relatively poor understanding of these new predator populations, some indirect evidence shows that European predators have substantial effects on their prey. In an analysis of the potential impacts of predation by Eurasian lynx, grey wolf, brown bear and red fox (hereafter referred to as lynx, wolf, bear and fox respectively) on populations of roe deer and moose, Gervasi et al. (2011) found that lynx predation had the strongest effect on prey (increasing lynx predation by 50% reduced roe deer population growth by 8%); followed by wolves, then foxes, with bears having the least impact. Predation, primarily by wolves and lynx, accounts for over 50% of the natural mortality in roe deer populations in the Bialowieza Primeval Forest in Poland and numbers from other areas suggest that this is not unusual (Aanes et al. 1998, Jedrzejewska et al. 2005). While, foxes and bears are not typically considered predators of large herbivores, they can be a substantial source of mortality for neonates. Research at Swedish sites has found that fox and bear predation were responsible for the deaths of 24% of roe deer fawns (Liberg et al. 1993) and 26% of moose calves (Swenson et al. 2007), respectively. Roe deer and wild boar populations are negatively associated with predator numbers, but the strength of this relationship appears to be dependent on climate and environmental productivity (Jedrzejewska et al. 2005, Melis et al. 2006, Melis et al. 2009). It has been shown repeatedly that predation can increase during snowy winter conditions (Cederlund and Lindström 1983, Okarma 1995, Nilsen et al. 2009b). This complexity could make it particularly challenging to estimate the effects of climate change on ungulate populations in sites where predators are present.

Roe deer population dynamics and their drivers

Roe deer, once extirpated from much of Europe due to over-hunting, are now the most numerous of European ungulates (Danilkin 1996, Lovari et al. 2008). The range of this species has expanded greatly over the past century and is expected to increase further, presenting challenges for managers as they balance the wishes of hunters and other public groups (e.g. farmers) (Cederlund et al. 1998, Linnell et al. 1998a). The roe deer is a useful species for studies of climate effects on ungulates because the complexities of roe deer population dynamics are representative of other temperate ungulate populations. As with other European ungulates, roe deer populations are likely to be strongly affected by the bottom-up effects of climate via vegetation and the top-down effects of predation and harvest-related mortality (e.g. Jedrzejewska et al. 2005, Melis et al. 2009; more detail below). Also, like many large herbivores (Gaillard et al. 1998a, Gaillard et al. 2000b), roe deer have age-structured population dynamics with vital rates influenced by an interaction between resource availability and population density (Gaillard et al. 1998b). Roe deer survival is lowest and most variable among fawns (generally defined as individuals < 1 year old) and highest and least variable among adults (approximately 2 to 7 years old) (e.g. Gaillard et al. 1993). Similarly, the reproductive rates of subadult roe deer (1 year old) are lower and more variable than those of older individuals (e.g. Strandgaard 1972, Hewison 1996). For a brief survey of the vital rates of roe deer from published studies see Appendix 1 (Text A1.1 and Table A1.1).

Climate variation plays an important role in roe deer dynamics and can synchronise changes in roe deer population growth across large geographic distances (approximately 200 km; Grotan et al. 2005). Climate and vegetation-driven changes in roe deer vital rates are generally mediated by changes in roe deer body condition (typically measured through body mass) (Gaillard et al. 1998b). Body mass has been related to rates of reproduction (Gaillard et al. 1992, Hewison 1996), and the survival of fawns (Gaillard et al. 1997, Gaillard et al. 1998b). The growth of fawns (< 1 year old) can have knock-on effects for individual fitness later in life (creating cohort effects where annual conditions affect the overall performance of the deer born that year; Kjellander 2000, Pettorelli et al. 2002, Pettorelli et al. 2005a, Kjellander et al. 2006). In general, spatial variation in roe deer densities and population growth has been positively related to environmental productivity and negatively related to harsh winter conditions (Melis et al. 2009, Melis et al. 2010). Several studies have highlighted winter as a critical period for roe deer survival (usually relating to snow depth; Fruzinski and Labudzki 1982, Cederlund and Lindström 1983, Mysterud and Ostbye 2006), and climate and vegetation conditions in the spring and summer as drivers of fawn survival and body mass (Gaillard et al. 1996, Gaillard et al. 1997, Pettorelli et al. 2006, Gaillard et al. 2013). Negative effects of population density on roe deer are common (Gaillard et al. 1993, Putnam et al. 1996, Kjellander 2000, Pettorelli et al. 2003, but see Mysterud and Ostbye 2006, and Andersen and Linnell 2000). The ultimate effects of climate on roe deer vital rates, operating via changes in resource availability and population density will likely result in delayed effects of climate on roe deer population dynamics.

Roe deer are a convenient size for Europe’s large mammalian predators (Linnell et al. 1998a) and are heavily preyed upon by wolves, lynx, and red fox throughout much of the continent (Aanes et al. 1998). Melis et al. (2009) demonstrated that roe deer population densities are lower where wolf and lynx are present and that this limiting effect is stronger in low productivity environments. Roe deer are the dominant prey of lynx throughout much of Europe (Okarma et al. 1997, Aanes et al. 1998, Herfindal et al. 2005b, Molinari-Jobin et al. 2007, Basille et al. 2009, Mejlgaard et al. 2013) and lynx predation can reduce roe deer survival by 10% or more (Nilsen et al. 2009a, Heurich et al. 2012). Roe deer are relatively less important as a prey source for wolves, but the proportion of roe deer in wolf diet varies based on ungulate community composition (Okarma 1995, Aanes et al. 1998); in some areas roe deer alternate with wild boar as prey species of choice (Okarma 1995). Red foxes are generalist predators that sometimes specialise on roe deer fawns (Aanes et al. 1998, Dell'Arte et al. 2007, Panzacchi et al. 2008). Predation by foxes can have a strong negative impact on roe deer populations by reducing recruitment (Liberg et al. 1993, Lindström et al. 1994, Kjellander and Nordström 2003, Jarnemo and Liberg 2005). The combined effect of predation by lynx, wolves, and foxes is not well understood, but the different forms of mortality could have additive effects on roe deer survival (Lindström et al. 1994, Aanes et al. 1998, Jarnemo and Liberg 2005) and this could result in a situation that requires delicate management. European roe deer have already been pushed toward extinction once by over-harvest (Lovari et al. 2008) and that was during a time when large predators were much rarer. For these reasons, population models designed to enable responsible management will need to consider the additive effects of harvest and predation by more than one predator.

Study sites

Much of the understanding of European ungulate dynamics comes from several sites within Europe (e.g. the Isle of Rum in Scotland, Clutton-Brock et al. 1985, Trois Fontaines in France, Gaillard et al. 1993, Bialowieza Primeval Forest in Poland, Jedrzejewska et al. 1997, the Isle of Hirta in Scotland, Coulson et al. 2001). However, wildlife managers face a wide range of challenges as they deal with the variety of ungulate communities present throughout Europe (e.g. there are five native species of ungulates in Bialowieza Primeval Forest compared to the two or three species in many sites; Okarma 1995). Many of the best-studied ungulate populations are in areas where mortality due to hunting and predation is very limited (Gaillard et al. 2000b, Nilsen et al. 2009a). It is, therefore, important to examine a range of sites and assess how widely findings are likely to apply across sites. Moreover, projecting future population dynamics accurately is dependent on data for many processes. There are extensive datasets on many managed populations, but funding constraints and changing management goals mean that these datasets may contain gaps that limit such analyses. Identifying these gaps will help establish priorities for future research.

In this thesis, I focus on three sites with managed roe deer populations: Alpe di Catenaia (hereafter Catenaia) in Italy, Bogesund on the eastern coast of Sweden and the Grimsö Wildlife Research Area (hereafter Grimsö) in central Sweden (Fig. 1.4).

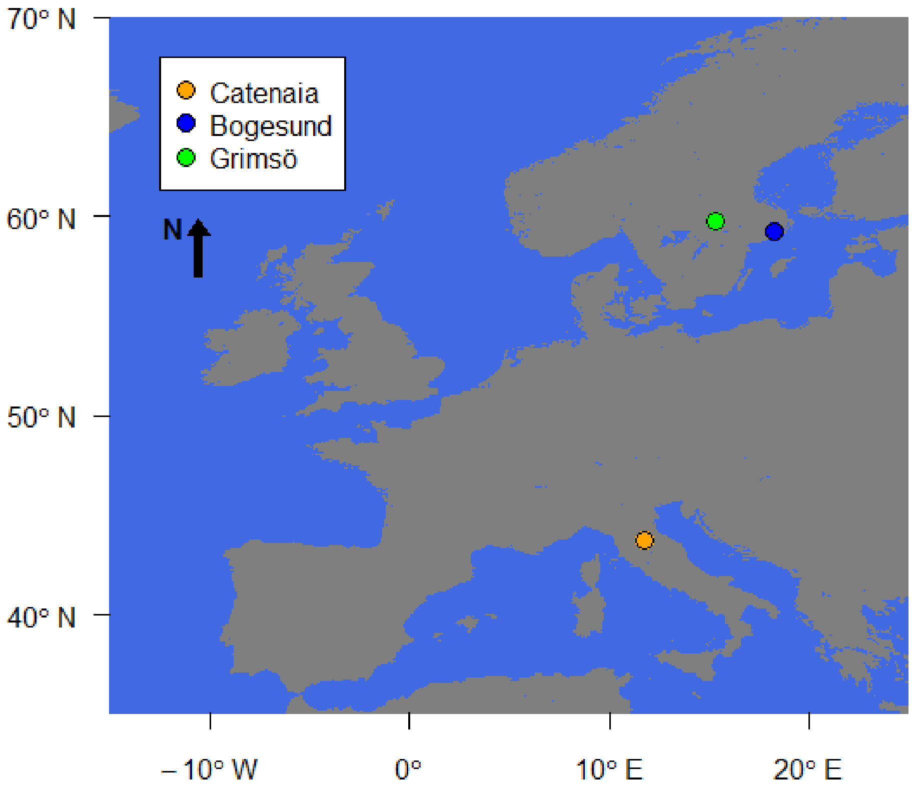

Fig. 1.4: The locations of the three focal sites examined in this thesis. The first site, Catenaia is located in north-eastern Tuscany. The other two sites, Bogesund and Grimsö are located approximately 150 km apart in Sweden. The GlobCorine 2009 land cover dataset (© ESA 2010 and Université Catholique de Louvain) was used to create the underlying map of Europe.

The contrast in climate among these sites (Table 1.1) is of interest because the climatic drivers of vegetation production at the two northern sites are likely to be very different from those in the sub-Mediterranean climate of Catenaia. The intensive roe deer monitoring programs at the Swedish sites span more than two decades and allow the examination of temporal variation in roe deer dynamics. Additionally, differences in the carnivore species inhabiting Bogesund and Grimsö allow a comparison of roe deer populations with different levels of predation pressure (more detail below). At Catenaia, monitoring of wolves and wild boar in addition to roe deer allows for an examination of predation from a different perspective. In particular, nearly ten years of data on wolf diet is used to investigate temporal variation in prey selection. Detail on the climate, vegetation cover, and ungulate community unique to each site is provided in the following paragraphs.

Table 1.1: Seasonal climate conditions at the three study sites [a]

Study site	Winter Tmp (°C)	Winter Pre (mm)	Summer Tmp (°C)	Summer Pre (mm)
Catenaia	1.91	149.99	18.01	144.5
Bogesund	-1.43	90.5	15.88	155.79
Grimsö	-4.44	140.41	14.21	224.62

[a] Mean climate conditions were calculated based on monthly data from the Climate Research Unit (CRU 3.1 dataset ;Mitchell et al. 2004, Mitchell and Jones 2005) for the 1973-2009 period (see methods in Ch. 2 and Ch. 3 for more detail on calculation methods). Winter metrics were calculated using data from the December, January and February months (the “1973” winter includes data from December 1972, January 1973 and February 1973). Summer conditions were calculated using data from the June, July and August months. Temperatures (Tmp) were averaged across months. Precipitation (Pre) was summed across months.

Catenaia is a 120 km^2 forested area in the Apennine mountains in the north-eastern part of Tuscany (Arezzo province, 43.80° N, 11.82° E). Altitude within Catenaia ranges from 300 to 1414 m above sea level (a.s.l.). While Catenaia is surrounded by a number of small agricultural areas, vegetation cover within the site is mainly composed of mixed deciduous hardwoods (76% of total area), with coniferous forests (7%) and open scrubland areas (16%) also present. The climate in Catenaia is sub-Mediterranean with hot, dry summers, and relatively mild winters (Table 1.1). The Catenaia area supports populations of roe deer and wild boar with red deer occasionally observed in the area. There are two predators of roe deer and boar in Catenaia: red foxes (which concentrate on neonates) and wolves (which prey on all age groups) (Bassi et al. 2012). Wolves were first observed in the study area in 1998.

Bogesund is located in east-central Sweden (59.38° N, 18.25° E) in the inner reaches of the Stockholm Archipelago, on the coast of the Baltic Sea. As such, the site is surrounded by water and the movement of wildlife in and out of the area is limited. The elevation of the 26 km^2 area never exceeds 60 m a.s.l. Approximately 65% of the Bogesund site is covered by highly productive mixed coniferous-deciduous forest while another 25% is occupied by farmlands (bedrock and bogs make up the remaining 10%). Due to its location on Sweden’s south-eastern coast, the climate in Bogesund is harsh compared to that of Catenaia, but is relatively mild when compared to the climate in Grimsö (Table 1.1). During the winter months, December through February, there is an average of 4.0 cm of snow on the ground (mean from 1973-2009, data from Stockholm; Swedish Meteorological and Hydrological Institute 1972-2009). In Bogesund, there are large populations of roe deer and of wild boar. Also, young male fallow deer (*Dama*

dama) are occasionally observed in the site. Wild boar were re-introduced to Sweden in the 1970's and their range is expanding (Welander 2000, Truve and Lemel 2003). The first contemporary and documented boar reproduction to take place in Bogesund was in 2000. The only natural predator of ungulates currently in Bogesund is the red fox.

The third and final study area, Grimsö, is a 130 km^2 area located in south-central Sweden (59.67° N, 15.42° E). Grimsö consists primarily of coniferous forest (74% of area) interspersed with bogs, mires, and fens (18%), farmland (3%), and lakes and rivers (5%). The landscape is relatively flat ranging from 75 – 180 m a.s.l. Grimsö is approximately 150 km (2.6°) northwest of Bogesund. Compared to Bogesund, Grimsö has a harsh climate, a low proportion of farmland, and generally low vegetation productivity. Winters in Grimsö are characterized by cold temperatures and large amounts of precipitation (Table 1.1) which are associated with an average snow depth of 18.60 cm during the winter months (mean from 1973-2009, data from Ställdalen; Swedish Meteorological and Hydrological Institute 1972-2009). While there are several bodies of water in the Grimsö area (including a large permanent lake and recurring seasonal ponds), it is not surrounded by water. So, unlike Bogesund, the movement of wildlife in and out of Grimsö is relatively unrestricted. Grimsö is inhabited by three species of ungulates including roe deer, moose and, since 2006, wild boar. Occasionally red deer are also observed in the area. There are currently three natural predators of roe deer in Grimsö: lynx, red foxes, and wolves. Lynx and wolves were not present throughout the whole of the study period; lynx arrived in 1996 and wolves in 2003.

Aims and thesis structure

The over-arching aim of this study was to model the impacts of climate change on roe deer population dynamics. Meeting this goal required multiple interconnected steps, which form the basis of the chapters in this thesis. Furthermore, because each step was analytically intensive and made strenuous demands of finite datasets, these analyses prompted ancillary assessments of the uncertainties involved at each stage. These assessments of uncertainty were used to examine the feasibility of using available data to meet the objectives set in each chapter.

In Chapter 2, I explore the relationship between climate and temporal variation in NDVI, an index of vegetation production, at Catenaia, Bogesund and Grimsö. Two different methods are implemented: one which aims to describe a general relationship between climate and NDVI across Europe and one which develops individual models for the three focal sites. The contrasting performance of these two approaches is discussed.

In Chapter 3, I use a variety of predictors (mostly climate, vegetation, harvest, and predation-related) to model roe deer survival in Bogesund and Grimsö. The results of binomial models and capture-mark-recapture models, which use different aspects of the available data on individually marked roe deer, are compared. The discussion explores the relative importance of non-climatic and indirect climatic drivers of roe deer survival.

In Chapter 4, I investigate the role of climate, vegetation, deer density, and predation as drivers of roe deer reproduction at Bogesund and Grimsö. Models of ovulation and early fawn survival are constructed and integrated into simulations of per capita reproductive success. The uncertainty surrounding simulations is explored and guidance is provided regarding future research that could address the highlighted data gaps.

In Chapter 5, I mechanistically integrate the models of vegetation, survival and reproduction developed in previous chapters into matrix population models in order to simulate changes in roe deer density at Bogesund and Grimsö. The uncertainty in the simulations attributable to each modelled process is evaluated. The matrix models are used to project roe deer population dynamics at Bogesund given climate change and to explore the levels of harvest which might be required to maintain stable roe deer populations in the future. The effect of data limitations on the ability to produce confident projections of roe deer dynamics is discussed and priorities for future research are highlighted.

In Chapter 6, I relate variation in wolf diet to the relative availability of wild boar and roe deer at Catenaia. The ramifications of sampling error for the uncertainty surrounding estimates of prey selection are evaluated. The discussion addresses the potential influence of wild boar abundance on the use of roe deer by wolves and highlights the importance of accounting for sampling uncertainty when drawing conclusions regarding predation.

Chapter 2 – The relationship between net primary productivity and annual climate conditions

Abstract

Many of the effects of climate change on ecological communities are likely to operate indirectly via changes in the vegetation-related food resources exploited by consumer populations. Here, I investigate the relationship between climate and inter-annual changes in net primary productivity using a remotely-sensed index of vegetation production, NDVI. I model the annual sum of NDVI values, integrated NDVI (INDVI), as a response to precipitation and temperature-based climate metrics and CO_2 concentrations and use the models to project future INDVI given climate change. Analyses were conducted at two spatial and temporal scales: at 103 sites distributed across Europe on an annual scale and within key study sites (Catenaia, Bogesund, and Grimsö) on a monthly scale. Inter-site variation in INDVI dominated intra-site (inter-annual) variation. Consequently, although the best annual model of INDVI across Europe included the major expected drivers (CO_2 concentrations, plus seasonal temperature and precipitation), it performed poorly at explaining temporal changes in vegetation production within the study sites. By contrast, the site-specific monthly models performed relatively well. These results highlight difficulties in the use of NDVI as an index of inter-annual changes in vegetation across large geographic areas. When used to project future INDVI at the study sites, the best models from both methods suggested increased vegetation production under three greenhouse gas emission scenarios. There remains, however, an urgent need for a better understanding of the drivers of vegetation productivity at a community level – especially the likely consequences of changing CO_2 concentrations – in order to make projections most useful to ecological managers.

Introduction

It is increasingly evident that climate change will have numerous consequences for the Earth’s ecosystems (IPCC 2007a). Most studies to date have focused on climate-driven shifts in the phenology and geographic range of specific taxa, but there has recently been a call for research that reaches deeper into the dynamics of ecological communities, addressing changes driven by interactions among trophic levels (Barnard and Thuiller 2008, Huntley et al. 2010). Climate-driven changes could permeate all trophic levels by altering vegetation productivity. Herbivores, their predators and competitors are all likely to be affected by changes in primary production either directly or indirectly. These consequences could be manifested in many ways including not only range shifts (as have already been documented for some species), but also as changes in population growth rates and cycles.

Primary production is increasing globally. Nemani et al. (2003) used satellite observations to estimate a 6% increase in global vegetation production from 1982 to 1999. A similar increase has been documented in Europe (Slayback et al. 2003); however, this upward trend is not consistent across all regions. While Northern Europe is expected to experience increased productivity due to longer, warmer growing seasons, parts of Central and Southern Europe may see a decrease in primary productivity (Boisvenue and Running 2006, Fronzek and Carter 2007, Penuelas et al. 2007). The combined effects of warmer temperatures and decreased summer rainfall in areas which are already water-limited (such as the Mediterranean) may cause an eventual decline in primary productivity (Boisvenue and Running 2006, Parmiggiani et al. 2006, Penuelas et al. 2007, Prieto et al. 2009). Climate change effects and the potential for droughts to become more frequent and more severe in future have already caused concern over possible declines in the productivity of both forested and agricultural areas (Boisvenue and Running 2006, Hermans et al. 2010). By contrast, climate-driven increases in productivity in other areas, have been seen as beneficial, raising hopes of heightened agricultural production (Hermans et al. 2010) and increased vegetation biomass which, in turn, might facilitate carbon storage (Lee et al. 2011). Changes in primary productivity, whether positive or negative, are likely to have important consequences for ecological systems and need to be assessed to understand more fully how climate change will impact on communities. For example, roe deer

(*Capreolus capreolus*) and wild boar (*Sus scrofa*) densities are positively related to net primary productivity across Europe (as measured through remotely-sensed satellite indices; Melis et al. 2006, Melis et al. 2009). Any changes in the population dynamics of these widespread herbivores are likely to require adapted management efforts.

Few studies have directly related vegetation productivity to climatic conditions or created projections of productivity under climate change. Nemani et al. (2003) and Piao et al. (2011) documented changes in productivity but did not relate these temporal changes to the potential climatic drivers. Simple mathematical models have been developed to relate climate to spatial variation in net primary productivity (NPP) across wide geographic scales (Lieth and Whittaker 1975, Friedlingstein et al. 1992, Dai and Fung 1993), but these models are not generally used to simulate fine-scale temporal responses. Fronzek and Carter (2007), for example, used the Miami Model index (Lieth and Whittaker 1975), based on the mean temperature and annual precipitation of an area, to estimate primary productivity in Europe. They then contrasted current productivity with that given projected mean climates for the 2071-2100 period; they did not examine how climate might alter NPP of locations over the intervening period. More commonly, large-scale studies of vegetation production make use of satellite-derived indices, which can provide global coverage and also long-term data on fine (sub-monthly) temporal scales. For example, the Normalized Difference Vegetation Index (NDVI) is an index of vegetation productivity and is globally available for the 1982-2006 period at a bimonthly resolution. NDVI correlates directly with vegetation production and biomass, and the annual sum of NDVI provides an index of NPP (Tucker 1980, Running 1990, Reed et al. 1994, Field et al. 1995). NDVI has been widely used to model temporal relationships between vegetation and animal populations (Pettorelli et al. 2005c). Yet, surprisingly, studies that model NDVI’s response to climate usually examine spatial variation rather than making use of the available long-term NDVI time-series (Potter and Brooks 1998, Larsen et al. 2011). Additionally, the few studies that do examine temporal relationships use monthly NDVI data from specific months or seasons of interest (Pettorelli et al. 2007, Mysterud et al. 2008) or use methods which allow prediction only 1-4 months in the future (Funk and Brown 2006) rather than evaluating NDVI response to climate across years as a proxy for net primary productivity.

Many studies to date have investigated geographic variation in net primary productivity and NDVI as a response to spatial variation in climate (Lieth and Whittaker 1975, Dai and Fung 1993, Potter and Brooks 1998, Larsen et al. 2011). These analyses are valuable; however, in order to understand the temporal dynamics of animal populations in response to changing vegetation production, information on how productivity changes over time (ideally on an annual scale) in response to a changing climate would be more relevant. A large portion of spatial variation in productivity likely reflects differences in species assemblages among communities which have developed over centuries as a response to available resources, mean climatic conditions and biogeographical history. The first responses of both productivity and wildlife populations to climate change are likely to take place on much shorter time scales, during which there might be limited opportunity for community composition to change substantially (Etterson and Shaw 2001, Neilson et al. 2005, Parmesan 2006, Bennie et al. 2010). Thus, spatial relationships between climate and vegetation production are unlikely to describe the short-term temporal response of a location's vegetation to climatic change. An approach which explicitly examines the temporal effects of climate on vegetation productivity will help create more accurate projections of vegetation production given climate change. Such projections would enable future investigations of how climate-driven changes in productivity could translate into altered wildlife population dynamics and impact on a given community.

In this chapter, I explore the temporal relationship between climate and NDVI in Europe using two modelling techniques. I use 25 years of data (1982-2006) from three study sites (two in northern Europe, one in the Mediterranean), supplemented with data from 100 randomly selected sites throughout Europe. In doing so, I explore the potential use of the annual sum of NDVI (known as integrated NDVI) as a proxy for NPP on ecologically relevant scales that could be useful for predicting the future management of wildlife populations. My main goals in this chapter are to answer the following questions:

1) Is climate a good predictor of variation in integrated NDVI (INDVI) among years? In particular, how well does it explain variation in INDVI at the three study sites of interest?
2) Which climatic metrics best explain variation in INDVI among years?

  - Do bioclimatic predictors (growing degree days and dryness) or strictly climatic predictors (temperature and precipitation) have more explanatory power?
  - Do seasonally summarised predictors (e.g. summer precipitation) have more explanatory power than annually summarised ones (total annual precipitation)?

3) Based on models of INDVI as a response to climate and given expected climate change for the 21st Century what, if anything, can be concluded about the future trajectory of INDVI (and thus net primary productivity) at the three study sites?

Methods

Focal sites

Three study areas were used in these analyses: Catenaia, Italy; Bogesund Sweden; and Grimsö, Sweden (see locations in Fig. 2.1 further below). In this chapter, I refer to these sites as “focal sites” in order to distinguish these areas from the randomly selected sites (more detail below). In contrast to the two Swedish sites, where harsh cold winters and short growing seasons mean that vegetation is likely to be strongly limited by temperature, in Catenaia, precipitation and associated droughts are likely to be important factors affecting productivity. These sites are described in detail in Chapter 1.

Extraction of observed climate data and CO_2 concentrations

I obtained observed climate data from the Climate Research Unit (CRU). The CRU 3.1 dataset contains global data at a 0.5° resolution (approximately 1,585 km^2 for the Swedish sites and 2,240 km^2 for Catenaia) for the period 1901-2009 in monthly time-steps (Mitchell et al. 2004, Mitchell and Jones 2005). I overlaid focal site polygons with the CRU data grid and extracted observed climate for the CRU cell containing each of the focal areas.

Many studies relating vegetation and climate do not take the direct effects of CO_2 concentrations into account. Because CO_2 concentrations affect plant physiology and can increase photosynthetic rates and water-use efficiency, the omission of direct CO_2 effects from vegetation models could give a misleading impression of the response of vegetation to climate change (Rickebusch et al. 2008). I obtained time-series of mean global CO_2 concentrations from NOAA's Earth System Research Laboratory (Conway et al. 1994, Conway and Tans 2011). This dataset is available at both monthly and annual resolutions for the entire period covered by both the NDVI and climate data (1982-2006). The monthly datasets include both recorded CO_2 concentrations throughout the season (which respond to seasonal changes in vegetation growth) and seasonally de-trended time-series; I used the seasonally de-trended series in models (see Table 2.1, further below, for abbreviations of CO_2 variables used in models).

Extraction of projected climate data and CO_2 concentrations

I downloaded climate projections (2001 – 2100) for all of Europe from the ALARM website (http://www.alarmproject.net/alarm/). The ALARM dataset (Mitchell et al. 2004, Spangenberg 2007) consists of projected climates for the 21st Century from the HadCM3 General Circulation Model down-scaled to a 0.17° resolution (roughly 175 km^2 in the Swedish sites and 250 km^2 at Catenaia). Down-scaling by the ALARM project was achieved using the "delta-change approach" in which simulated anomalies (from the projected period means) are added to baseline climate time-series that are available on a smaller spatial scale (see Wilby et al. 204, Mitchell et al. 2004 for more detail, Tabor and Williams 2010). ALARM provides climate projections for three greenhouse gas (GHG) emission scenarios (A1FI, A2 and B1) from the IPCC Special Report on Emission Scenarios (Nakicenovic et al. 2000, Table SPM-3a; see also scenario description in Ch. 1). In terms of emissions and expected climate change, the A1FI is the most extreme of these (associated with high emissions) and B1 scenario is the least extreme (with low emissions) (see Ch. 1 for more detail; Nakicenovic et al. 2000). I overlaid the ALARM climate grid with the focal site polygons and extracted data from all overlapping cells. Due to the finer resolution of the ALARM data (compared to the 0.5° resolution of the CRU grid) each focal site included multiple ALARM cells (Grimsö included 5 cells, Bogesund and Catenaia each included 3 cells). I averaged climate metrics across the cells associated with each focal area.

The finer spatial resolution of ALARM projections relative to the CRU 3.1 dataset causes some differences in the climate metrics from the two datasets. To correct for this, I downloaded the observed climate dataset provided by the ALARM project which is at the same 0.17° resolution as the ALARM projections. I calculated difference anomalies between the two observed datasets (CRU 3.1 and ALARM) and added the mean anomalies (for each climate metric) to the ALARM projections for the 21st Century. This removes any systematic differences between the datasets. The observed data provided by ALARM, and used in this correction, is derived by downscaling data provided by CRU to a 0.17° resolution. Unfortunately, this ALARM dataset of observed climate only extends until the year 2000; I used the CRU 3.1 observed dataset to fit my models, despite its coarser 0.5° resolution, because it extends to 2009, thus better encompassing the time period spanned by NDVI datasets.

The ALARM project also provides the global mean CO_2 concentrations associated with the scenarios at a decadal resolution. I used cubic splines to interpolate these values to annual or monthly time-scales for use in analyses. The CO_2 concentrations and climatic changes projected for the focal sites under each of these scenarios are compared to observed period means (CRU 3.1 data, 1982-2006) and summarised in Appendix 2 (Table A2.1).

Climate metric calculation

Both the CRU and ALARM datasets provided monthly information on mean temperature (Tmp_m), total precipitation (Pre_m), and either equilibrium evapo-transpiration (Eet_m, ALARM) or potential evapotranspiration (Pet_m, CRU); however, the CRU dataset lacked information on growing degree days above 5° C (Gdd_m) or a measure reflecting overall climate aridity. Gdd_m was calculated by interpolating the monthly temperature data to a daily resolution using cubic splines and summing the temperature for all days within each month that were above a base temperature of 5 °C, in accordance with the method used for ALARM. An index of overall dryness (Dry_m) was calculated as $\mathrm{Pre}_m - \mathrm{Pet}_m$ for each month. For the ALARM projection data Eet_m was converted to Pet_m using a multiplier of 1.32 as recommended by Hobbins et al. (2001) and Gerten et al. (2004). See Table 2.1 for a list of the abbreviations for the variables that are used in the models presented here.

Using the observed and projected data for each period and scenario I summarised the climate data on an annual basis and separately for the spring (March, April, May), summer (June, July, August), and autumn seasons (September, October, November) for the 1901 – 2100 period (see Table 2.1 for variable abbreviations). Tmp_m and Dry_m were averaged across months, whereas Pre_m and Gdd_m were summed.

Finally, an independent index of net primary productivity (NPP) based on the Miami Model (Lieth 1975) was calculated for each year for all sites (Miami index, Table 2.1):

$$\mathrm{NPP} = \min \begin{Bmatrix} 3000/(1+\exp\,(1.315 - 0.119 \cdot \mathrm{Tmp})) \\ 3000 \cdot (1 - \exp\,(-0.000664 \cdot \mathrm{Pre})) \end{Bmatrix} \qquad \text{[Equation 2.1]}$$

where NPP is measured in grams dry matter $\mathrm{m}^{-2}\mathrm{y}^{-1}$, and Tmp and Pre are the average temperature and precipitation conditions for a location measured in °C per year and mm per year respectively. The Miami model was developed empirically to estimate global geographic variation in productivity and was not originally intended to estimate temporal changes at a location. While more complex physiological and plant-community based models may be ideal for estimating temporal change in productivity, the implementation of such models is beyond the scope of this study in which I aim to examine broad relationships between productivity and climate spanning large geographic areas. The Miami model provides a simple temperature and precipitation-based productivity index which been shown to generate realistic patterns of NPP (Friedlingstein et al. 1992, Dai and Fung 1993, Adams et al. 2004, Zaks et al. 2007), and has already been used in climate change impact research (Fronzek and Carter 2007). The Miami index has often been used as baseline for comparing different spatial models of NPP (Adams et al. 2004). An understanding of the Miami Model’s suitability (or lack thereof) as an index for modelling temporal changes in productivity could be of great practical interest to climate change impact research.

Extraction and processing of NDVI data

Normalised difference vegetation index (NDVI) is based on the ratio of red (RED) to near-infrared (NIR) light that is reflected from the Earth and is used as an index of vegetation productivity:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + \mathrm{RED}} \qquad \text{[Equation 2.2]}$$

Table 2.1: Variables used in models of INDVI.

	Abbreviation and definition [a]		
Variable	Monthly resolution	Seasonal resolution	Annual resolution
Integrated NDVI	**INDVI$_m$**: sum of two bimonthly NDVI values within each month.		**INDVI**: sum of 24 bimonthly NDVI values from January to December.
Temperature	**Tmp$_m$/ Tmp$_{m\text{-}1}$ / Tmp$_{m\text{-}2}$**: monthly mean temperature.	**Spring Tmp**: mean Tmp$_m$ from Mar. – May **Summer Tmp**: mean Tmp$_m$ from Jun. – Aug. **Autumn Tmp**: mean Tmp$_m$ from Sep. – Nov.	**Tmp**: mean of Tmp$_m$ from Jan. – Dec. of each year.
Precipitation	**Pre$_m$ / Pre$_{m\text{-}1}$ / Pre$_{m\text{-}2}$**: monthly sum of precipitation.	**Spring Pre**: sum of Pre$_m$ from Mar. – May **Summer Pre**: sum of Pre$_m$ from Jun. – Aug. **Autumn Pre**: sum of Pre$_m$ from Sep. – Nov.	**Pre**: sum of Pre$_m$ from Jan. – Dec. of each year.
Growing degree days	**Gdd$_m$ / Gdd$_{m\text{-}1}$ / Gdd$_{m\text{-}2}$**: monthly sum of degrees above 5° C (see text).	**Spring Gdd**: sum of Gdd$_m$ from Mar. – May **Summer Gdd**: sum of Gdd$_m$ from Jun. – Aug. **Autumn Gdd**: sum of Gdd$_m$ from Sep. – Nov.	**Gdd**: sum of Gdd$_m$ from Jan. – Dec. of each year.
Dryness	**Dry$_m$ / Dry$_{m\text{-}1}$ / Dry$_{m\text{-}2}$**: Pre$_m$ minus monthly potential evapo-transpiration (see text)	**Spring Dry**: mean Dry$_m$ from Mar. – May **Summer Dry**: mean Dry$_m$ from Jun. – Aug. **Autumn Dry**: mean Dry$_m$ from Sep. – Nov.	**Dry**: mean of Dry$_m$ from Jan. – Dec. of each year.
Global CO$_2$ concentration	**CO$_{2\ m}$**: monthly global CO$_2$ concentration (seasonally de-trended; see text).		**CO$_2$**: annual mean global concentration of CO$_2$ (see text)
Miami model index			**Miami index**: index of net primary productivity (see Equation 2.1)
Month of the year	**Month**: factor representing the 12 months of the year		
Distance to sea	**Sea distance**: distance of sites to coastlines (no temporal variation; used in multi-site annual models)		

[a] Abbreviations used are in bold. Original data were obtained from a number of independent sources in different forms and resolutions (see text for details). For monthly predictors, subscripts "*m*", "*m*-1", and "*m*-2" indicate time-lags of 0, 1, and 2 months relative to the INDVI$_m$ response being modelled.

Any single time-step value of NDVI can vary between -1 and 1, but typically observed values range between 0 and 1 with values between 0 and 0.2 representing areas that are either sparsely vegetated or covered by snow. Within any given year, the NDVI at a temperate site usually shows a seasonal curve peaking in the summer and declining to a minimum value during winter in the absence of green vegetation. This pattern was reflected in the monthly sum of NDVI values (monthly integrated NDVI or INDVI_m) for each of the three focal sites when averaged for each month across all years (Appendix 2, Fig. A2.1). Site-specific absolute NDVI values are affected by land cover type and, in particular, areas with more water bodies create what is known as a “mixed cell effect” where the NDVI range may be lower than would otherwise be expected. This is probably the case for the Bogesund focal site, which shows lower NDVI on average than does Grimsö, despite the similarities between the two areas.

Pre-calculated NDVI data were obtained from the Global Inventory Modelling and Mapping Studies (GIMMS) website (http://glcf.umiacs.umd.edu/data/gimms/). The GIMMs data are global in extent (0.07° resolution; roughly 30 km^2 at the Swedish sites and 45 km^2 at Catenaia) and cover the July 1981- December 2006 time period at bimonthly (15 day) intervals resulting in 24 data points pixel^{-1} y^{-1} (Pinzon et al. 2005, Tucker et al. 2005). The GIMMS dataset is smoothed and corrected for the following anomalies/biases: instrument changes (satellite succession), cloud contamination, aerosol contamination from major volcanic eruptions, and satellite drift. The maximum NDVI value observed was recorded for each two-week period; this form of data compositing helps correct for negative errors in NDVI due to cloud and snow contamination (see Pettorelli 2005 for more detail). Spatial NDVI data for each bimonthly time-step were overlaid with the site polygons and values were extracted for all NDVI cells which overlapped by at least 1% of cell area. The Bogesund, Grimsö, and Catenaia sites overlapped with 6, 11, and 7 NDVI cells, respectively. I manually examined changes in NDVI value for each NDVI cell in each focal site for the entire covered period and investigated all cases where sudden drops (> 0.2) followed by quick recoveries (> 0.15) were observed (a sign of possible contamination by, for example clouds or snowfall). Suspicious values were substituted with the average value from the preceding and following two-week periods for that cell. Area-weighted means of bimonthly NDVI (across cells) were then calculated for each focal site.

For each site I created a monthly INDVI$_m$ time-series by summing the two bimonthly NDVI values within each month (Table 2.1); this measure has previously been used as a proxy for vegetation biomass (Pettorelli et al. 2007). For each year (1982 to 2006; data for 1981 were incomplete so this year was excluded) I calculated three NDVI metrics as indices of net primary productivity: annual integrated NDVI (hereafter just INDVI), growing season integrated NDVI, and the maximum observed NDVI for a given year (Pettorelli et al. 2005c). INDVI is the sum of all 24 bimonthly NDVI values over a given year and is a measure of annual vegetation production (Table 2.1). Growing season integrated NDVI is calculated similarly but summed over only the growing season months (May through October, inclusive). Maximum values of NDVI for a year are simply taken from the time-step with the highest NDVI value (typically some time in June or July) recorded during a given year; as an index of overall vegetation production, this metric can be sensitive to extreme values. Preliminary analyses of all three yearly indices suggested no substantial differences among their responses to climate so I only present analyses of INDVI here.

Random site selection

To characterize general relationships between vegetation and climate I boosted models using randomly selected sites distributed throughout Europe. I identified 100 additional sites by randomly selecting European cells from the CRU 0.5° climate grid (Fig. 2.1). I constrained the cells selected to those within temperate regions (i.e. between 23° and 66° N). To minimise spatial auto-correlation, cells were selected to ensure a minimum separation of 1.5 degrees (~166 km).

The proportional land cover of sites could affect the relationship between NDVI and climatic predictors. However, constraining the random sites to those with at least 75% forest cover (similar to the focal areas) did not improve model fit; consequently, random site selection was not constrained by land cover type. I extracted and processed the climate data for all time-steps associated with the climate cell defining each of the 100 random sites. I then overlaid the area of each random site (defined by one 0.5° x 0.5° climate cell) with the GIMMs NDVI data. Due to the relatively large size of the CRU climate cells defining the sites, each random site overlapped with approximately 40-60 NDVI cells. For each bimonthly time-step and each site I calculated the average of the NDVI for the CRU cell area, weighted by the area of overlap between the CRU climate cell and each NDVI cell associated with it.

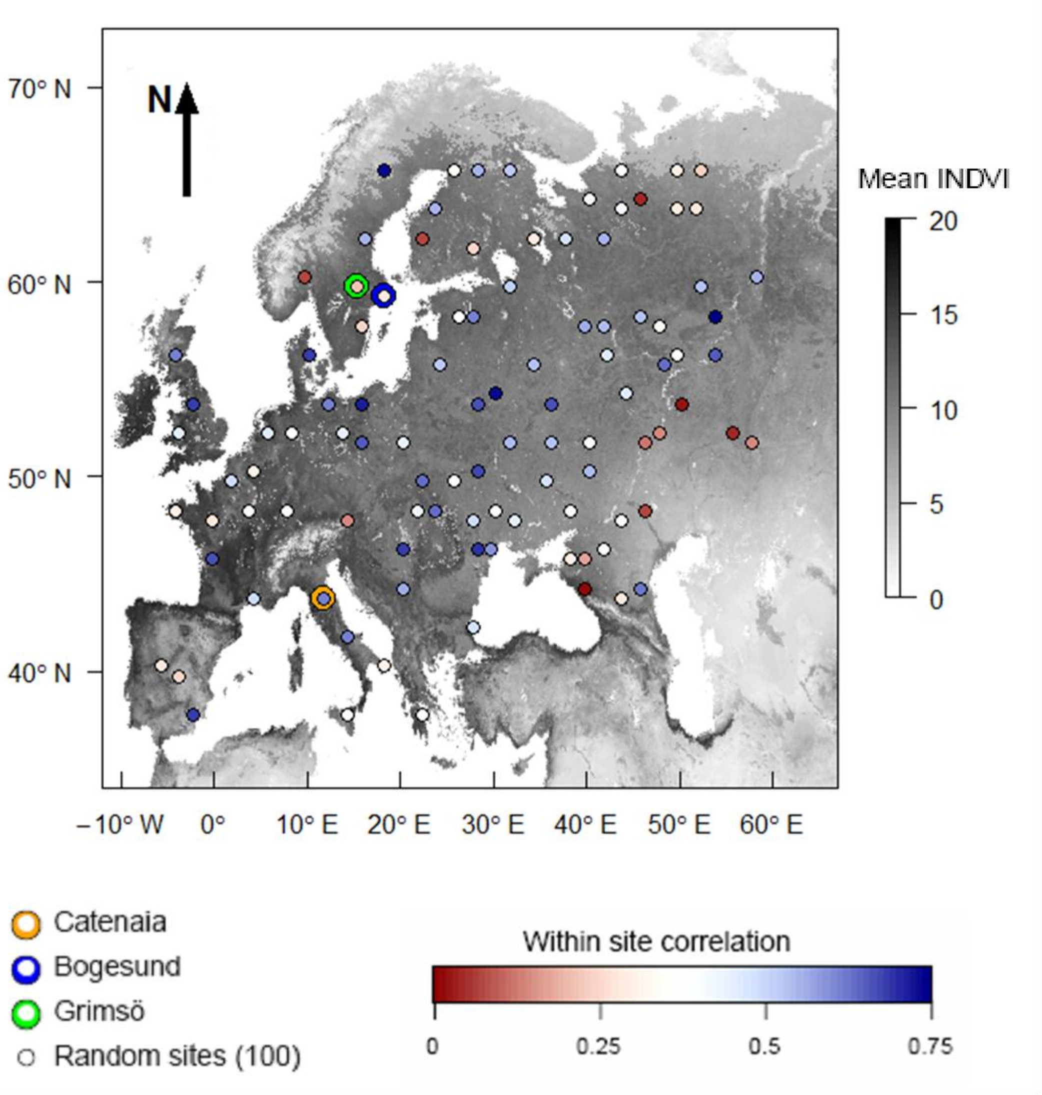

Figure 2.1: Location of sites used in analyses of INDVI in response to climate. The primary goal of analyses was to model time-series of INDVI at the three focal sites. Two of these sites, Bogesund (large blue circle) and Grimsö (large green circle) are located in southern Sweden. The third focal site, Catenaia (large orange circle), is located in northern Italy. Data on INDVI and climatic metrics from these sites were used in both the multi-site yearly and single-site monthly analyses. In order to boost the sample size for the multi-site yearly models, 100 additional sites within temperate Europe (between 23^{o} and 66^{o} N) were randomly selected (small black circles). The grey-scale of the background represents geographic variation in mean INDVI across 25 years (1982-2006). The colour with which circles are filled indicates the within site-correlations (Pearson's *r*, n = 25 in all cases) between observed INDVI values and estimates of INDVI from the selected multi-site yearly model (see results for more detail).

Modelling analysis

Multi-site yearly models

To identify the climatic drivers of inter-annual variation in NPP at sites across Europe, I compared the ability of seven candidate models (and three associated null models) to explain variation in INDVI within and across sites. Models were compared using Akaike's Information Criterion (AIC) and Akaike model weights (Anderson et al. 2000, Burnham and Anderson 2002).Three models were dependent on strictly climatic variables (temperature and precipitation). Of these, one (the "annual" model) used climate metrics summarised for the entire year; one (the "full seasonal" model) used climate metrics summarised for the spring, summer, and autumn seasons, with interactions for variables within all periods; and one (the "reduced seasonal" model) used only spring and summer climate metrics, with only interactions for the summer season (when drought conditions are most likely). Three analogous models (an annual model, a full seasonal model and a reduced seasonal model) used bioclimatic variables (growing degree days and dryness) as predictors, rather than strictly climatic variables. The seventh model included the calculated Miami model index as a predictor. Finally, two other "control" models and a null model, which did not represent *a priori* hypotheses explaining INDVI, were included to compare the relative importance of model components including the intercepts, CO_2, and the site-specific spatial variable Sea distance (Table 2.1; more below). In preliminary analyses, annual (global) CO_2 concentration was found to be a strong predictor of INDVI. To control for the potentially important effects of CO_2 fertilization on productivity (Ainsworth and Long 2005, Rickebusch et al. 2008), I included it in all models of the *a priori* model set. I also tested for an interaction between CO_2 and precipitation variables, because higher CO_2 concentrations can decrease the stomatal conductance of plants thus increasing the water-use efficiency of vegetation (Ainsworth and Long 2005, Gerten et al. 2005); however, these effects did not improve model AIC. Because sites nearer to large bodies of water may consistently experience milder climates (with less extreme temperature variations), the distance of each site to coastlines (Sea distance) was included in all models to account for some variation in INDVI due to site location.

The response variable (annual INDVI for the 25 year period from 1982-2006) is the yearly sum of 24 values between 0 and 1 of each year. Owing to this constraint, INDVI values were logit-transformed before analysis. Models included a random effect, allowing different intercepts for each of the 103 sites. These intercepts account for variation in mean INDVI among sites while allowing deviations from the means (the anomalies) to be modelled as responses to the climatic predictors. Additionally, I included a first order auto-regressive term (Phi) which models possible effects due to the previous year's INDVI (temporal auto-correlation).

Preliminary analyses suggested that alternative spatial factors (including elevation and latitude) were uninformative relative to models including Sea distance. Interactions between latitude and climatic predictors also failed to improve model fit. Finally, I investigated non-linear treatment of predictors through the use of generalised additive models (using 10 equally spaced spline points along the range of each predictor; Wood 2006), non-linear mixed effects models (modelling INDVI as two parameter logistic functions of the climate variables), cubic regression splines and quadratic terms. However, these results are not presented here because these approaches generally had poor explanatory power compared to the more parsimonious linear mixed effect models.

Plots of the model residuals were examined for deviations from the assumptions of independence, normality and homoscedasity and for signs of spatial auto-correlation. In order to test the predictive ability of the best AIC model, I used a cross-validation technique. Specifically, data from a subset of years were randomly excluded, and then the model was re-fitted and used to reproduce values from the excluded years for all 103 sites. This process was repeated for 25 iterations excluding 1 year at a time and for 1000 iterations each excluding between 2 and 5 years at a time. Upon completion of each set of simulations (in which 1, 2, 3, 4, or 5 years were excluded), I calculated the estimation Root Mean Squared Error (RMSE) and Pearson's correlation coefficient between observed and estimated responses for the excluded data for each iteration. I also recorded the estimated model parameters for each simulation. This was done to document the effects of sample size on model fit.

Finally, using the model fitted with all the data (no years excluded) I compared the estimated INDVI time-series for the three focal sites to that observed for the 1982-2006 period. I then used the best AIC model to project INDVI into the future for the three focal sites under the climate conditions described by the A1FI, A2 and B1 IPCC scenarios. I considered projections of the best model with and without the inclusion of CO_2 effects because of inherent uncertainty concerning the realistic strength and form of CO_2 fertilization effects outside the ranges of CO_2 concentrations observed to date. Confidence intervals for model estimates were calculated using a parametric bootstrap in which data were simulated from the fitted model 1000 times with noise added by sampling the error distribution defined by the residual mean squares and the estimated temporal correlation of the residuals (see Gelman and Hill 2006 for an overview of parametric bootstrapping techniques). The model was refit to the simulated data, and then used to estimate confidence intervals for model expectations under current climate and to project future INDVI under climate conditions described by the three emissions scenarios. The 95% quantiles of these projections were used to describe the confidence intervals of the model projections.

Single-site monthly models

Poor performance of the multi-site yearly models (see results for more detail) suggested that inter-annual variation in INDVI was low and that most of the intra-site variation in productivity might be occurring within years (as a part of seasonal cycles; Appendix 2, Fig. A2.1), rather than among years. It is likely that some information on the relationship between NDVI and climate is lost by using annually summarised INDVI as the immediate response variable in the multi-site yearly models. To investigate the climatic drivers of variation in NDVI on a finer temporal scale, and thus avoid the loss of intra-annual information, I fitted monthly models for each of the three focal sites (Catenaia, Bogesund and Grimsö); the larger sample size available at this scale enabled the use of single-site models.

Seasonal cycles, with data points on a finer (monthly) time-scale created higher temporal dependence and highlighted the possibility of lagged effects. In order to identify the correct lags and avoid missing potentially important variables I used an “all subsets” technique, in which I tested all possible combinations of up to five climatic variables with time-lags of up to two months prior to the month being modelled. Variables tested in this way included Tmp_m, Pre_m, Dry_m, and Gdd_m (see Table 2.1 variable definitions). CO_2 concentrations for the current month ($CO_{2\ m}$) were also tested although no time lags for this variable were included. I allowed for any possible two-way interaction between these predictors, given that they involved the same time-lag (i.e. an interaction between the previous month's temperature and precipitation could be included but not one between the current month's temperature and previous month's precipitation). The immediate response variable was INDVI_m, the sum of the two bimonthly NDVI values of a given month, logit-transformed to constrain values between 0 and 2. Estimated monthly values were then back-transformed and summed to yield the annual INDVI response estimated by the model for each year. Month (Table 2.1) was included as a categorical factor in all models along with a first order auto-regressive term (Phi_m), which accounted for the possible correlation with the previous month's INDVI_m.

All possible models meeting these criteria were compared using the AIC. When considering models from this set, I followed the nesting rules of Richards (2008) by disregarding any more complex nested models that did not have a lower AIC than simpler nested models. I then selected the subset of models with a Δ AIC ≤ 6 and ranked them according to their Akaike weights (Anderson et al. 2000, Burnham and Anderson 2002, Richards 2008). I calculated the relative importance of predictors appearing in this subset as the sum of the weights of all models including that predictor. I then tested the predictive ability of the best model for each of the three focal sites using the same cross-validation procedure described above to compare observed INDVI values to those estimated by the model for each year. The site-specific best models were then used to project the associated site's annual INDVI into the future given the climate conditions of the A1FI, A2 and B1 scenarios. Confidence intervals around model projections were calculated using a parametric bootstrap procedure as described above (for the multi-site yearly models) and accounted for uncertainty given the auto-correlation structure of the model.

All data preparation, GIS and statistical analyses were conducted using program R 2.13.0 (R Core Development Team 2011).

Results

Multi-site yearly models

The yearly models were based on a large sample size including 103 sites with 25 years per site (2575 observations total; Fig 2.1). The best performing model was the reduced seasonal model including the strictly climatic variables (those based on temperature and precipitation) which had been summarised for only the spring and summer seasons (Appendix 2, Table A2.2). All of the other models tested performed relatively poorly with a combined weight < 0.001; the model based on the Miami index was ranked a distant second with a Δ AIC = 34.4. The Miami index model and the annual Tmp and Pre model (Δ AIC = 37.7) were similarly ranked and both performed notably better than the models with bioclimatic variables (all the models including variables based on growing degree days and dryness had Δ AIC > 47). Neither of the highly parameterised full seasonal models performed well. As suggested by preliminary analysis, CO_2 was an important predictor of INDVI and the inclusion of this variable alone led to a Δ AIC = 68.8, accounting for a large proportion of the improvement of parameterised models over the null model with Δ AIC = 268.3 (Table A2.2).

In all models INDVI was found to increase close to the sea where one might expect to find milder climate conditions. Similarly, in all models, carbon dioxide concentrations showed a strong positive effect on INDVI within sites; the magnitude of the CO_2 effect in all models translated approximately to a 0.1% increase in INDVI per ppm CO_2. In the best model, INDVI was positively related to spring temperature and precipitation, and to the interaction between summer temperature and precipitation.

Results from the cross-validation simulations implied that estimation errors were small relative to among-site variation in INDVI but large relative to the inter-annual variation within single sites (Fig. 2.2a). The root mean square error (RMSE) of the model estimates was not strongly impacted by the number of years excluded when fitting the model (Fig. 2.2a). Additionally, the coefficient of variation (CV) across the 1000 iterations for the model parameters increased little with the number of years excluded (ranging from 0 to 5). For eight of the nine parameters, the CV increased by less than 0.1, implying that the number of years excluded (and thus the sample size) had little effect on the confidence in the parameter estimates (Fig. 2.2b). Observed INDVI values and those estimated by the model were highly correlated (Pearson's r = 0.985, $P < 0.001$; Fig. 2.2c), but this correlation was largely due to the random Site ID intercept term included in the model. This component controlled for variation among sites and, when this known variation was ignored, the correlation between observed and estimated values was much weaker (Pearson's r = 0.408, $P < 0.001$; Fig. 2.2d).

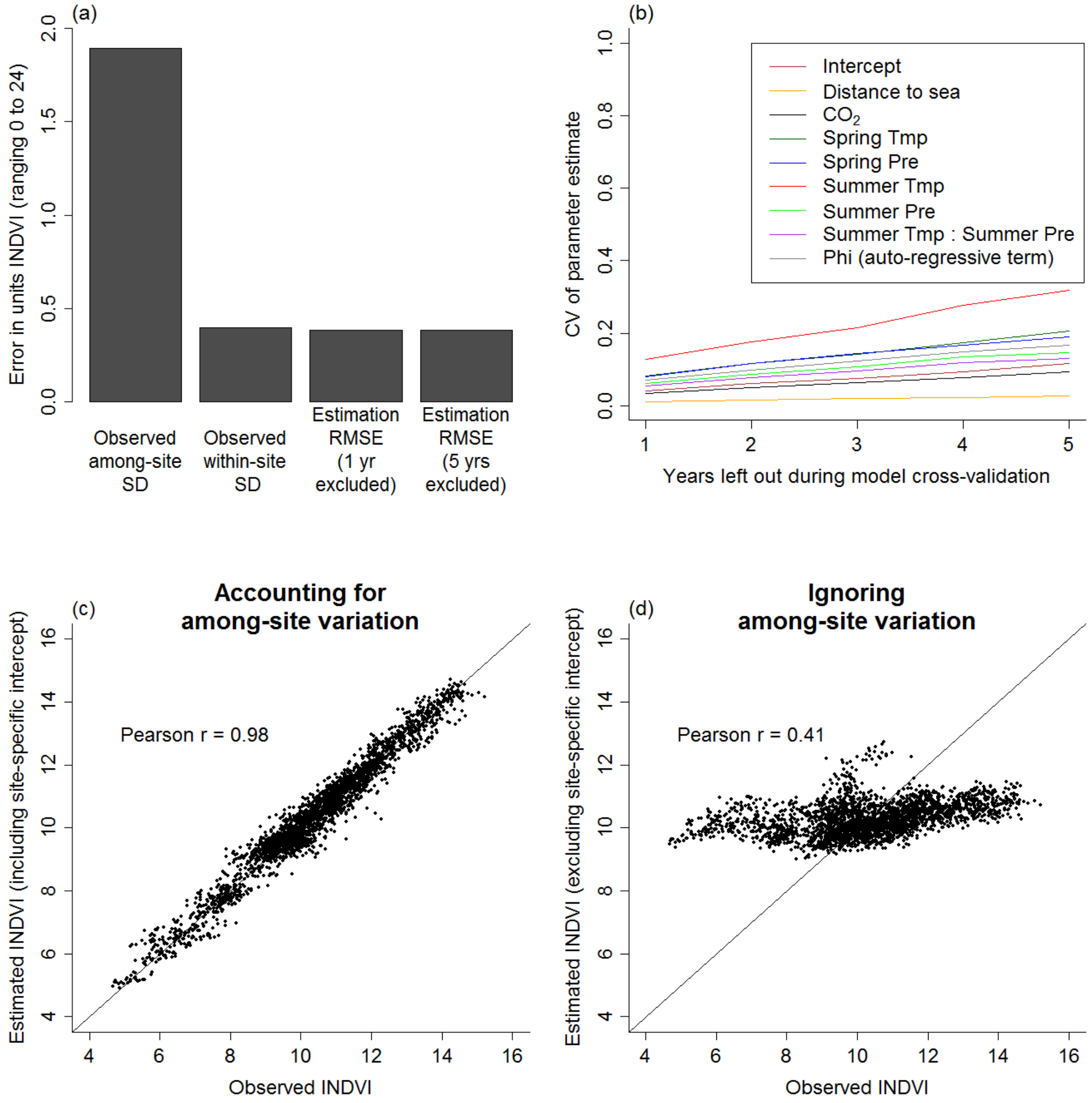

Figure 2.2: The performance of the AIC best multi-site yearly model of INDVI was investigated using a cross-validation procedure. A random effect was included in the model to control for variation in mean INDVI values among sites. In the cross-validation analysis, data from randomly chosen subsets of years were excluded, the model was re-fitted, and used to estimate the excluded data for all sites (see text for model details). The estimation Root Mean Square Errors (RMSE's) for iterations in which 1 and 5 years were excluded are compared to the within- and among-site standard deviation of the observed data (panel a). The uncertainty surrounding parameter estimates was evaluated by examining the coefficient of variation (CV) of the parameter estimates across iterations (panel b); see text and Table 2.1 for variable definitions. Finally, using only the iterations in which just one year was excluded at a time, the correlation between estimated and observed INDVI for the excluded years was examined; this was done both when the among-site variation was accounted for (i.e. the site-specific random intercept was included in the estimation process, panel c) and when this variation was ignored (and the site-specific intercept was excluded from estimation, panel d).

Within-site correlations between observed INDVI and the INDVI values estimated by the model varied greatly, but showed little geographical pattern (see Fig. 2.1, in Methods). The relatively large size of estimation error compared to within-site INDVI variation was highlighted by the model's poor ability to capture inter-annual variation in INDVI within the focal sites even when all data were used to fit the model (no years excluded; Fig. 2.3). The predicted year-to-year variations at the focal sites often did not reflect the time-series of observed change in INDVI from one year to the next. Correlations between the observations and model estimates (25 pairs at each site) were variable across the focal sites (Fig. 2.3, panels d, e, and f); the model performed best in reproducing yearly INDVI in Catenaia with a Pearson's $r = 0.62$ ($P < 0.001$; Fig. 2.3) and less well in Bogesund (Pearson's $r = 0.28$, $P = 0.172$) and Grimsö (Pearson's $r = 0.22$, $P = 0.290$).

Using the best model ("Reduced seasonal Tmp and Pre"; Appendix 2, Table A2.2), I projected INDVI for the three focal sites for the A1FI, A2, and B1 climate change scenarios. Because of uncertainty over how accurate the estimated contribution of CO_2 might be (see discussion), I made projections including and excluding CO_2 from the models. All three focal sites were projected to experience increases in INDVI by the end of the 21st Century (Fig. 2.4); unsurprisingly, increases were greatest in magnitude for all three sites under the extreme A1FI scenario and smallest under the more conservative B1 scenario (see Methods for scenario descriptions). Under the A1FI scenario, rates of INDVI increase asymptotically toward the end of the century, a result of approaching the maximum possible INDVI value of 24. When the effect of CO_2 is excluded from the model, the projected INDVI increase is much less; in the A1FI scenario all sites experience an increase of < 0.5 by 2100 (contrasting with the increases of > 4 in the models including CO_2; see Appendix 2, Table A2.3 for exact values). Using the selected model, most of the projected increase in INDVI from 2001 to 2100 is due to the more-or-less steady increase in CO_2 concentrations associated with the IPCC scenarios. The inter-annual fluctuations shown in projections are due to the effects of the climatic variables included in the model (spring and summer temperature and precipitation levels).

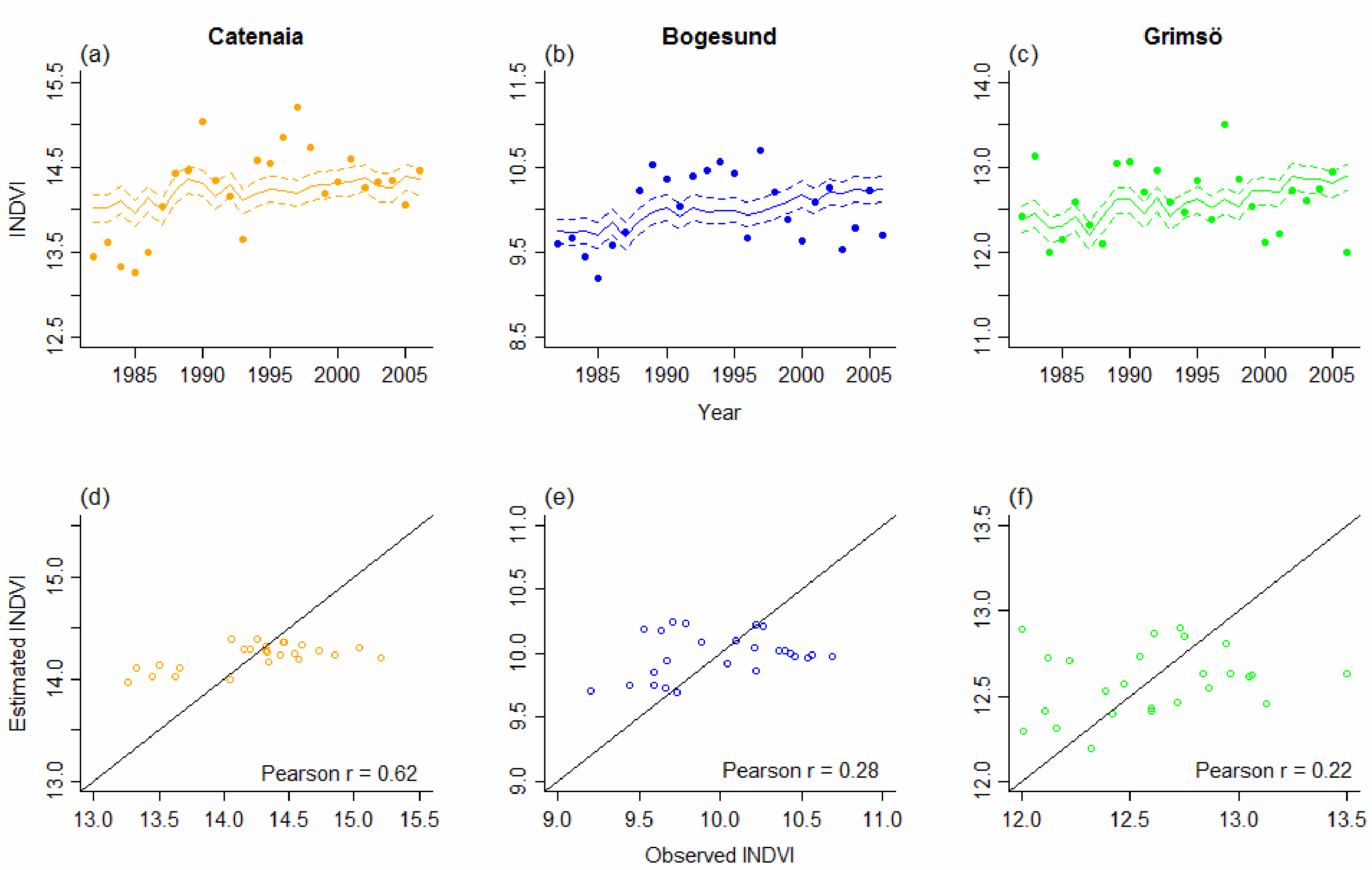

Figure 2.3: The performance of the AIC best multi-site yearly model of INDVI was evaluated by comparing model estimates against observed INDVI values from the three focal sites (Catenaia, orange, panels a & d; Bogesund, blue, panels b & e; and Grimsö, green, panels c & f). This model included the effects of seasonal temperature and precipitation metrics (from the spring and summer seasons) on annual INDVI at each site (see text and Appendix 2, Table A2.2 for more detail). In panels (a), (b), and (c) solid lines represent site-specific model estimates (with 95% CI, dashed lines) and points represent observed INDVI across years. The correlations between estimated and observed INDVI at Catenaia, Bogesund and Grimsö is illustrated in panels (d), (e), and (f) respectively.

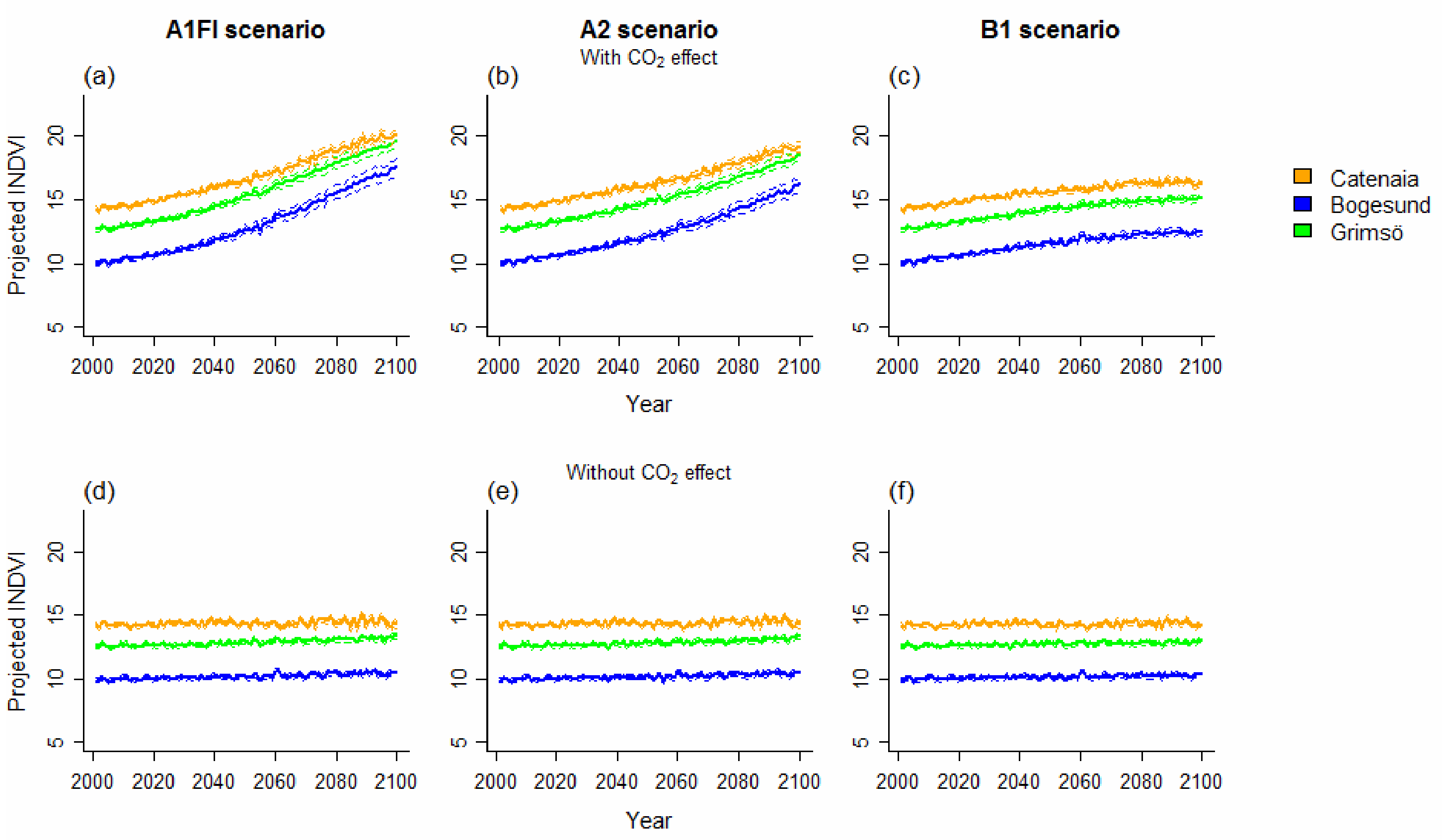

Figure 2.4: Using the best AIC multi-site yearly model, INDVI was projected into the future for each of the focal sites (Catenaia, orange lines; Bogesund, blue lines; and Grimsö, green lines). Climatic conditions from three different IPCC scenarios, the A1FI, A2 and B1 scenarios were used as predictors to create these projections (see text and Appendix 2, Table A2.1 for scenario descriptions). The best AIC model included global CO_2 concentrations, and seasonal temperature and precipitation conditions (from the spring and summer) as predictors of INDVI. Because of inherent uncertainty associated with the realistic strength and form of the CO_2 effect (see text for detail), projections were created with (panels a, b, & c) and without the effect of CO_2 (panels d, e, & f). The model used to create the projections excluding CO_2 was generated by refitting the best model without using CO_2 as a predictor (but including the other selected predictors). See text and Appendix 2, Table A2.2 for more detail on model specification and selection. Solid lines in all panels (a-f) represent projected INDVI; dashed lines represent the 95% confidence intervals surrounding the projections.

Single-site monthly models

I used focal site-specific models on a monthly time-scale to estimate INDVI_m (NDVI integrated on a monthly scale) based on climatic conditions of the current month and the two months prior; I then summed monthly estimates for a year to produce an estimate of INDVI (on an annual scale) for that site. Model selection resulted in distinct models being identified as “best” for each of the three focal sites. However, there were similarities among sites in both best models and the selected model sets in the relative importance of predictors and in the direction of estimated relationships with INDVI_m. For example, Dry_m of the current month was a relatively important predictor and had a negative effect in the best models for all three focal sites (Table 2.2 below).

Twelve competing models (with Δ AIC ≤ 6) were selected for Catenaia (Italy) (for a list of selected models in all sites, see Appendix 2, Table A2.4) and these models relied heavily upon the inclusion of climatic variables from the current month; time-lagged predictors were less important (Table 2.2). The best model included a negative relationship with Dry_m, and a positive relationship with $\text{CO}_{2\ m}$ and with the interaction of Pre_m and Gdd_m. The strength of $\text{CO}_{2\ m}$ as a predictor in this model translated approximately to a 0.12% increase in INDVI per ppm CO_2 similar to that observed in the yearly multi-site models. Interactions between Gdd_m and either Pre_m or Dry_m were important (Table 2.2) and were included in 10 of the 12 models selected. The results for Bogesund (Sweden) were similarly uncertain, with 7 models having Δ AIC ≤ 6. Bogesund’s top model included a positive relationship with temperature and negative relationship with dryness for both the current month and the one prior. Additionally, this model included relationships with temperatures from both of the two previous months ($\text{Tmp}_{m\text{-}1}$ and $\text{Tmp}_{m\text{-}2}$) and with growing degree days from two months prior to the NDVI response being modelled ($\text{Gdd}_{m\text{-}1}$ and $\text{Gdd}_{m\text{-}2}$). In keeping with this pattern, many of the other variables that were included in Bogesund’s competing model set were based on time-lags of one or two months. For Grimsö (Sweden), only two models had Δ AIC ≤ 6. The top-ranked model had a weight of 0.93; as with Bogesund, this model included Tmp_m and Dry_m as predictors. This model also included a positive term for the interaction between the lagged $\text{Tmp}_{m\text{-}1}$ and $\text{Dry}_{m\text{-}1}$ variables (from 1 month prior to the NDVI being modelled). The only competing model for this site had a weight of

0.07 and was very similar to the top model differing only by the inclusion of the current month's Pre_m as a predictor instead of Dry_m.

Table 2.2: Relative importance of climate predictors occurring in single-site monthly models of $INDVI_m$

	Relative importance of predictors in competing model set (Δ AIC ≤ 6)[a]		
Climatic predictors[b]	Catenaia (12 models)	Bogesund (7 models)	Grimsö (2 models)
Tmp_m	0.02	0.82 (bm)	1.00 (bm)
Pre_m	1.00 (bm)[a]	0.13	0.07
Gdd_m	1.00 (bm)		
Dry_m	1.00 (bm)	0.76 (bm)	0.93 (bm)
$CO_{2\,m}$	0.65 (bm)		
$Tmp_m : Pre_m$	0.02		
$Pre_m : Gdd_m$	0.65 (bm)		
$Pre_m : Dry_m$	0.13		
$Gdd_m : Dry_m$	0.25		
$Tmp_{m\text{-}1}$		1.00 (bm)	1.00 (bm)
$Pre_{m\text{-}1}$	0.07		
$Gdd_{m\text{-}1}$	0.03	0.19	
$Dry_{m\text{-}1}$	0.14		1.00 (bm)
$Tmp_{m\text{-}1} : Gdd_{m\text{-}1}$			
$Tmp_{m\text{-}1} : Dry_{m\text{-}1}$			1.00 (bm)
$Tmp_{m\text{-}2}$		0.92 (bm)	
$Gdd_{m\text{-}2}$		0.79 (bm)	
$Dry_{m\text{-}2}$		0.02	
$Tmp_{m\text{-}2} : Gdd_{m\text{-}2}$		0.29	

[a] The relative importance of a predictor is calculated as the sum of the weights of all competing models (with Δ AIC ≤ 6) including that predictor (see Appendix 2, Table A2.4 for site-specific model sets). The notation "(bm)" after a value indicates inclusion of that predictor in the AIC best model for the site listed. Model fit and predictive ability is addressed in the Results section of the text and also in Figures 2.5 and 2.6.

[b] Predictors listed with a subscript of "*m*" are from the same month as the $INDVI_m$ response being modelled. In predictor names suffixes of "*m*-1" and "*m*-2" denote a one and two month time-lag respectively.

Similar to results seen in the cross-validation analyses of the yearly multi-site model, the number of years excluded in cross-validation of the monthly models appeared to have little impact on predictive ability (Fig. 2.5). In contrast to the poor predictive ability of the multi-site yearly models, the best monthly models for the Swedish sites performed relatively well (Pearson's correlations between observed and estimated values were high: 0.55, $P < 0.01$ for Bogesund and 0.60, $P < 0.01$ for Grimsö). The Pearson's correlations observed between observations and estimates for Bogesund and Grimsö in the leave-one out cross-validation were 0.47 ($P < 0.05$) and 0.56 ($P < 0.01$) respectively (Fig. 2.5d, e, and f). Furthermore, estimates of the monthly models selected for Bogesund and Grimsö reflected inter-annual variation in INDVI

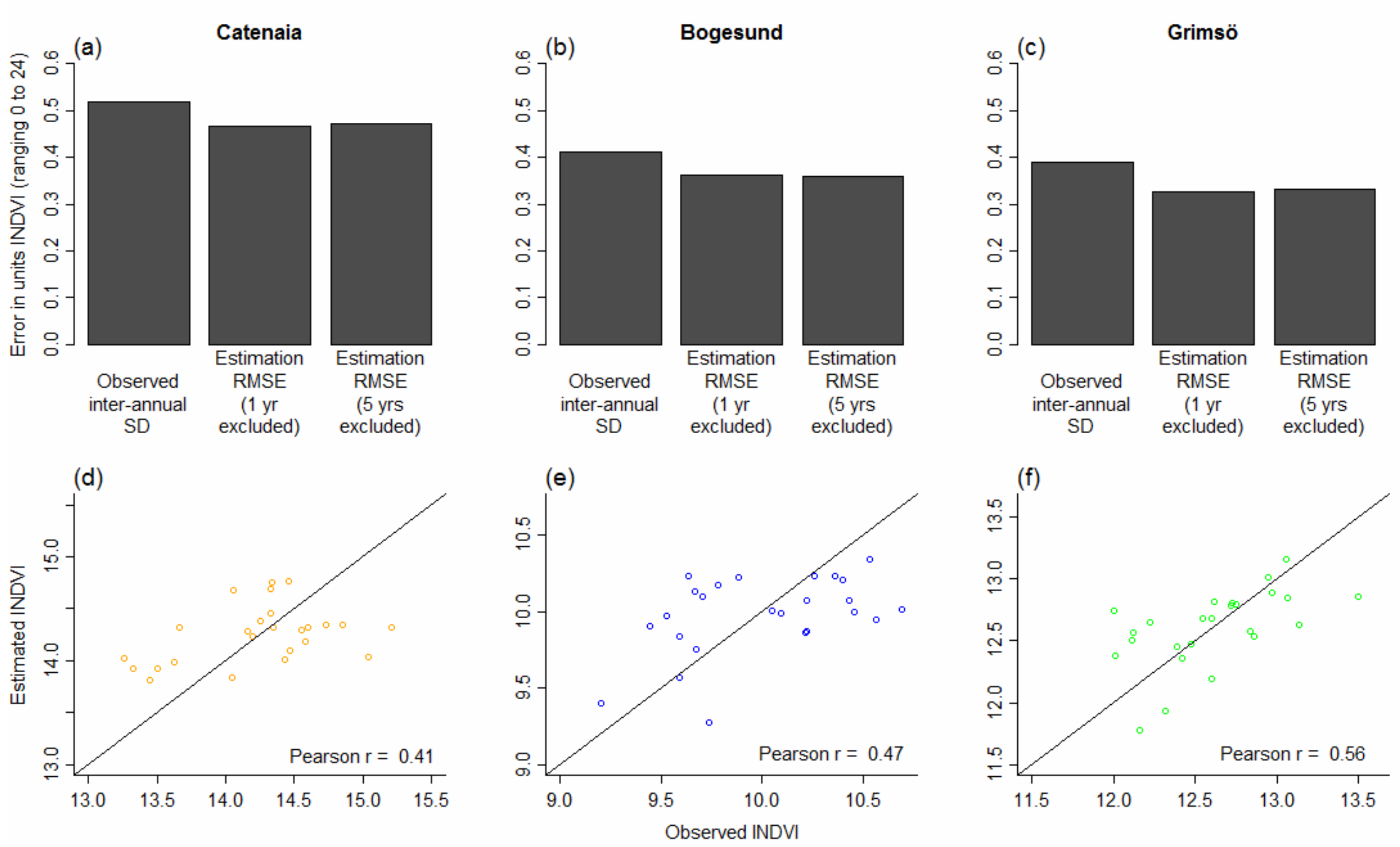

Figure 2.5: The performance of the site-specific AIC best monthly models was investigated using a cross-validation procedure. In these models, monthly NDVI sums ($INDVI_m$) were modelled in response to climate conditions. Estimates of $INDVI_m$ were summed to produce estimates of annual INDVI. During cross-validation, data from randomly chosen subsets of years were excluded from the datasets, models were refitted, and used to estimate the excluded data. The estimation Root Mean Square Errors (RMSE's) for iterations in which 1 and 5 years were excluded are compared to the standard deviation of the observed data within the associated site (Catenaia, panel a; Bogesund, panel b; Grimsö, panel c). Using the iterations in which one year was excluded at a time, the correlation between estimated and observed INDVI for the excluded years was examined (Catenaia, panel d; Bogesund, panel e; Grimsö, panel f).

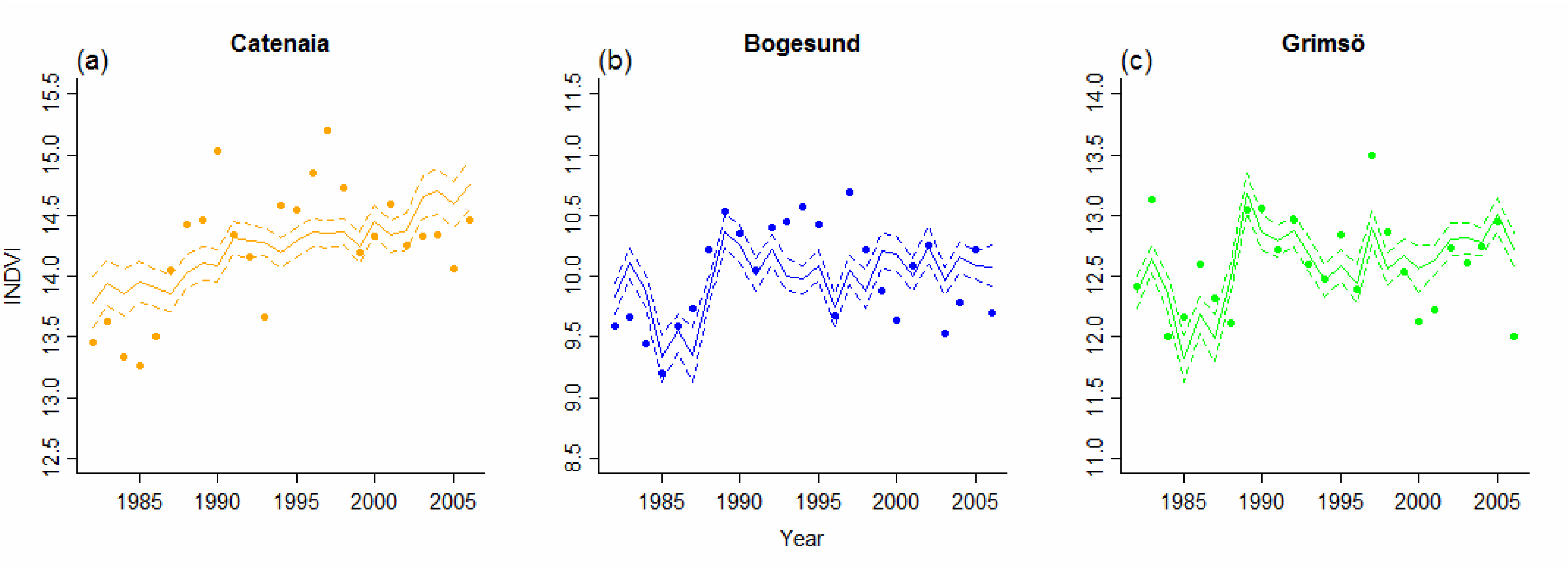

Figure 2.6: The performance of the AIC best single-site monthly models was evaluated for Catenaia (orange, panel a), Bogesund (blue, panel b), and Grimsö (green, panel c). The sum of bimonthly NDVI measures (INDVI_m) were modelled as response to monthly climate conditions. Model fitting and model selection was site-specific (see text and Table 2.2 for details on methods and on the parameters selected in each site). Estimates of the INDVI_m resulting from the fitted models were summed within years to give estimates of annual INDVI at each site. In each panel, solid lines represent the site-specific estimates of annual INDVI (with 95% CI, dashed lines) and points represent observed INDVI across years.

well, capturing, for example, the dip in productivity seen in the mid-late 1980's and the subsequent peak in INDVI in both sites which occurred in 1989 (Fig. 2.6b and c).

The monthly models for Catenaia performed less well. Errors surrounding the estimates of the best model for Catenaia were relatively large (compared to the estimation errors calculated for the other sites; Fig. 2.5a). The ability of Catenaia's best monthly model to reproduce the observed trend in INDVI at the site was mediocre (Fig. 2.6a). The Pearson's correlation between the observations and estimates of the best model was lower than at the Swedish sites ($r = 0.50$, $P < 0.05$) and this was also true for the leave-one out cross-validation ($r = 0.41$, $P < 0.05$; Fig. 2.5d). Increasing INDVI estimates for Catenaia were primarily driven by the steady rise in CO_2 concentrations observed throughout the study period. Inter-annual fluctuations in estimated INDVI (the sum of the monthly estimates within a year) were small relative to observed variation in INDVI (Fig. 2.6a). Because CO_2 increased steadily across seasons and years, its effect could obscure seasonal effects on INDVI. Preliminary exploration of the third-ranking monthly model for Catenaia, which did not include CO_2 as a predictor (Appendix 2, Table A2.4), led to a very poor simulation of observed INDVI (the correlation between observed INDVI values and those estimated by this model were negative, although non-significant).

Projections based on the top-ranked model chosen for each of the Swedish sites implied a slight but steady increase in INDVI under all climate scenarios (Fig. 2.7a, b and c). For example, under the A1FI scenario Grimsö's INDVI is projected to reach a mean value of 13.68 during the 2051-2100 period, compared to a mean of 12.60 which was observed from 1982-2006; the increase for Bogesund is similar but slightly smaller. These increases are considerably smaller than those projected by the yearly model which included CO_2 but on a similar scale to increases projected by the yearly model when CO_2 was excluded (Appendix 2, Table A2.3). The monthly model for Catenaia resulted in a large projected increase in INDVI by 2051-2100 in all scenarios (ranging from 3.09 to 6.20 higher than the observed mean of 14.23; Fig. 2.7a). This projected change in INDVI was larger than that projected by the yearly multi-site model for this area (Appendix 2 Table A2.3). Given the poor overall performance of this monthly model in simulating observed INDVI for Catenaia, the resulting projections for this site should be viewed with great scepticism.

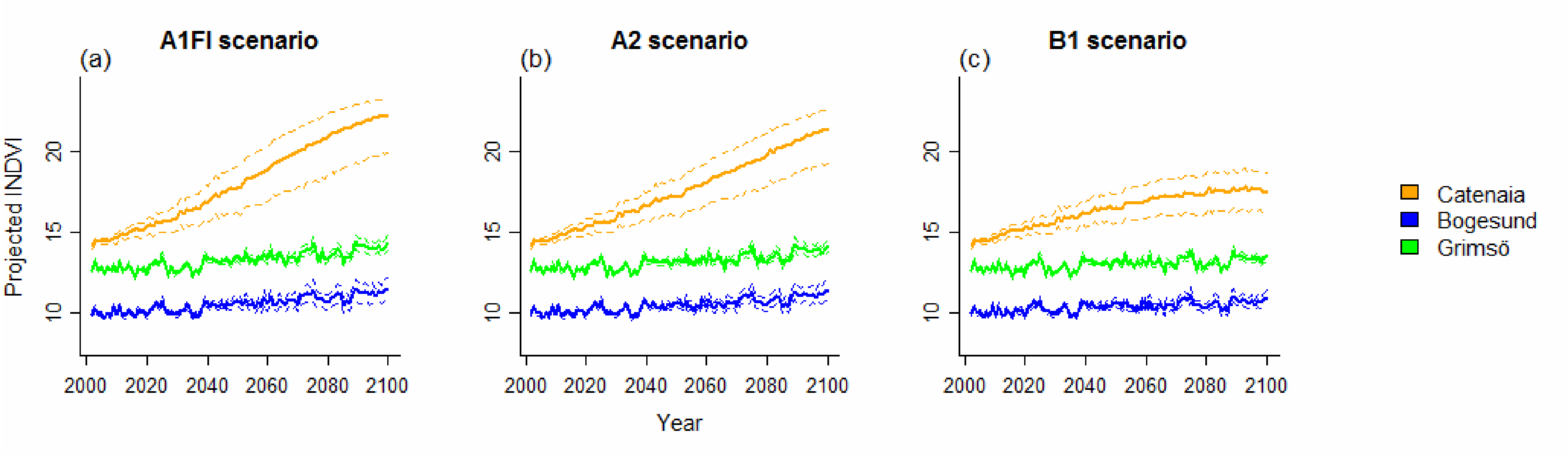

Figure 2.7: Using the site-specific best AIC single-site monthly models, INDVI (the sum of all monthly INDVI$_m$ estimates within the same year) was projected into the future for each of the three focal sites (Catenaia, orange lines; Bogesund, blue lines; and Grimsö, green lines). Climatic conditions from three different IPCC scenarios, the A1FI (panel a), A2 (panel b) and B1 (panel c) scenarios were used as predictors to create these projections (see text and Appendix 2, Table A2.1 for scenario descriptions). Solid lines in all panels (a-c) represent projected INDVI; dashed lines represent the 95% confidence intervals surrounding the projections.

Discussion

The results of the analyses presented here suggest that under some conditions, climate might be a good predictor of INDVI at specific sites. However, they also highlight some difficulties associated with using NDVI as an index of inter-annual changes in vegetation, especially when modelling large geographic areas. Considering the link between INDVI and net primary productivity, it is rather surprising that temporal variation in INDVI values is not more consistently well estimated by annual climate conditions. In general, annually integrated NDVI (INDVI) might be better suited to distinguishing among geographically distributed vegetation types, rather than tracking temporal productivity changes. Others, while not explicitly investigating the use of INDVI in this manner, have occasionally suggested that this might be the case; for example, Potter and Brooks (1998) found that seasonal extreme NDVI values (maximum and minimum) did not show a predictable response to annual climate conditions. As these authors propose, adaptation of plant species to long-standing local climate cycles may buffer against immediate responses to annual climate (see also Bennie et al. 2010). Indeed, as seen in this study, the magnitude of inter-annual variation in INDVI is miniscule compared to that among locations; this is a formidable challenge when modelling temporal change across a large geographic area.

INDVI response to annual climate across Europe

The yearly models treating INDVI as a response to yearly climate conditions appeared to perform well across sites, but performed very poorly when reproducing differences in INDVI at an inter-annual scale within the focal sites; this suggests relationships between productivity and climate may be site-specific and, in the future, single-site models might be more appropriate. Despite this, the comparison among *a priori* models lends insight into some of the factors driving vegetation productivity in sites across Europe. The best performing model relied on a limited number of seasonally-based climate metrics (specifically temperature and precipitation in spring and summer), a fact which emphasises the importance of sub-annual time periods, not all of which are equally important drivers of vegetation productivity. Models depending on the bioclimatic variables, growing degree days and dryness, were consistently less well supported than their temperature and precipitation-based counterparts.

Additionally, it is interesting to note that the model based on the traditional Miami Model (Lieth and Whittaker 1975), while not competing (with Δ AIC = 34.4), was the second best model of those tested and performed slightly better than the annual Tmp and Pre model. Both these models were based on annual temperature and precipitation, but the Tmp and Pre model required the estimation of more parameter coefficients than the model using the Miami index; this is likely due to the minimization function built into the Miami model (see Equation 2.1) which “designates” only Tmp or Pre as limiting productivity under any given climatic conditions. In the future, a modification of the Miami model incorporating seasonal measures of temperature and precipitation might generate improved estimates of NPP and be worth pursuing.

These analyses also underline the need to understand better the effects of CO_2 on vegetation productivity, not only for single plant species, but at a more general community level that will be most useful to ecological managers. It appears that CO_2 concentration was the single most important predictor of INDVI in these models. It is well established that elevated CO_2 concentrations can facilitate photosynthesis, thus increasing vegetation productivity, but the strength of this effect is debated (Long et al. 2006, Rickebusch et al. 2008, Lee et al. 2011). The (CO_2) effect size in the models presented here is roughly equivalent to a 0.1% increase in INDVI per ppm CO_2. While this is broadly consistent with existing literature (Ewert et al. 2005, Long et al. 2006, Hermans et al. 2010), this similarity is unremarkable given the uncertainty surrounding not only the magnitude of CO_2 enrichment effects but also the functional form (linear vs. asymptotic vs. hyperbolic) of vegetation response to increasing concentrations of this gas. Current studies, most notably the Free Air Carbon Enrichment (FACE) experiments (Nowak et al. 2004, Ainsworth and Long 2005), are helping to define the relationship between CO_2 concentrations and vegetation production; however, much of what is known is limited to individual agricultural species and work on broader species assemblages suggests a lack of generalities among vegetation-CO_2 relationships that is not conducive to making reliable predictions (Ainsworth and Long 2005, Lee et al. 2011). The magnitude of vegetation response to CO_2 and the point at which this response becomes saturated (as other factors limit productivity) is greatly debated; for example, Curtis and Wang (1998) suggest a saturation point as low as ~550 ppm, while Long et al. (2006) assert that saturation is likely to occur between 800 and 2000 ppm. Because these proposed saturation points in the relationship between CO_2 and INDVI lie outside the small range of CO_2 concentrations observed over the study period, quantifying such non-linearities in the relationship is currently impossible. Furthermore, in the time-series based models presented here, the uncertainty is complicated by the fact that other aspects of environmental change (e.g. nitrogen deposition) are developing simultaneously to increasing CO_2 concentrations, probably confounding the INDVI variation attributed to CO_2 alone. For all these reasons, it is difficult to establish the relationship between CO_2 and productivity with confidence.

INDVI response to monthly climate

The monthly analysis, which modelled INDVI time-series in the focal sites as a response to monthly climate predictors, addressed some of the issues which could have caused the poor performance of the yearly models discussed above. In addition to allowing for site-specific variation in productivity-climate relationships by modelling each site separately, these models used data on a finer temporal scale, calculating INDVI as the sum of monthly estimates. This approach is more mechanistically reflective of the manner in which NPP is likely to respond to climate conditions and of the way in which INDVI is calculated. The hope was that this method would exploit the large intra-annual variation in NDVI and climate and provide insight into important drivers of productivity which may have been overlooked. In Bogesund and Grimsö, the selected best models relied heavily on temperature and dryness as predictors including interactions and lagged effects of these metrics from up to two months prior to the month whose productivity was being modelled. This is consistent with other studies, which have found that NDVI is affected by both temperature and rainfall from one and two months prior (Potter and Brooks 1998, Parmiggiani et al. 2006, Pettorelli et al. 2007). Even though the uncertainty surrounding estimates was large (indicated by wide confidence intervals), these monthly models performed relatively well and generated realistic INDVI time-series for the observed period in Bogesund and Grimsö.

The single-site monthly analysis was not very successful at modelling INDVI in Catenaia. Similar to the multi-site yearly models, the monthly model chosen for Catenaia did a poor job of reflecting inter-annual changes in INDVI observed over the study period. The concentration of CO_2 was an important predictor leading to a gradual increase in INDVI, but model estimates did not adequately represent shorter term variation in the response. Despite the apparent importance of predictors related to dryness (Dry_m and interactions of Dry_m and Pre_m with Gdd_m), without the inclusion of CO_2 in the models these climate metrics on their own were very poor at estimating INDVI in this site. One possible reason for the mismatch between observed and estimated INDVI in Catenaia is the relatively complex topography of the area. Compared to the Swedish sites which are both generally flat and low altitude, Catenaia is in the foothills of the Italian Alps. The high degree of altitudinal variation in the area could lead to poor accuracy of the down-scaled global climate datasets (observed and projected) because topography generates fine scale variation in climates. The relatively coarse scale of the climate datasets used in this analysis (the CRU datasets have a resolution of 0.5^o) means that fine scale variation in climate, as might be driven by topography, is poorly described (Cook et al. 2010). This observation error may be more pronounced in the monthly datasets as some of the error would cancel out when averaged over a year.

Finally, it is important to note that while $CO_{2\ m}$ was included in the top-ranking monthly model for Catenaia, this predictor was not in all the competing models for this site and did not feature in models selected for either of the Swedish sites. This is in sharp contrast with the importance of CO_2 as a predictor in the yearly multi-site analysis. This may be due to inter-site variation in the response of vegetation to increased CO_2 concentrations. Increased concentrations of carbon dioxide can facilitate water-use efficiency (plants decrease stomatal apertures thus reducing transpiration; Ainsworth and Long 2005, Gerten et al. 2005). Therefore, it is likely that increasing concentrations of this gas have a stronger positive effect on vegetation in areas that are more water-limited; this would explain the occurrence of $CO_{2\ m}$ as a predictor in the best model for the sub-Mediterranean site, Catenaia, and its absence from the model sets for the northern Swedish sites which are likely to be limited by temperature (not water availability). Additionally, it is likely that CO_2 concentration was no longer highlighted as such an important predictor in the monthly analyses because the seasonal variation of NDVI within years is much greater than that observed between years. As seasonally de-trended measurements of CO_2 were used in these analyses, estimated $CO_{2\ m}$ concentrations varied little within years (except for a small, gradually positive change). This contrasts with a well known intra-annual cycle of atmospheric CO_2 concentrations that could be used instead, as a covariate in the models. However, it is generally accepted (Enting 1987, Bonan and Shugart 1989, Nemry et al. 1999) that CO_2

uptake by vegetation drives these cycles as opposed to the other way around. Given the goal of these analyses to model productivity as a response to potential climatic change which is, in part, driven by gradually increasing CO_2 concentrations, the seasonally de-trended CO_2 time-series seemed most appropriate.

INDVI projections, implications, and uncertainty

The projections generated by all of these models (yearly and monthly) should be regarded with some caution. However, at least for the Swedish sites, the projections generated by monthly models are worth considering. Given the poor performance of the monthly model in Catenaia, Italy, and the uncertainty surrounding the parameterisation of CO_2 effects on vegetation production ($CO_{2\,m}$ was an important predictor in this site), it is inadvisable to draw any conclusions regarding the response of productivity to climate change in this area. In Bogesund and Grimsö, the monthly models represented the observed time-series fairly well, so projections using these models could be considered a useful first approximation of potential productivity trajectories for these sites for the 21st Century. Unlike the yearly models, in these two Swedish sites, the monthly models have the advantage of excluding CO_2 effects (this variable was not in the best models for these sites) and the uncertainty associated with their parameterisation. It is reassuring that the magnitude of productivity increase projected by these models is just slightly higher than that projected by the yearly models excluding CO_2; this suggests that the estimation of INDVI increase due to other climate predictors was fairly robust. The projections of steadily increasing productivity for Bogesund and Grimsö are consistent with other research suggesting that longer, warmer growing seasons will result in higher productivity in Northern Europe where temperature is limiting (Slayback et al. 2003, Fronzek and Carter 2007, Penuelas et al. 2007). Increased productivity could have numerous knock-on effects for entire ecological communities. For example, herbivore populations could fluctuate more dramatically from one year to the next; these populations might respond to increased productivity with faster growth, and, then, could crash abruptly during occasional years of poor productivity (Wilmers et al. 2007a, Wilmers et al. 2007b). Such populations, exhibiting more dramatic cycles of “boom and bust,” would impact upon co-existing species, including both predators and competitors, and will likely necessitate more aggressive wildlife management regimes (such as culling) to regulate their abundance.

The potential ecological ramifications of changing primary productivity levels are far-reaching.

Considering the ecological consequences of the projected changes in productivity presented here requires caution. A great deal of uncertainty is inherent in these climate change projections, not all of which is illustrated by the confidence intervals surrounding the projected values of INDVI (Mitchell et al. 2004, Giorgi 2005). Some of the uncertainty that is not illustrated by the confidence intervals is encompassed by the IPCC scenarios; these scenarios include variation in greenhouse gas emissions and in the global development of human society. Some of the uncertainty is due to lack of knowledge concerning climate response to greenhouse gas concentrations and can be further investigated by examining other global climate models (only the HadCM3 model is used here). Uncertainty is compounded by ignorance regarding the form of vegetation response to climate metrics, particularly beyond the observed range of climates for European sites to date. This is a key hurdle to overcome before more reliable projections can be produced and currently constrains models to using simplistic linear effects. A non-linear treatment of predictors would be ideal, but constructing such relationships without more advanced knowledge about the response of vegetation to climate is largely speculative, given that an observed response to today’s climate (linear or otherwise) might not be accurate when extrapolating to projected conditions.

Conclusion

Results from this study generally support previous predictions of increased productivity for locations in Northern Europe and highlight an immediate need for more information about the climatic drivers of productivity. There is a need to describe climate-productivity relationships for the climatic conditions expected with climate change, not just those currently existing, so that they can be translated into mechanistically realistic models. In order to develop ecological models which can be applied on a site level and then incorporated into climate change mitigation plans, these relationships should be defined not only for specific plant species but on a more general community-wide scale. Additionally, I found that annually integrated NDVI for European sites generally shows limited variation from one year to the next and, therefore, may not provide an ideal index for estimating the response of vegetation to the changing climatic conditions expected over the next century. These caveats need to be taken into account when using projections of INDVI into the future. However, the monthly models for the two Swedish sites performed well at reproducing contemporary INDVI patterns, and, therefore, provide a basis for initial projections of future vegetation productivity at Bogesund and Grimsö. These projections can be used in analyses of the implications of climate change for herbivore populations at these two sites. While such analyses must be undertaken with caution, they provide one avenue to an understanding of how animal populations may have to be managed in response to climate change.

Chapter 3 – The climatic and non-climatic drivers of ungulate survival: a case-study of two roe deer populations

Abstract

Research on climate change impacts has focused on projecting changes in the geographic ranges of species, with less emphasis on the impacts of climate on the vital rates giving rise to species distributions. Additionally, studies of the role of climate in population dynamics often focus on the direct climatic effects while overlooking potentially important indirect climatic and non-climatic drivers. In this study, I model the survival of roe deer at two Swedish study sites, Bogesund and Grimsö, using a variety of direct climatic, indirect climatic and non-climatic predictors. I use two modelling methods: generalised linear models and capture-mark-recapture models. The best models consistently included one climatic predictor (direct or indirect) and one non-climatic predictor, the latter associated with predation or human harvest. The model estimates replicated observed survival well (Pearson's r = 0.55 – 0.69 across sites and modelling methods). Despite consideration of a large pool of candidate predictors with noisy datasets, the results were generally consistent across sites and modelling methodologies. Furthermore, models performed well when evaluated through cross-validation. Strong positive relationships with INDVI (an index of vegetation production) in three of these models highlighted the potential for climate to affect roe deer survival indirectly via climate-driven changes in vegetation. Climate change is likely to drive increased vegetation productivity in northern Europe, so roe deer survival might increase in the future. The inclusion of negative relationships with lynx presence (Grimsö) and human harvest (Bogesund) reflect differences in the ecology of the two sites (one with predators and one without), suggesting factors that might reduce roe deer population growth and thus counteract the effects of climate change. These results stress the importance of simultaneously considering indirect climatic and non-climatic drivers when describing the response of wildlife populations to climate change.

Introduction

Climate change impact research, to date, has focused on identifying where species are likely to find suitable climate in the future without considering how well populations will persist in the “climatically suitable” areas that are identified (Hill et al. 2002, Araujo and Guisan 2006, Thuiller et al. 2006, Huntley et al. 2008, Elith and Leathwick 2009). The species distribution models used in many of these analyses generally assume that species are in equilibrium with their environment and ignore the dynamic processes giving rise to species ranges (Guisan and Thuiller 2005, Pagel and Schurr 2012). Filling this gap requires mechanistic models of population dynamics that incorporate climate effects and can produce projections of population growth that can inform management decisions (Barnard and Thuiller 2008, Thuiller et al. 2008, Huntley et al. 2010, Dormann et al. 2012).

Population growth models have two major components, survival (this chapter) and fecundity (see Ch. 4), both of which could be affected directly and indirectly by changing climatic conditions. For example, some herbivore populations experiencing increased survival due to milder winter temperatures (direct effect due to lower risk of hypothermia) might also experience increased survival due to climate-driven increases in vegetation productivity (indirect effect). Additionally, in many wildlife populations, the survival component of population growth is further complicated by the potentially density-dependent impacts of predation and hunting. Including these factors in models of climatic impacts on survival is crucial, not only because they can obscure relationships between survival and climate, but because predators and human harvest provide important mechanisms for managing the fluctuations of wildlife populations (Sinclair 1997, Ballard et al. 2001, Apollonio et al. 2010). Predation could mitigate the impacts of climate change by reducing variation in population growth and vital rates, thereby dampening the fluctuations of prey populations (Wilmers et al. 2006, Wilmers et al. 2007a, Gilg et al. 2009). Only by simultaneously considering the potential effects of climate, climate-driven changes in food resources, predation, and human management can researchers develop models of survival to underpin mechanistic simulations of population growth and inform effective management plans in the face of climate change.

Large amounts of data, from relatively complex ecological systems, are likely to be required to build predictive population models that incorporate both climatic and non-climatic drivers. Temperate ungulates provide an opportunity to examine different drivers of survival simultaneously. Analyses of long-term datasets have furthered the understanding of ungulate population dynamics (e.g. Clutton-Brock et al. 1985, Gaillard et al. 1993, Jedrzejewska et al. 1997, Coulson et al. 2001). Yet, many of these studies come from sites without predators or human harvest, thus omitting two potential drivers of survival that influence many wildlife populations (Gaillard et al. 2000b, Nilsen et al. 2009a). Additionally, studies addressing climate-driven population dynamics in herbivores often suggest that lagged effects of climate are mediated by altered vegetation production (Forchhammer et al. 1998, Wang et al. 2002, Griffin et al. 2011), without including explicit vegetation measures to examine this link.

Roe deer (*Capreolus capreolus*) demonstrate complex, age-structured, population dynamics that are driven by both climatic and non-climatic factors such as density-dependence and predation pressure (Liberg et al. 1994, Gaillard et al. 1998b, Festa-Bianchet et al. 2003, Nilsen et al. 2009a). Recent increases in their populations are associated with large economic costs from vehicular collisions, and damage to both forest vegetation and crops (Cederlund et al. 1998), but are also beneficial for recreation-based economies (e.g. hunting). Identifying the contribution of climate-driven changes in survival to variation in population dynamics across time and space is necessary to understand how roe deer populations will be affected by climate change. Similar to other ungulates (reviewed by Gaillard et al. 1998a), prime-age roe deer (adults, 2-7 years old) experience high survival that is relatively consistent among years. Any reductions in adult survival can have large impacts on population growth (i.e. adult survival has a high elasticity on lambda; Gaillard et al. 1998b, Nilsen et al. 2009a). The survival of subadults (one year olds) is more variable among years but typically has a smaller effect on population growth (Gaillard et al. 1998b).

A multitude of factors have the potential to influence roe deer mortality rates and must be considered in survival models. Studies of roe deer repeatedly suggest that winter is the critical period for survival, with harsh climate conditions increasing mortality rates (Fruzinski and Labudzki 1982, Cederlund and Lindström 1983, reviewed by Gaillard et al. 1998b). In particular, snowfall has been identified as an important indirect cause of mortality because deep snow impedes mobility and feeding on ground vegetation and can lead to starvation (Cederlund 1982, Fruzinski and Labudzki 1982, Mysterud et al. 1997, Mysterud and Ostbye 2006). Conversely, inter-annual variation in net primary production of vegetation (NPP) could be an important source of variation in survival; food availability throughout the year may contribute to the accumulation of body mass which can affect winter survival (Gaillard et al. 1998b, Gaillard et al. 2000a, Pettorelli et al. 2006). This possibility is consistent with studies linking higher NPP to higher population densities and growth rates (Melis et al. 2009, Melis et al. 2010). Finally, hunting by humans and predation by lynx (*Lynx lynx*) are likely drivers of mortality among all age classes of roe deer. Lynx are stalking predators specialising on roe deer, commonly killing adults and maintaining high kill rates even when roe deer densities are low (Aanes et al. 1998, Nilsen et al. 2009b, Mejlgaard et al. 2013). Despite this knowledge, analyses of survival have generally been limited to a small subset of possible drivers and have emphasised hypothesis testing rather than building predictive models which could be used to simulate population dynamics.

In this chapter, I use data from two sites in Sweden with long-term roe deer monitoring programs to investigate the importance of non-climatic and direct and indirect climatic drivers of roe deer survival rates. The ultimate goal of this analysis is to build predictive models of roe deer survival that, in combination with models of fecundity (see Ch. 4), can be used to simulate inter-annual fluctuations in roe deer population growth (see Ch. 5). In order to consider indirect climatic effects explicitly in my models, I use a widely available remotely-sensed index of vegetation productivity, NDVI (Normalized Difference Vegetation Index), as a potential predictor. I investigate non-climatic predictors by considering the effects of population density, human harvest and predation in model selection. Specifically, I use these models to address the following questions:

1) How does variation in annual roe deer survival relate to climatic conditions?
2) Does the direct inclusion of a measure of vegetation (NDVI) rather than strictly climatic predictors improve models and the understanding of roe deer survival?
3) Do the effects of climate and climate-driven variables on survival differ between the two study populations and is there evidence that any observed differences are related to the presence of predators in one of the sites?

4) Are the data available from such well-monitored sites sufficient to construct models of survival observed throughout the study period?

Data collection methods

Study sites and management

I use data from two sites in Sweden: Bogesund and Grimsö. In addition to the differences in management and community composition described in this chapter, these sites differ in terms of climate and productivity. Compared to Bogesund, Grimsö has harsher winters and lower vegetation productivity (see Ch. 1 for detail).

Researchers in Bogesund began manipulating the local roe deer population for a density-dependence experiment in 1988 (Kjellander 2000) and, since then, various research objectives and shifts in management authority have led to changes in the harvest rates imposed on the population. Detailed records of these management plans and harvest restrictions are not available, but the number of deer shot each year was recorded (see section on “Annual harvest records” below). Initially, the Bogesund site was divided into two areas, X-area, the experimental area (12.5 km^2; generally indicated by the distribution of box-traps in Fig. 3.1a) on the western part of the peninsula; and C-area, the control area (13.5 km^2) in the East. In X-area human harvest was halted from 1988 until the winters of 1992-93 and 1993-94 when more than 300 deer were culled (about 75% of the population; Kjellander 2000). After 1993, low harvest rates were implemented and managers allowed the density in X-area to recover. Since 1994 the two areas have been manipulated simultaneously through hunting regulations with the main goal of building harvest models (see Fig. 3.2 below for a timeline of management goals). Because the population in X-area was more closely monitored than that of C-area, the data I used are based on the X-area population. Hereafter, X-area is referred to simply as the Bogesund study area.

The Grimsö Wildlife Research Area (GWRA; containing the Grimsö site) has been loosely managed since the 1970s with the goal of allowing natural processes (e.g. climate, predation and density-dependence) to regulate the population. Managers aimed to allow hunting which helped to limit population growth without decreasing deer abundance. The data used here come from a “study area” of approximately 80 km^2, within the GWRA (Fig. 3.1b). Deer have been monitored with box-traps and radio-

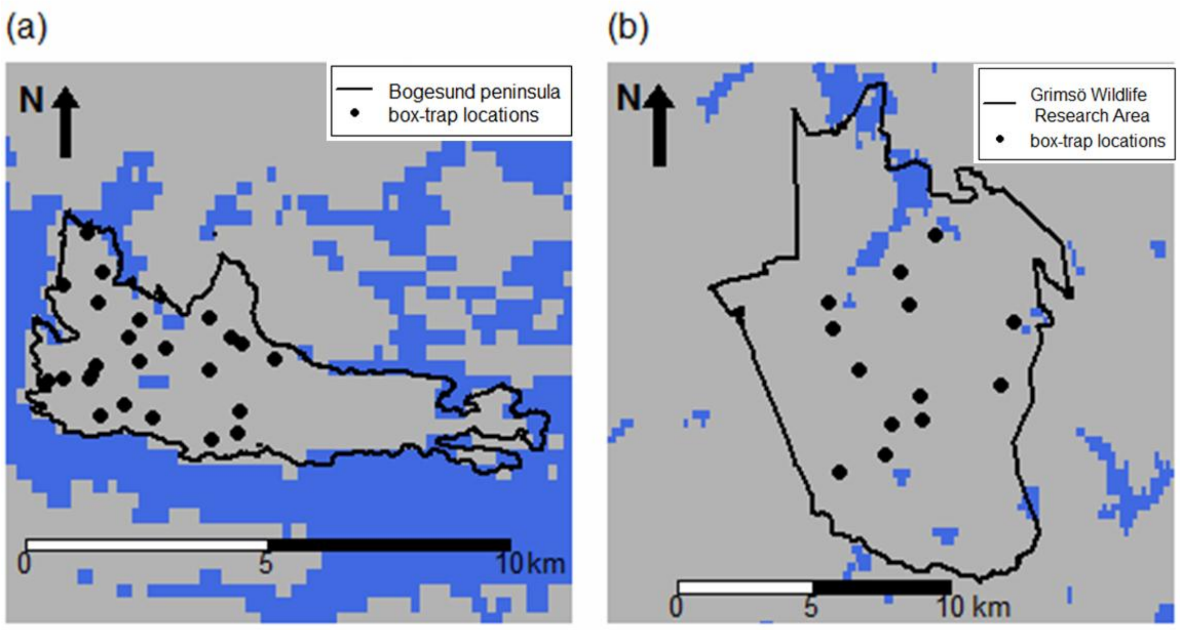

Figure 3.1: The outlined areas represent the boundaries of the Bogesund peninsula (panel a) and the Grimsö Wildlife Research Area (GWRA; panel b). The box-trap grid in Bogesund and Grimsö covered a sub-portion of these areas equal to approximately 12.5 km^2 (also known as the "X-area" within Bogesund; see text) and 80 km^2 respectively; these sub-areas define what is, hereafter, referred to as the Bogesund and Grimsö study sites. The data associated with deer captured at these box-trap locations were used in the survival analyses presented here (and the reproduction analysis, see Ch. 4). Blue areas represent the Baltic Sea surrounding the Stockholm Archipelago in panel (a), and inland lakes and ponds in panel (b). The underlying maps were created using the GlobCorine 2009 land cover dataset (© ESA 2010 and Université Catholique de Louvain).

collars in Grimsö since the 1970s (see below). Protection of radio-collared individuals varied during the early part of the study period (until 1994; see timeline in Fig. 3.2). In these analyses, I use data from 1985 onward, thus avoiding the earlier years when a majority of radio-collared individuals were shot to retrieve collars. To account for these management changes, protection policy was initially included as a categorical variable (protected, protected in all but a 3 km^2 area in southern Grimsö, not protected) in models of roe deer survival; however, this variable proved uninformative in explaining survival rates and was not considered further.

Deer monitoring

Annual harvest records

In both Bogesund and Grimsö there is close cooperation between hunters and researchers. In addition to recording information on the individuals they shoot (sex, ID if marked, and date of death), enabling accurate records of the deer harvested each year, hunters partake in management activities as volunteers and, in many cases, record

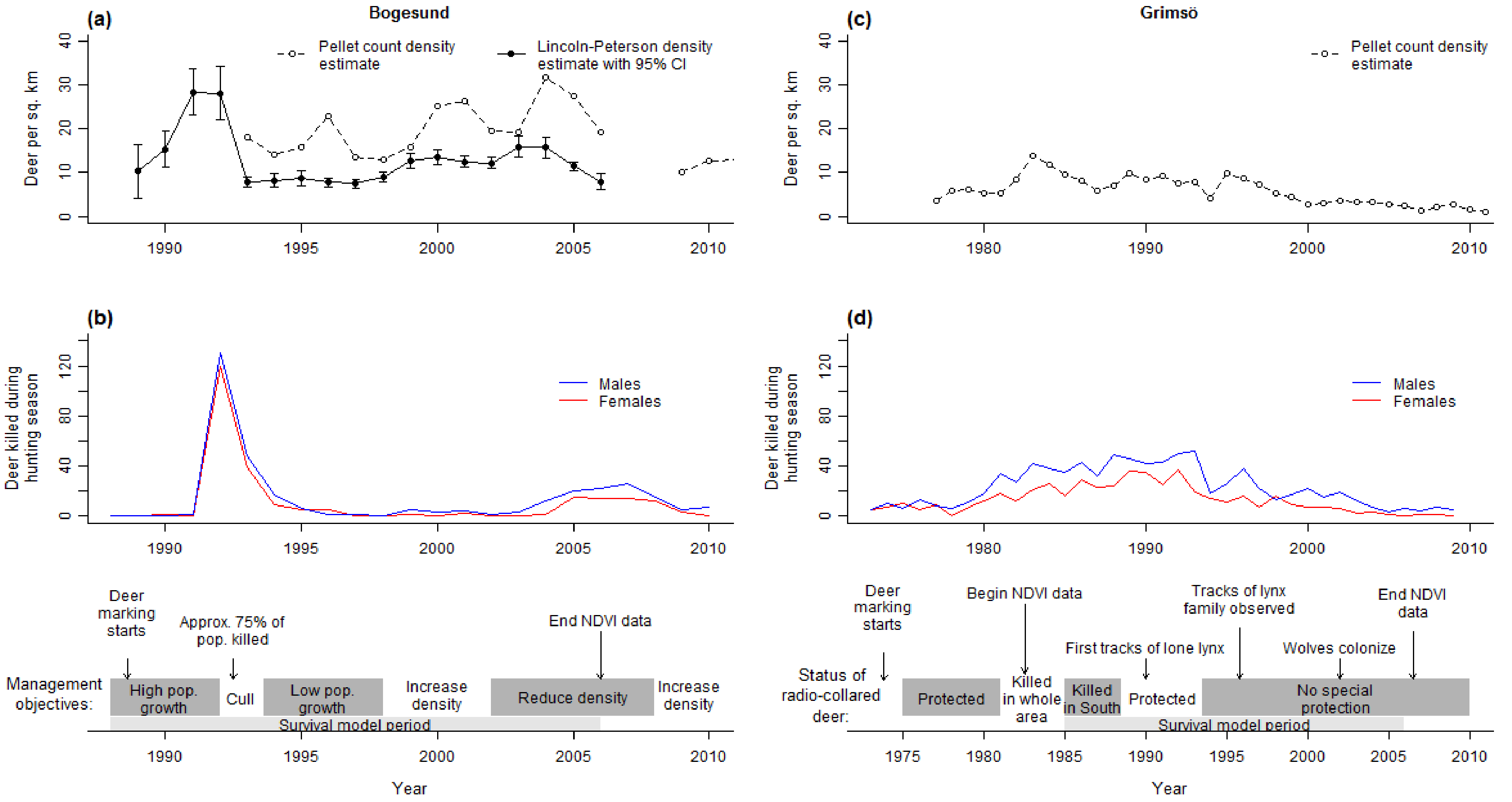

Figure 3.2: The modelled period in each site was limited by data availability and within-site management activities (see timelines at bottom). In Bogesund, (panel a) deer density has been manipulated through annual harvests (panel b). In Grimsö, roe deer densities are comparatively low (panel c). Harvests in Grimsö are not highly regulated, but have been relatively small (panel d).

sightings of roe deer and their predators. Hunting restrictions, including seasons and quotas (limits on the maximum number of deer to be shot annually), are adhered to. For males ≥ 1 year old the hunting seasons lasts from August 16th until January 31st. For fawns (< 1 year old) the season lasts from September 15th to January 31st. The hunting of females (≥ 1 year old) is more restricted with a hunting season lasting from October 1st to January 31st each year. In Bogesund, the quotas set each year are generally met and, therefore, the observed number of deer harvested is a good record of that year's quota. In Grimsö, no quotas have been set because hunting pressure is believed to be low considering the size of the area. In order to have a variable reflecting hunting pressure that could be compared between the two sites, I calculated the per capita harvest (Harvest; Table 3.1 below) as the number of individuals (marked and unmarked) killed each year, divided by the most recent estimate of deer abundance. Deer abundance was estimated as density multiplied by the area surveyed; densities used were based on annual September surveys in Bogesund and April surveys in Grimsö (September surveys did not take place in Grimsö; see density estimation methods below).

Deer capture and marking methods

Researchers began capturing and marking deer in Bogesund in the winter of 1988-89 (Kjellander 2000). Since then, animals have been captured using box-traps each winter (Fig. 3.1a). The traps were baited with livestock forage pellets, left overnight and checked the following morning. During the winters of 1988-89 and 1989-90, only six and eight trapping locations were used, respectively. Over the years, several long-term trapping sites were added and an average of 15.5 ± 2.76 (mean ± SD, from 1990-91 to 2005-06) trap locations were used each year. All of the 2,997 captures took place between November 1st and April 30th; the median date of capture was February 11th across all trapping years (1988-89 through 2010-11). Few records on the frequency of trapping have been kept in Bogesund and, due to changes in research staff over the study period, effort is likely to have been variable. For this reason, I calculated the number of unique capture dates (CapDates) achieved each winter as an index of trapping effort (23.0 ± 13.56 [SD] dates from 1988-89 until 2005-06; see next paragraph for more discussion of this measure).

Similar methods have been used to capture roe deer in Grimsö since 1973 (see box-trap locations in Fig. 3.1b). In 1973-74, seven capture sites were established. Since then, numbers and locations of traps have varied for logistical reasons. Detailed records of trapping effort are not available until 1989. From 1989-90 until 2005-06 there were 10.8 ± 1.40 trap locations (mean ± SD) with 21.6 ± 3.42 box traps active across those sites. Of the 2,709 captures recorded between 1973-74 and 2010-11, all but 4 (1 in October, 3 in May) captures took place from November to April. The median date of the November-April captures across all trapping years (1973-74 through 2010-2011) was February 12th. From 1989-90 until 2005-06, average effort was 411.5 ± 135.31 trap-nights each winter. Because measures of trapping effort before 1989 were not available, I calculated the sum of unique capture dates observed in a given winter (24.6 ± 8.92 from 1984-85 to 2005-06) as an index of trapping effort over the entire study period. This measure was highly correlated (Pearson's $r = 0.86$, $P < 0.001$) with trap-nights (a more standard measure of trapping effort) and was available for the entire study period at both study sites; therefore, the number of capture dates (CapDates) was used as a measure of trapping effort in analyses. There is inherent circularity in this measure because high capture success will result in more capture dates; however, in the absence of trap-night data for the study period it provides the best estimate of trapping effort available as evidenced by the high correlation with trap-nights (see further on this issue in the Discussion).

Captured deer were generally handled, measured, and tagged in the same manner at Grimsö and Bogesund (method implementation in Bogesund is described by Kjellander 2000). Individuals captured for the first time were marked using plastic ear-tags with individual ID numbers and colour combinations and, when possible, were fitted with radio-collars (lifespan approx. 3.5 years, 151MHz, Televilt International, Lindesberg, Sweden). The age of individuals at first capture was estimated based on tooth eruption and body characteristics (for fawns), or on tooth wear (for deer 1 year and older; Cederlund et al. 1991a). Recaptured individuals were identified and an estimate of their current age was recorded based on their estimated age at first capture and the assumption of a June 1st birth date (most roe deer births take place between the beginning of May and end of June; pers. comm., Kjellander 2012).

Observations of marked individuals and their deaths

Observations of marked individuals were recorded in both Grimsö and Bogesund throughout the study period. These observations are an amalgamation of data from a number of sources and, in combination with death records (described below), form the response data used in the binomial, beta-binomial and capture-mark-recapture models of survival (see "Modelling methods"). Many marked individuals were recaptured in box traps in the winter and all such capture events were recorded. Additionally, individuals fitted with radio-collars were located at least once a month throughout the year and as often as once a week during the winter. Over the years, researchers estimate that 38 ± 16.2% (mean ± SD) of the population at Bogesund has been collared (pers. comm., Kjellander 2012); for Grimsö this percentage is not known. Finally, throughout the study period, the date, location and ID of any deer observed were recorded by researchers while driving, walking or conducting fieldwork.

Records of the deaths of marked individuals were also obtained from three sources: first, inactivity of radio-collared deer triggered a "mortality signal", prompting further investigation; second, hunters were required to report any deer they shot; third, any known deer found dead incidentally by researchers (or reported by locals) were recorded. Obvious causes of death (as with shot individuals) were recorded. Less obvious causes were investigated further. If the body was emaciated or found under ice in a river, cause of death was recorded as "natural". If the deer carcass was found on the side of the road and with signs of vehicle-impact, it was recorded as "human-related". If there were signs of predator activity on or around the carcass (and no other cause was implicated) then the cause of death was listed as "likely predation". Finally, if the death was not recent or there was little or mixed evidence for the cause of death, then it was recorded as "unknown".

Observations of young fawns

Researchers began tagging neonate fawns in 1997 in Bogesund and 2000 in Grimsö. Because these data were not collected for most of the study period and because the drivers of fawn survival can be very different from those affecting older deer (e.g. red fox, *Vulpes vulpes,* prey heavily on young fawns; Aanes et al. 1998, Linnell et al. 1998b), I excluded these and other summer (from May until September) fawn records from these analyses. I model the survival of young (< 4 months old) fawns separately (see Ch. 4).

Density estimates

Researchers estimated the density of deer in Bogesund every April and September using the Lincoln-Petersen (L-P) method (Caughley 1977) from 1989 until 2006 and every April using pellet counts from 1993 until 2006. The L-P estimates were based on the ratio of marked and unmarked deer observed during dawn and dusk observation periods each April. Details of these methods and the 1989-2003 estimates are reported in Kjellander et al. (2006). The pellet-based density estimates were calculated using the number of pellet groups within 10 m^2 circular plots distributed along transects spaced 400 m apart throughout the study area (there were approximately 220 plots sampled per year). A defecation rate of 22 pellet groups per deer per day was assumed based on results from a study in another Swedish roe deer population (Wallin et al. unpubl.); these methods are described by Kjellander (2000). While giving different absolute densities, these methods produced similar abundance patterns for the deer population (Fig. 3.2). Given the longer period covered by the L-P estimates, I used the L-P estimates in my analyses (the pellet-based estimates are presented for comparison). April L-P estimates were used as measures of deer density in models (Den; Table 3.1 below), while September L-P estimates were used in the calculation of per capita harvest, as described above.

Researchers have estimated roe deer density in Grimsö since 1977 using pellet counts; L-P estimates were not completed. Pellets were counted within rectangular plots 10 m^2 in size. The grid included 439 ± 141.5 sampling plots (mean ± SD over 20 years) and covered an area of 25 km^2 (methods described by Lindström et al. 1994). In 1997, a new, larger grid was established comprising 32 squares (1 km^2), systematically distributed throughout the GWRA. Clusters of pellet plots were arranged every 200 meters along the perimeter of each square. Each cluster contained four 10 m^2 circular sampling plots (one in each cardinal direction). The mean pellet count from each cluster of four plots was used in analyses. The same system of 32 squares (except with different sampling plots) was used for moose (*Alces alces*) density estimates and is described by Månsson et al. (2011). As in Bogesund, density estimates were calculated assuming a defecation rate of 22 pellet groups per deer per day. These April pellet count surveys were used as measures of density in models (Den; Table 3.1 below) and, because no autumn measures of density were available, in the calculation of per capita harvest for Grimsö.

Potential covariates of roe deer survival

Climate and vegetation

The CRU 3.1 dataset, assembled by the Climate Research Unit (CRU), provides global climate data at a 0.5° resolution for the 1901-2009 period (Mitchell et al. 2004, Mitchell and Jones 2005). These data were spatially overlaid with outlines of the Grimsö and Bogesund areas and the observed climate for the 0.5° cell containing each site was extracted. I used these data to generate climate predictors (see Table 3.1 for calculation descriptions) including winter temperature (WinTmp), winter precipitation (WinPre), annual precipitation (Pre) and annual growing degree days (Gdd). Growing degree days were calculated using a baseline temperature of 5 °C (see Ch. 2 for calculation details). Annually summarised predictors were calculated across the calendar year (January through December) because this allows easy integration of climatic datasets, often available on a calendar year basis. Therefore, the relationship between these variables and survival (defined Feb 15th – Feb 14th) includes a slight time-lag.

Snow depth data were obtained from weather stations near the sites (Grimsö data from Ställdalen, 39 km to the Northwest; Bogesund data from Stockholm, a few kilometres to the South) (Swedish Meteorological and Hydrological Institute 1972-2009). Mean snow depth (Snow; Table 3.1) for each cold season was derived from daily measurements from November through April (following Cederlund 1982). As in Chapter 2, integrated NDVI (INDVI; Table 3.1) was used as an index of vegetation production within each study site.

Predators

Red fox (*Vulpes vulpes*) are the only natural predator of roe deer in Bogesund. In Grimsö there are foxes, lynx, and wolves (*Canis lupus*). Foxes prey on young fawns (Lindström et al. 1994, Aanes et al. 1998, Kjellander and Nordström 2003, Jarnemo and Liberg 2005) but not older deer. A male-female pair of wolves first established a territory in the Grimsö area in 2003, but the first wolf-related death of a marked roe

Table 3.1: Potential covariates of roe deer survival

Metric	Abbrev.	Sample dates[a]	Description
Survival	Survival_t	Feb. 15, 1995 – Feb. 14, 1996	Dates delineating the effective survival period are approximate. The estimation of survival and the definition of relevant period depends on the type of model used (binomial vs. capture-mark-recapture). See Methods for more detail.
Climate and Vegetation predictors			
Annually summarised [b]			
Annual integrated NDVI	INDVI_t	Jan. 1995–Dec. 1995	Sum of monthly NDVI in calendar year overlapping survival period.
	$\text{INDVI}_{t\text{-}1}$	Jan. 1994–Dec. 1994	Sum of monthly NDVI in calendar year preceding survival period.
Annual precipitation	Pre_t	Jan. 1995–Dec. 1995	Sum of monthly precipitation in calendar year overlapping survival period.
	$\text{Pre}_{t\text{-}1}$	Jan. 1994–Dec. 1994	Sum of monthly precipitation in calendar year preceding survival period.
Annual growing degree days	Gdd_t	Jan. 1995–Dec. 1995	Sum of growing degree days (> 5 °C) in calendar year overlapping survival period.
	$\text{Gdd}_{t\text{-}1}$	Jan. 1994–Dec. 1994	Sum of growing degree days (> 5 °C) in calendar year preceding survival period.
Seasonally summarised			
Winter temperature	WinTmp_t	Dec. 1995–Feb. 1996	Mean monthly temperature in winter at the end of survival period.
	$\text{WinTmp}_{t\text{-}1}$	Dec. 1994–Feb. 1995	Mean monthly temperature in winter preceding survival period.
Winter precipitation	WinPre_t	Dec. 1995–Feb. 1996	Sum of precipitation in winter at the end of survival period.
	$\text{WinPre}_{t\text{-}1}$	Dec. 1994–Feb. 1995	Sum of precipitation in winter months preceding survival period.
Snow depth	Snow_t	Nov. 1995–Feb. 1996	Mean daily snow depth in cold season at the end of survival period.
	$\text{Snow}_{t\text{-}1}$	Nov. 1994–Apr. 1995	Mean daily snow depth in cold season overlapping start of survival period.
Other predictors			
Roe deer density	$\text{Den}_{t\text{-}1}$	Apr. 1994	Density from April of year prior to survival year being modelled.
Per capita harvest	Harvest_t	Aug. 1995–Jan. 1996	Number of deer harvested divided by the most recent deer abundance estimate.
Lynx family density	LynxDen_t	Feb. 1995	Density of lynx families (regional surveys) in winter at beginning of survival period.
Lynx presence	LynxPres_t	Jan. 1995–Dec. 1995	Inferred from regional family density and signs in study site (see Methods).

[a] Unless otherwise stated sample dates given are inclusive of the entire start and end months

[b] Annually summarised predictors from time *t* include a slight time lag (approximately 6 weeks) relative to the survival period being modelled. See Methods for details.

deer was not observed until 2006. Thus, wolves were unlikely to be an important driver of deer survival during the modelled period (1985-2006) (this was supported by preliminary analyses). Consequently, only lynx effects are considered in this chapter.

In Sweden, the number of lynx family groups per 1000 km^2 has been estimated since 1994 (Andrén et al. 2002). There are nine “lynx bio-regions”, designated to cover all of Sweden; two of these (16,484 km^2 and 15,872 km^2 in size) overlap with Grimsö. Researchers averaged density estimates from these two regions to create lynx density estimates for the study area (LynxDen; Table 3.1). During the 1994-2006 period there has been an average of 2.44 ± 0.653 (SD) family groups per 1000 km^2 in Grimsö. Tracks of lynx families were not observed in the study area until 1996 (pers. comm., Kjellander 2012) and signs of predation by lynx were only observed regularly after that time. Given these observations, a density of 0 lynx per km^2 was assumed (at the regional level) prior to 1994. On the local (study site) level, I inferred colonization of the area by lynx at the time when tracks of a lynx family were first observed and constructed a categorical variable indicating lynx presence as of 1996 (LynxPres; Table 3.1).

Modelling methods

Survival was modelled using two different approaches to take advantage of two different data sources. First, beta-binomial and binomial (collectively BB) models used data on deer observations collected throughout the year. These models estimate survival (S) based on the ratio of observed mortalities to observed live individuals. Second, capture-mark-recapture (CMR) models used individual capture histories composed from observations across two sub-annual periods. This latter method exploits the fact that deer were individually marked. CMR models estimate survival from one three-month-long primary sampling period (see section on CMR models for definition) to the next, based on live observations, observed deaths, and the lack of live observations throughout the year. Because the majority of deer observations came from box-traps and took place in late winter, it was most efficient to use January through March as the primary sampling period in the CMR models. Thus, the CMR models generate annual estimates of survival from one January-March sampling period to the next. For comparability between the two approaches, response data for the BB models were also summarised from one February to the next (considering February 15th as the midpoint of the January-March closed periods in the CMR models). All data preparation and analyses were performed in program R 2.13.0 (R Core Development Team 2011).

Binomial and beta-binomial survival models

Estimating survival based on records of live individuals and their deaths

Data on uniquely marked individuals observed alive and observed dead were collated for each year (lasting February-February). Survival (S) was estimated from the ratio of dead to live observations; this assumes that variation in observation effort similarly affects observations of live and dead individuals. The BB models used with these data assume a binomial distribution of errors. The beta-binomial models (as opposed to the simple binomial models) contain an extra parameter to account for extra-binomial variation that is common in this type of data.

Preliminary selection of climatic and vegetation variables

I chose six metrics reflecting climate and vegetation conditions that are likely to affect roe deer survival from one winter to the next: WinTmp, WinPre, Snow, Pre, Gdd, and INDVI (Table 3.1). Because of the potential for lagged effects on survival, climate and vegetation conditions from the current year (t; overlapping with the year of survival being modelled) and the previous year (t-1) were considered. For a complete list of these variables see Table 3.1.

Density dependence is important in some roe deer populations and is likely to affect mortality via food availability. I included the previous year's density ($\text{Den}_{t\text{-}1}$; Table 3.1) as a potential predictor in models. For consistency, I used the density estimate from the April survey for both sites (surveys only took place in April at Grimsö). The current year's deer density could affect survival rates. However, density estimates took place after the late winter-early spring period during which deaths most commonly occurred; thus, survival rates should be positively correlated with "current" density because individuals survived the winter to be counted in spring, not because density impacted survival. For this reason, I considered only the previous year's density in models.

In total, there were 13 potentially important climate and vegetation related predictors (including the previous year's density) identified *a priori*. To reduce the number of variables considered in final models and to select the predictors that best explained climate-related roe deer mortality in each site, I constructed preliminary models based only on the potentially climate-related roe deer mortality. This meant excluding records of deer deaths that were most likely caused by predators and humans and afforded some protection against drawing conclusions based on spurious relationships between climatic predictors and non-climate related mortality. I ran models with all combinations of the 13 predictors, but allowed a maximum of two in each model (in addition to sex and age group) in order to avoid over-fitting. Only those variables which appeared in the models with a Δ AIC ≤ 6 for a given site were considered further in the site-specific analyses.

Specification of final binomial and beta-binomial model sets

When constructing the final BB model sets of survival (S), I used data on all deaths. I considered all possible two-variable combinations of the selected climate and vegetation variables, density, harvest, lynx family density and lynx presence. Although lynx were never present in Bogesund during the study period, I included the same lynx covariates in the analyses of both sites; if lynx-related variables were selected in the Bogesund models, this would highlight a potentially spurious effect. Combinations of variables that were strongly correlated with Pearson's $r \geq 0.4$ (see Appendix 3, Table A3.1; c.f. Freckleton 2011) were removed from the model set. I included age group and sex as categorical variables in all models. Individuals were classified as fawns (> 3 months and < 1 year old), subadults and adults (1 to 7 years old), or senescents (> 7 years old). I investigated the use of a fourth age group, including only subadults (1 year olds), but the extra parameters required were uninformative and led to models with higher AIC scores. I calculated the AIC for all models and ranked them according to Δ AIC and model weight (ω_i; Anderson et al. 2000, Burnham and Anderson 2002). Only models with Δ AIC ≤ 6 were included in the selected model set. Complex models with a higher AIC relative to simpler nested models (with fewer variables) were excluded (Richards 2008).

Model evaluation and cross-validation

I evaluated the predictive ability of the AIC best model for each site by examining the correlation between the observed and estimated rates of survival (S). I did this for the entire dataset using the best model (fitted using the complete dataset) and for a subset of data excluded from model-fitting in a cross-validation procedure. For cross-validation, I excluded 1 to 5 randomly chosen years of data from the datasets, re-fitted the model using reduced datasets and used the model to reproduce the omitted data. This was repeated 1000 times for each number of years left out (2-5 years) or once for each year (when 1 year was excluded). I also used this cross-validation method to evaluate the robustness of the parameter estimates to outliers and reductions in sample size. I compared the mean and 95% quantiles of parameter estimates (i.e. 95% confidence intervals) across the iterations given models fitted leaving 1-5 years out of the dataset.

Capture-mark-recapture models of survival

The Barker model and estimating survival based on individual capture histories

Capture-mark-recapture (CMR) models use individual encounter histories to estimate survival. In these analyses I use Barker models, a form of CMR model that incorporates both live and dead observations into encounter histories (Barker 1997, Barker and Kavalieris 2001). The basis for Barker models and, arguably, for all CMR models, is the relatively simple CJS model (Cormack 1964, Jolly 1965, Seber 1965). In CJS models, individual capture histories are composed using live recaptures from relatively short sampling occasions during which the population is assumed to be closed (i.e. no deaths, births, or emigrations). In practice, this assumption of closure is often relaxed, as closed population capture-recapture methods have been found to be relatively robust to violations of closure (Kendall 1999, Lindberg 2010). The probability of survival is estimated across the intervening “open” population periods when no observations are taken (and when individuals can join and leave the population). To accomplish this, one additional “control” parameter, capture probability (p) during the closed sampling periods, must be estimated. These models can be limiting because they do not allow the incorporation of live observations or known deaths of individuals from the intervening open population period. Additionally, due to their relatively simple parameterisation CJS models only allow the estimation of apparent survival (typically denoted ϕ) which can be affected by losses due to emigration as well as mortality (Thomson et al. 2008).

Barker models are an extension of CJS models which allow the incorporation of “auxiliary” information consisting of dead “recoveries” and live “resightings” from the open population intervals in between the "closed" or "primary" sampling periods (hereafter referred to as primary sampling periods). These "open" or "secondary" sampling periods extend from the end of one primary sampling period to the start of the next. The incorporation of these extra data can substantially increase the precision of estimates of survival probability (from one primary sampling period to the next), but requires the estimation of several additional "control" parameters (Barker and Kavalieris 2001). Two of these control parameters are related to site fidelity (see F and F' defined below) and result in the estimation of emigration (1- F) from individual capture histories. By accounting for this process, Barker models have the added advantage of estimating "true" survival (S), defined by mortality alone, rather than apparent survival (ϕ; see CJS model description above). For an in depth description of Barker models and the underlying theory, see Barker (1997). In Program MARK (White and Burnham 1999), the parameters estimated for the Barker model are defined as follows:

S_i = the probability that an individual alive at primary period i is alive at $i+1$

p_i = the probability that an individual at risk of capture (in the sampling area, i.e. not emigrated or dead) at primary period i is captured at i.

r_i = the probability that an animal that dies in the secondary sampling period i, $i+1$ is found dead and reported.

R_i = the probability that an animal that survives from primary period i to $i+1$ is resighted (alive) in the intervening secondary period.

R'_i = the probability that an animal that dies in between primary period i and $i+1$ is not found dead and is resighted alive in the secondary period i, $i+1$ before it died.

F_i = the probability that an animal at risk of capture at primary period i is also at risk of capture at primary period i+1 (site fidelity, i.e. the probability the animal has not emigrated).

F'_i = the probability that an animal not at risk of capture at primary period i is at risk of capture at $i+1$ (i.e. the probability that an animal has returned to the site; this allows for emigration to be temporary).

Program MARK uses capture histories (one for every individual marked in the study) to produce estimates of all these parameters over the model period; maximum likelihood parameters are estimated simultaneously using a multinomial model with a logit link. An individual's capture history is structured as a sequence of single digits composed of alternating primary and secondary period entries; for example, over three primary and secondary sampling periods, a capture history would take the form of PSPSPS (P for primary period and S for secondary period). Individuals are classified as either observed or not in the primary period while in the secondary period they are classified as not observed, observed alive or recovered dead. If an individual was observed alive prior to being found dead only the death was recorded.

Model assumptions and parameter specifications

Similar to other CMR models, Barker models assume that the primary sampling period is relatively short compared to the intervening secondary period. To meet this assumption, I defined January through March of each year as the primary sampling period. This meant that the primary sampling period incorporated the winter months when the majority of live observations (due to the winter box-trapping season) took place. A shorter primary period would be an inefficient use of the available data and could result in less precision surrounding estimated parameters. This resulted in one three-month long primary period and one nine-month long secondary period (April-December) per year. When deaths, occurred during the primary sampling period, this death was attributed to the closest open period (i.e. the date of death was shifted back or forward). This meant that 88 deaths had to be "moved" an average of 21.5 ± 14.77 (SD) days in Bogesund and 69 deaths had to be "moved" 21.8 ± 13.29 days in Grimsö. Such violations of the closure assumption are likely common in field situations and, as previously stated, CMR models are relatively robust to violations of the closure assumption (Kendall 1999, Lindberg 2010). Given that the primary sampling period is short relative to the intervening secondary periods the main effect of such violations on survival estimation is to blur the definition of the secondary period across which survival is estimated. Thus, estimated recovery rates (r_i) may be higher during each open period and there is uncertainty regarding the exact length of the survival interval, but this should not bias survival rates presented on an annual basis.

In these CMR models, it is also assumed that marks are not lost and all marked individuals have the same probability of recapture and survival (aside for the variation accounted for by covariates). While direct tests of these assumptions are not possible, I included several covariates with the goal of controlling for heterogeneity not associated with the temporal changes in survival that were of interest in this analysis. Firstly, I controlled for heterogeneity in observation probabilities during the secondary period, which could be caused by the disproportionate monitoring of radio-collared individuals. A large portion of data used in secondary sampling period entries comes from observations of radio-collared individuals, which are likely to have higher observation probabilities. Therefore, in all models, I included whether or not an individual was radio-collared as a covariate of r_i and R_i (the effect of radio-collared status on R'_i was examined but found to be non-significant in both sites).

Secondly, I added constraints to the parameters describing site fidelity. The F and F' parameters relate to the probability that an individual will emigrate from ($1-F$) or return to (F') the study site during the secondary sampling period. Roe deer are typically sedentary, aside from an initial “natal dispersal” which takes place when deer are about 1 year old. In Grimsö, preliminary estimates suggest a dispersal distance of 24 ± 4.4 km (mean ± SE; Markussen 2002), so emigration outside the study area could be relatively common. In this site, I therefore considered age as a covariate of F and allowed only individuals turning 1-year-old during the secondary sampling period (captured as fawns during the primary sampling period) to have a separate emigration probability from older deer. Older deer were assumed to have the same probability of emigration irrespective of their exact age. In Bogesund, emigration outside the site is unlikely because dispersal distances are small (median distance = 3 km; Liberg et al. 1994, Gaillard et al. 2008) and because the study site is mostly surrounded by water (see Fig. 3.1). Indeed, initial models fitted to the Bogesund data would not converge when emigration was to be estimated. This is consistent with near-zero emigration rates that would result in numerical errors on the scale of the linear predictor (models incorporated a logit-link). Therefore, I assumed a site fidelity (F) of 1 (i.e. emigration, $1-F$, was set to 0) and set return rates (F') at this site as equal to 0 (because individuals cannot “return” to the study site given zero emigration).

Thirdly, I included a covariate for capture probability (p) to control for inter-annual variation in trapping effort during the primary sampling period. The majority of primary period observations came from individuals captured in box-traps; therefore, I included the number of unique capture dates (CapDates) as a covariate of *p* in all models. Other parameterisations allowing *p* to remain constant or to increase steadily across years were examined but were known not to reflect changes in capture effort and ultimately would have led to the same overall conclusions regarding effects on survival.

Finally, I constructed model sets for the Bogesund and Grimsö datasets by including covariates of survival (*S*). I considered survival models with all possible combinations of the selected climate predictors and non-climatic predictors for each site (listed in Table 3.1). As with the BB models, I included sex and age group in all models. I excluded models containing combinations of variables that were strongly correlated (Appendix 3, Table A3.1). I compared the candidate models for each site using AIC and model weights (ω_i).

Model evaluation

I evaluated the predictive ability of these CMR models by comparing model estimates to the observed survival data based on the records of roe deer and their deaths (estimates of survival, *S*, based on the same data used to fit the BB models). I examined the correlations between observed and estimated survival for all age-sex groups excluding fawns. Fawns were excluded because the fawn survival rates represented by the observed data were limited to records of fawns between four and twelve months of age and did not reflect the period of fawn survival estimated by the CMR models; the CMR models estimate survival of fawns from their first winter to the next when they are subadults (aged approximately 8-20 months). This is less of a problem for the other age groups (which cover longer periods of time, reducing the impact of this discrepancy). Owing to the different assumptions and data formats used in the BB and CMR models, the correlation between survival rates estimated by the CMR model and the survival rates estimated from the ratio of dead and live records is a substantial test of the agreement between the two estimation methods; however, a lack of agreement does not necessarily indicate a failure of the CMR model to estimate the survival rates indicated by the capture history data.

Results

Over the modelled period (1988-89 to 2005-06, 18 years), there were 275 recorded deaths of known individuals in Bogesund; 178 of these deaths were considered potentially climate-related (due to unknown or natural causes, not caused by humans or predators). There were 1,339 unique live observations across all years (i.e. the sum of unique individuals seen alive within each year). While many individuals appeared multiple times in these data across the study period, each individual was only counted once per year. At Grimsö, there were 1,449 unique live observations across years (22 years; 1984-85 to 2005-06), and 319 death records; 119 of the latter were considered potentially climate related. These data were used in the BB models. The CMR models used capture histories of 466 deer in Bogesund and 557 deer in Grimsö.

Preliminary selection of climate-predictors

Climate variables were selected using models based only on the number of potentially climate-related deaths recorded each year. Models (with Δ AIC ≤ 6) for both Grimsö and Bogesund generally included variables with the potential to act indirectly such as INDVI, snow depth, or predictors from the preceding year or winter (Appendix 3; Table A3.2). Five climate variables were selected for Grimsö: WinTmp $_{t\text{-}1}$, INDVI $_{t}$, INDVI $_{t\text{-}1}$, Pre $_{t\text{-}1}$, and Snow $_{t\text{-}1}$. Three were selected for Bogesund: INDVI $_{t\text{-}1}$, Gdd $_{t\text{-}1}$ and Pre $_{t\text{-}1}$. These variable sets were considered potentially important drivers of climate-related deaths and were included along with density, harvest and predation-related measures as candidate predictors in the complete survival analyses for each site. Overall, there were a large number of correlations amongst candidate predictors in the Grimsö dataset (compared to only one correlation with Pearson's $r > 0.4$ amongst predictors in Bogesund; Appendix 3, Table A3.1). Survival models including combinations of these correlated variables were removed from final model sets.

Effects of control parameters

The non-temporal covariates included in the models to account for heterogeneity in the data (sex and age group), consistently improved model fit (reduced model AIC scores) and were therefore included in all models at both sites (see Methods). In the CMR models, capture effort was positively related to p (the probability of capture during the primary sampling period) and radio-collared individuals had a greater probability of being observed (either dead or alive) during the secondary sampling period. Additionally, the Grimsö CMR models suggested that individuals that were approximately one year old (fawns during the primary capture season) had a greater probability of emigrating than older individuals; therefore, the models for this site were consistently improved by modelling emigration probability (1-*F*) as a function of age.

Models of survival in Bogesund

Of the 275 deaths of known individuals in Bogesund, 96 were human-related and 54 of these were shot during the designated hunting season. The majority of the remaining deaths were of deer found emaciated or drowned. Observed rates of survival (based on observed mortalities across all age-sex groups) ranged from 0.47 to 0.96 across years but survival rates were generally high and averaged 0.80 ± 0.034 (SE) across years (n = 18) (see Appendix 3,Table A3.3, for age-group and sex-specific rates). Unsurprisingly, survival in Bogesund differed very little between the period before lynx colonization of the Grimsö area (1988-1996) and the subsequent period (1996-2006; Fig. 3.3).

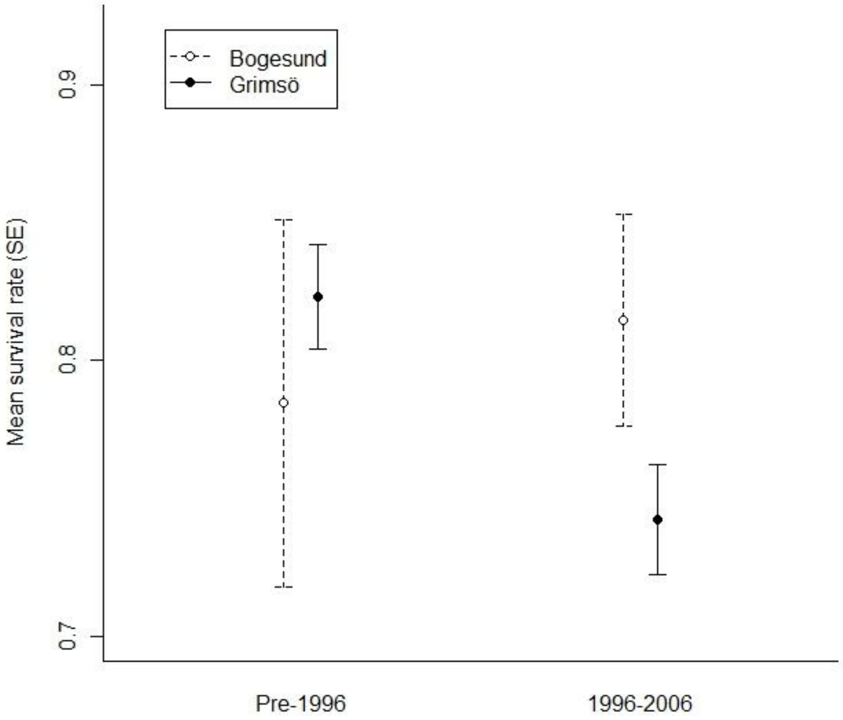

Figure 3.3: Mean survival rates (across years; all age-sex groups included) in Bogesund and Grimsö before and after lynx colonisation of Grimsö (in 1996; see Methods). Bars represent standard errors. Study periods lasted from 1985 to 2006 in Grimsö and from 1989 to 2006 in Bogesund.

Only two BB models for Bogesund had Δ AIC ≤ 6 (Appendix 3, Table A3.4) and both included a strong effect of the autumn harvest. The best performing model included a negative relationship with the autumn harvest ($\beta_{\mathrm{Harvest}(t)}$ = -4.0 ± 0.540 [SE]; Fig. 3.4a) and positive relationship with the previous year's INDVI ($\beta_{\mathrm{INDVI}(t\text{-}1)}$= 1.1 ± 0.275; Fig. 3.4b). This model had a weight (ω_i) of 0.88. The second ranked model (ω_i = 0.12; Appendix 3, Table A3.4) included a similarly strong effect of harvest ($\beta_{\mathrm{Harvest}(t)}$ = 3.9 ± 0.521) and a positive effect of precipitation from the year preceding survival ($\beta_{\mathrm{Pre}(t\text{-}1)}$ = 0.01 ± 0.002).

The best CMR model included the same predictors as the best BB model: harvest ($\beta_{\mathrm{Harvest(t)}}$ = -2.5 ± 0.407; Fig. 3.4a) and the previous year's INDVI ($\beta_{\mathrm{INDVI}(t\text{-}1)}$ = 0.92 ± 0.213; Fig. 3.4b). The effect sizes of the CMR parameters were generally similar to those of the best BB model (Fig. 3.4); this is further evidenced by the large overlap of (standardised) confidence intervals surrounding parameter estimates (for a comparison of standardised coefficients from all models see Appendix 3, Fig. A3.1). There were no other models in the selected model set (with Δ AIC ≤ 6); thus the top model had a weight of 1.0 (Appendix 3, Table A3.4).

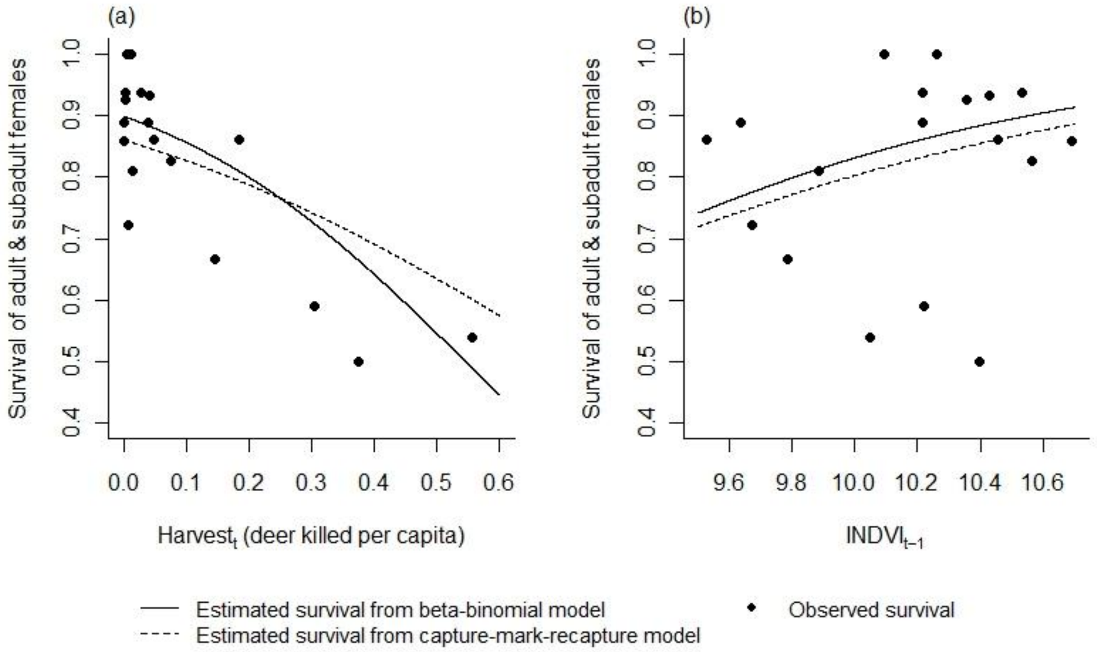

Figure 3.4: Estimated survival of adult and subadult females in relation to the observed range of (panel a) per capita harvest (Harvest$_t$) and (panel b) the previous year's INDVI (INDVI$_{t\text{-}1}$) from the best beta-binomial (BB) and capture-mark-recapture (CMR) models of roe deer survival in Bogesund. Estimated survival rates are conditional on (panel a) observed mean INDVI$_{t\text{-}1}$ (10.2 ± 0.34 [SD]) for Harvest and (panel b) observed mean Harvest$_t$ (0.10 ± 0.158) for INDVI. The 95% CI surrounding model estimates are illustrated in Fig. 3.5.

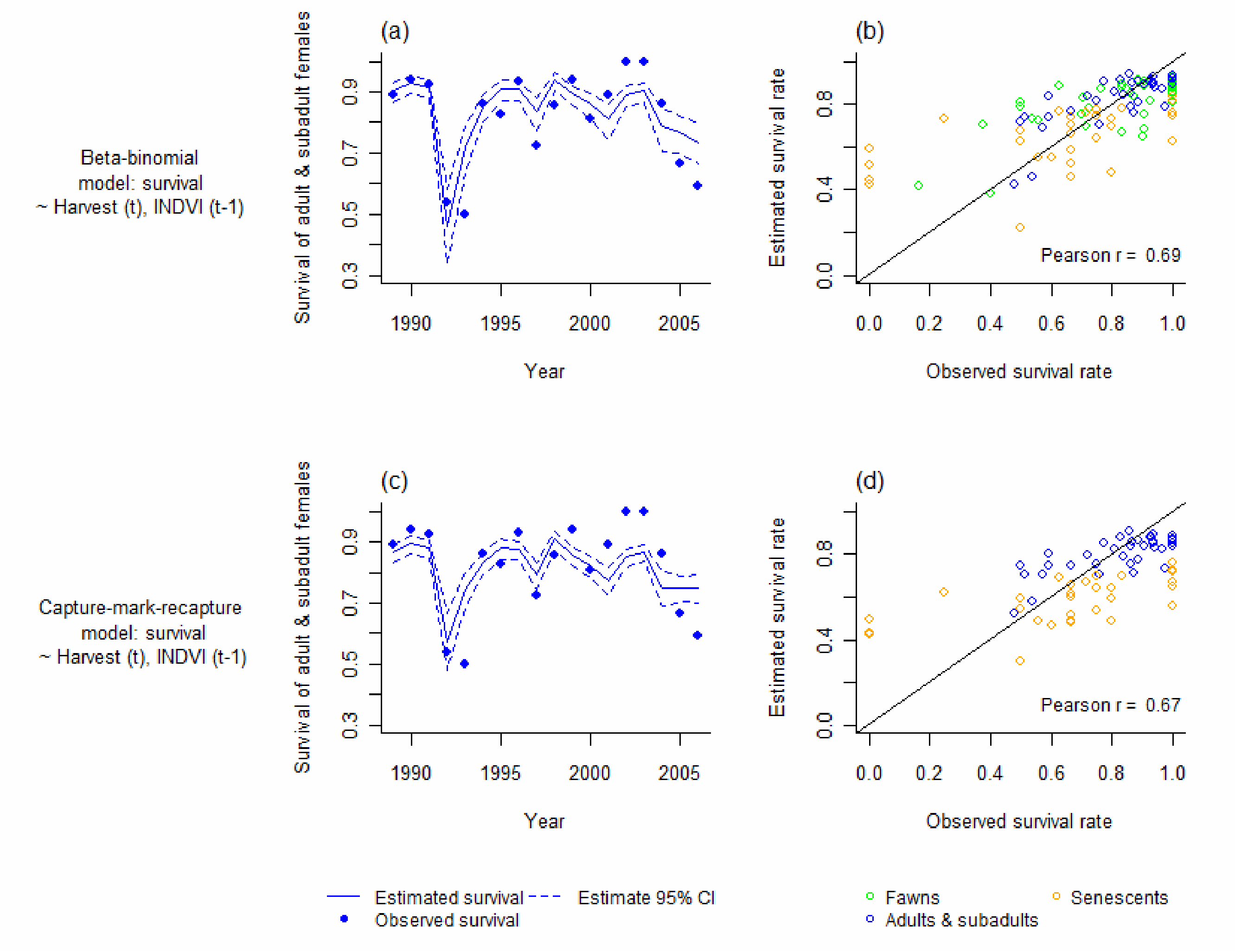

Figure 3.5: The performance of the AIC best models of survival in Bogesund was evaluated by comparing model estimates with observed survival rates. The best beta-binomial (BB) model (panels a & b) and the best capture-mark-recapture (CMR) model (panels c & d) included effects of the annual autumn harvest (Harvest $_t$) and the previous year's INDVI (INDVI $_{t-1}$).

Each of these models reproduced the observed survival data well (Fig. 3.5). Correlations between observed survival and the survival rates estimated by the models were relatively high (BB Pearson's $r = 0.69$, $P < 0.001$; CMR Pearson's $r = 0.67$, $P < 0.001$). While the model fits did not always capture the full magnitude of the year-to-year variation in observed survival, the temporal sequence of estimated survival rates resembled the changes in observed survival across years.

Cross-validation of the BB model shows that the exclusion of data only slightly reduced the predictive ability of the model. When reproducing the survival rates of excluded years, Pearson's r ranged 0.61-0.63 among the simulations in which 1-5 years were excluded. The quantile intervals for parameter estimates gradually widened as years were excluded; this is due to variation among model parameters fitted during iterations in which certain combinations of years were excluded (Appendix 3, Fig. A3.1). The fact that these intervals never overlapped with zero indicates that the effect size was relatively robust to decreases in sample size. Excluding the years 1992 and 1993 (associated with a large cull) did not decrease the estimated effect of harvest on survival, suggesting that these outliers did not disproportionately influence the final results.

Models of survival in Grimsö

In Grimsö there were 200 non-climate-related deaths including 104 deaths due to harvest and 68 due to predation. Most of these predation-related deaths (57) showed evidence of lynx involvement. Observed rates of survival (based on observed mortalities across all age-sex groups) were generally less variable across years in Grimsö than in Bogesund; survival in Grimsö ranged from 0.64 to 0.93 with a mean of 0.78 ± 0.016 across years ($n = 22$) (see Appendix 3, Table A3.3 for age-group and sex-specific rates). Mean survival prior to 1996 (0.82 ± 0.019 [SE]) was higher than the survival rates observed from 1996 through 2006 (0.74 ± 0.02) when lynx were present in the study area (Fig. 3.3).

Modelling results for Grimsö were less clear than those for Bogesund. The selected BB and CMR model sets (Δ AIC ≤ 6) included 11 and 6 models, respectively (Appendix 3, Table A3.5) indicating a high degree of uncertainty in model selection. The BB model with the lowest AIC was a binomial model including a negative effect of lynx presence ($\beta_{\mathrm{LynxPres}(t)} = -0.58 \pm 0.140$; Fig. 3.6a) and a positive effect of the current year's INDVI ($\beta_{INDVI(t)} = 0.45 \pm 0.182$; Fig. 3.6a) on survival. According to this model, lynx presence translates to an 11% decrease in roe deer survival (assuming mean INDVI conditions). This model had a weight (ω_i) of only 0.34 due to the presence of several other models with Δ AIC ≤ 6. Some of these models included $INDVI_{t-1}$, Den_{t-1}, $WintTmp_{t-1}$, and Pre_{t-1} as predictors but relationships were not very strong and often had low precision, thus 95% CI surrounding parameter estimates often overlapped with zero.

The top-ranked CMR model ($\omega_i = 0.29$) included a negative relationship between survival and lynx presence ($\beta_{LynxPres(t)} = -0.25 \pm 0.126$; Fig. 3.6b) and a positive but weak relationship with the previous winter's mean temperature ($\beta_{WinTmp(t-1)} = 0.05 \pm 0.030$; Fig. 3.6b). In this model, lynx presence translates to a 6% decrease in estimated survival rates (compared with lynx absence, all else being equal). Other models with Δ AIC ≤ 6 similarly included $WinTmp_{t-1}$ and lynx-related predictors (either presence, $LynxPres_t$, or density, $LynxDen_t$). The effect of $LynxDen_t$ in models was consistently negative, although non-significant with confidence intervals

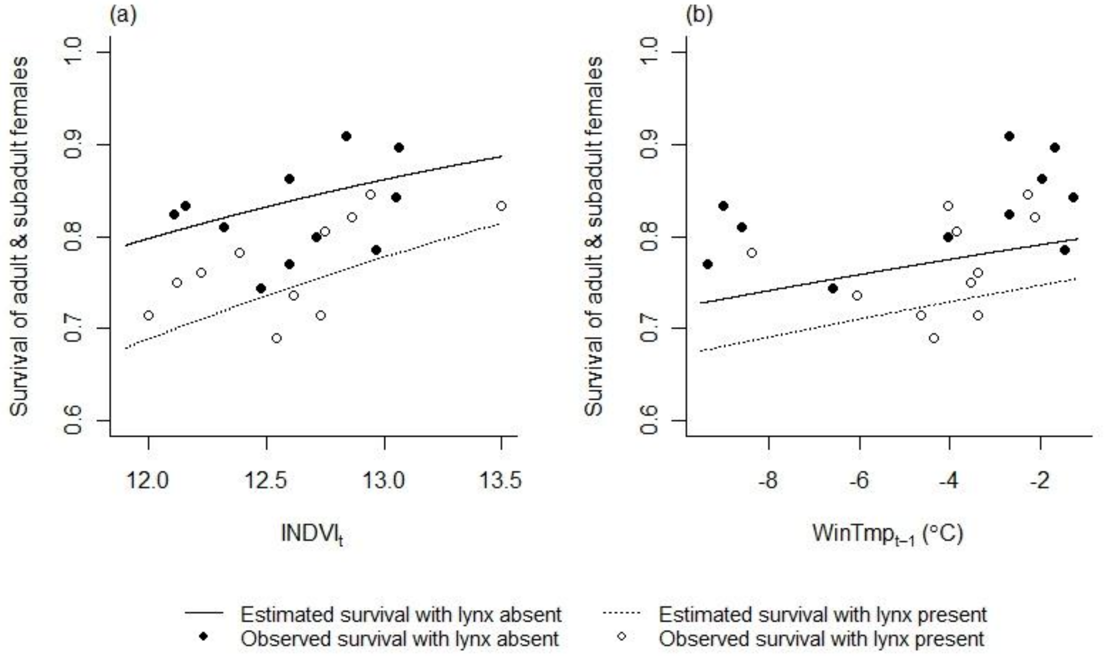

Figure 3.6: The estimated relationships from the AIC best binomial (BB; panel a) and capture-mark-recapture (CMR; panel b) models of roe deer survival in Grimsö are shown (for detail on modelling methods see text). Survival rates were estimated for the adult and subadult female group given the observed range of the current year's (panel a) INDVI ($INDVI_t$), and (panel b) the previous winter's mean temperature ($WinTmp_{t-1}$), including lynx (dotted lines) and excluding lynx (solid lines) in both cases. The 95% CI surrounding model estimates are illustrated in Fig. 3.7.

overlapping zero. The top-ranking model performed only moderately better than the CMR model including just age and sex effects on survival (Δ AIC = 2.37; Appendix 3, Table A3.5) suggesting little explanatory power was gained by the addition of temporal effects.

Lynx presence was included in the top model from both the BB and CMR methods. The final model set based on the BB method did not include the second variable highlighted in the top model from the CMR model set and vice versa. The BB model including LynxPres_t and $\text{WinTmp}_{t\text{-}1}$ (the parameters in the best CMR model) had a Δ AIC = 5.07 and the CMR model including LynxPres_t and INDVI_t (the parameters in the best BB model) had a Δ AIC = 2.38. While having Δ AIC ≤ 6 in each case, these models were removed from the model sets due to the superior performance of the simpler nested model including only LynxPres_t (as recommended by Richards 2008). All but one of the models (CMR and BB) with Δ AIC ≤ 6 included INDVI_t, $\text{WinTmp}_{t\text{-}1}$, or a lynx-related predictor (either presence or density) suggesting the relative importance of these predictors.

Despite the differences between the CMR and BB results, the top models from each method produced similar trajectories for estimated survival over time (Fig. 3.7); this likely reflects the correlation between the chosen climatic predictors, INDVI and $\text{WinTmp}_{t\text{-}1}$ (Pearson's $r = 0.44$, $P < 0.05$; Appendix 3, Table A3.1). The binomial model captured inter-annual variation in survival rates well and estimates of survival from this model were well correlated (Pearson's $r = 0.69$; $P < 0.001$) with observed data. Survival estimates generated by the CMR model were also correlated with observed survival (Pearson's $r = 0.55$, $P < 0.001$); however, the CMR survival estimates are noticeably lower than the calculated survival rates based on observations of live individuals and their deaths (Fig. 3.7).

The results of the cross-validation suggest that the BB survival model for Grimsö did well at reproducing the data excluded during model fitting. The correlation between observations and estimates of survival in excluded years was similar to that calculated for estimates based on the model fitted with the full dataset (Pearson's r ranged 0.66-0.67 across the different simulations). The quantile intervals surrounding the parameter estimates for INDVI_t and LynxPres_t changed very little as the number of years excluded was increased (Appendix 3, Fig. A3.1).

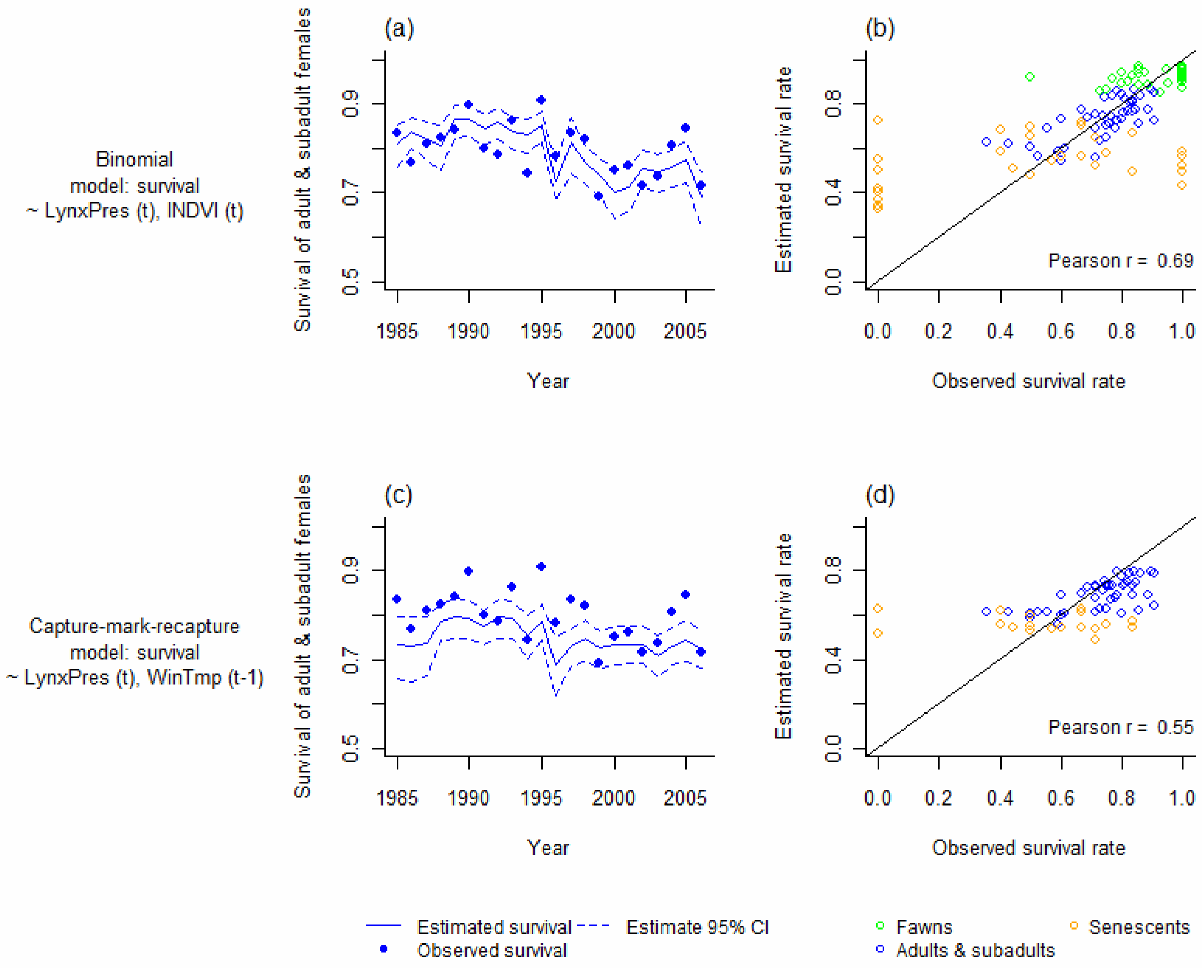

Figure 3.7: The performance of the AIC best models of survival in Grimsö was evaluated by comparing model estimates against observed survival rates. The best binomial model (panels a & b) included effects of lynx presence (LynxPres $_{t}$) and the current year's INDVI (INDVI $_{t}$). The best capture-mark-recapture model (panels c & d) included effects of lynx presence (LynxPres $_{t}$) and the previous winter's temperature (WinTmp $_{t-1}$).

Discussion

This analysis of roe deer survival emphasises the importance of simultaneously considering the impacts of climatic, indirect climatic, and non-climatic drivers when building predictive models of temporal variation in survival rates. This conclusion is supported by the results from two different modelling methods and two different study sites, one with natural predators (Grimsö) and one without (Bogesund). In both sites, the estimated age-group and sex-specific survival rates are generally within the range of those observed in other roe deer populations (e.g. adult females here had an average survival of 0.82 ± 0.036 [SE] in Bogesund and 0.80 ± 0.012 in Grimsö, compared with a range of 0.68-0.99 across other studies; see Table A1.1 in Appendix 1). Simple models (with a maximum of two temporal covariates) fitted observed survival rates well. In total, four model sets were constructed and four "top" models were selected: one for each combination of site and modelling method. These models of survival consistently included one climatic predictor (direct or indirect) and one predictor associated with mortality through natural predation or human harvest. In Bogesund, results were generally clear: harvest and INDVI were important predictors of survival. In Grimsö, while the results were less straightforward, models frequently included lynx presence and either INDVI or winter temperature. The emphasis on INDVI, an index of vegetation production potentially driven by climate, in both sites has general implications for future studies of this ungulate. This metric often outperformed purely climatic predictors and was included in three of the four top models. This suggests that the direct inclusion of vegetation effects (rather than strictly climatic parameters) in models can improve the understanding of roe deer survival and could potentially inform projections of their population dynamics given climate change.

Indirect climate effects on roe deer survival via vegetation and food availability

Despite support for INDVI as a predictor of roe deer survival in both sites, there were differences in the time-lag associated with the INDVI predictor selected and in the strength of support for that predictor. Previous research on roe deer and other ungulates has highlighted the importance of a detailed understanding of the factors driving population dynamics, which are potentially species and site-specific (Gaillard et al.

1993, Gaillard et al. 1997, Clutton-Brock and Coulson 2002, Månsson and Lundberg 2006, Martinez-Jauregui et al. 2009). In particular, Månsson and Lundberg (2006) drew upon an examination of precipitation-driven changes in herbivore food supplies to assert that indirect effects of climate are likely to be less easily generalised among systems than direct climate effects, due to the specificity of the mechanisms involved. This suggests that, for climate-driven models of population dynamics to be accurate, they will often have to be site-specific. The differences found here (and in the previous chapter) between the two study sites support this assertion.

In Bogesund, the previous year's INDVI (INDVI $_{t\text{-}1}$) was positively related to survival in both the best capture-mark-recapture model (CMR method) and the best beta-binomial model (BB method). These top models received strong support in both model sets, which provided little or no support for alternative climate-related variables. As an index of net primary vegetation productivity, INDVI (the annual sum of bimonthly NDVI values) is a potential indicator of indirect climate effects via food availability. Increased vegetation production likely allows individuals to increase growth rates and add to fat reserves, enabling higher rates of survival through the following year. This lagged effect of food availability is consistent with past studies of roe deer ecology, which emphasise lagged cohort effects on survival (Gaillard et al. 1998b, Pettorelli et al. 2002). Net primary production has previously been positively related to spatial variation in roe deer density and population growth (Melis et al. 2009, Melis et al. 2010). The results from this analysis add to this evidence and suggest that, in some sites, temporal variation in NPP (potentially driven by climate) could drive temporal variation in roe deer survival, influencing population growth within a site. The magnitude of the INDVI effect was remarkably similar in both the CMR and BB models and was robust to changes in sample size. Additionally, both models performed well when reproducing observed survival over time (Fig. 3.5). The only potentially competing model (in the BB model set; Δ AIC = 4) included a positive effect of previous years precipitation instead of INDVI. Effects of INDVI$_{t\text{-}1}$ and Pre$_{t\text{-}1}$, do not indicate mutually exclusive hypotheses. Similar to INDVI, precipitation would most likely have a positive impact on roe deer survival through food availability; higher precipitation in the previous year could be one factor leading to increased vegetation production. A negative relationship between monthly dryness (i.e. precipitation minus potential evapotranspiration) and NDVI was observed in both Grimsö and Bogesund (see Ch. 2), which is consistent with this interpretation. The fact that the model including precipitation performed less well than the model including INDVI may simply suggest the value of considering vegetation metrics directly in analyses of roe deer survival.

The results from the Grimsö analyses provide some additional support for the importance of vegetation production to roe deer survival, but the high degree of uncertainty in model selection at this site means that interpretations based on any single “top” model must be made tentatively. The best model from the BB modelling method included a strong positive effect of the current year’s INDVI (INDVI_t) similar in magnitude to that observed for the previous year’s INDVI ($\text{INDVI}_{t\text{-}1}$) in Bogesund (Appendix 3, Fig. A3.1). There was no time-lag associated with the INDVI effect in Grimsö as there was in Bogesund (where $\text{INDVI}_{t\text{-}1}$ was selected), which could be explained by the harsher climate in Grimsö (located further north and inland than Bogesund). Deer in Grimsö might be less able to accumulate fat reserves and, as a consequence, be primarily dependent on immediate vegetation conditions. None of the models in the final CMR model set included INDVI. The climate-related predictor in the best CMR model was the previous winter’s temperature ($\text{WinTmp}_{t\text{-}1}$). Warmer winter temperatures could increase roe deer survival over the following year because cold temperatures could cause physiological stress; during cold winters, individuals likely use more energy maintaining the body temperatures necessary to survive. Additionally, a warmer winter could be related to a longer growing season, which leads to increased vegetation production and survival rates. This second pathway is supported by the correlation between winter temperatures and INDVI (Pearson’s $r = 0.44$, $P < 0.05$; Appendix 3, Table A3.1) and by the positive relationship between monthly temperature and NDVI in this site (see Ch. 2). While both the CMR and BB models produced similar trajectories describing roe deer survival over time, the BB model including INDVI received more support relative to the model based on age and sex alone, and performed better than the CMR model when reproducing observed survival rates.

Non-climatic mortality drivers: predation and human harvest

The importance of human harvest as a predictor of roe deer survival in Bogesund is in keeping with the extensive management of this population for research purposes over the past two and half decades. The effect size of human harvest was relatively consistent across modelling methods and was robust to cross-validation. In Grimsö, where lynx are present and the roe deer population has not been as dramatically manipulated by humans, predictors related to predation effectively took the place of human harvest as the non-climatic driver of roe deer survival. The majority of the models in both CMR and BB model sets included a negative effect of lynx presence at Grimsö. The lower rate of survival that was observed in Grimsö during the later part of the study period (from 1996 onward) was not found in Bogesund (Fig. 3.3).The negative relationship observed between lynx presence and survival in the Grimsö models suggests that these predators, known to prey heavily on roe deer where available (Aanes et al. 1998), may partially drive differences in survival between the two study sites. Heurich et al. (2012) similarly found that roe deer survival decreased (by approximately 10%) after lynx re-colonisation of a site in Germany. These results further emphasise that the understanding of ungulate population dynamics would be improved by examining more datasets from sites with intact populations of natural predators (Gaillard et al. 2000b, Nilsen et al. 2009a).

The apparent importance of lynx to roe deer survival in Grimsö is noteworthy given the difficulties of estimating the impacts of predators on their prey. Four main points provide reassurance that the observed relationship with lynx is not spurious. First, both modelling methods for Grimsö led to the selection of a top model that included lynx presence, whereas the model sets for Bogesund, a nearby site without predators, did not include the lynx-related predictors. Second, the effect size of lynx presence in the BB model (c. 6-11% decrease in survival) was similar to that observed in other studies (Nilsen et al. 2009b, Heurich et al. 2012) and, furthermore, was robust to cross-validation even when more than 20% (5 out of 22 years) of the data were excluded in model-fitting (Appendix 3, Fig. A3.1). Therefore, it does not appear that this effect was driven by a few outlying years. Third, when included in models, lynx density had a negative, although weak, effect on survival, consistent with the estimated effect of lynx presence. Last, investigating correlations with the other candidate predictors in this site revealed that lynx presence was negatively related to human harvest and deer density but positively related to growing degree days (Appendix 3, Table A3.1). If these other environmental conditions were the true drivers of the observed lynx-survival relationships I would have expected survival to have increased during the period of lynx presence; smaller harvests should increase roe deer survival as should lower density and warmer weather. This was not observed, supporting the inference that lynx drove the reduced survival of roe deer at Grimsö from 1996 onwards.

General caveats and implications for model predictive ability

Temporal studies of this kind require long-term datasets. To meet this requirement these analyses used data from two managed populations of roe deer, monitored over three decades. Because data were collected primarily for management purposes and not necessarily with this particular analysis in mind there were inherent limitations. Care was taken to explore the consequences of departures from the assumptions of the modelling methods and ensure that relaxing these assumptions did not bias the results and conclusions. In particular, consistency was sought between two analytical techniques, which use different aspects of the dataset and make different assumptions.

The CMR models are more complex than the BB models; they involve more estimated parameters, making more demands of the data. For this reason, some caveats apply only to these models. First, CMR models assume population closure during the primary sampling period, but sampling a deer population requires a reasonable amount of time and some deaths inevitably occurred during this period. CMR models are reasonably robust to relaxing this assumption (Kendall 1999, Lindberg 2010); however, in order to minimise this problem the primary period was kept short as possible relative to the secondary “open” sampling period. Second, heterogeneity in capture probability can confound estimates of survival in CMR models, however, comprehensive data on capture effort were not available in either study site. The available metric, the number of unique capture dates (CapDates), was considered likely to reflect trends in capture effort thus providing a control for temporal variation in capture probability. However, this measure is imperfect because it does not account for the days when traps were set but no animals were captured. With this in mind, alternative parameterisations, such as constant and temporally increasing capture probability, were examined. Results were robust to these changes. Therefore, the number of unique capture dates, considered the most accurate reflection of variation in capture effort, was used in models. That the results of the CMR modelling method were very similar to the results of the BB modelling method provides considerable reassurance that my conclusions are not compromised by these data limitations.

More generally, two further concerns apply to both analysis methods; one applies specifically to the Grimsö data and one concerns the general exploratory approach of this study. First, when roe deer deaths were observed it was not always possible to distinguish between scavenging and predation. Consequently, in Grimsö, some deaths classified as “potentially climate-related” may have been caused by predation. This is unavoidable but should only impact the preliminary models used to select candidate predictors. In theory some of the uncertainty in the Grimsö analyses could be caused by these misclassified deaths. However, preliminary investigations suggested that the same candidate predictors were chosen even when some of the climate-related deaths in question were re-categorized; thus, this likely had little impact on the final results. Finally, on a much broader note, in this exploratory study the comprehensive consideration of climatic, indirect climatic and non-climatic drivers of survival, including lagged effects, led to a large initial pool of potential predictors. Many of these were inter-correlated, reducing the capacity of models to quantify unambiguously their independent effects on survival. Conclusions must therefore be cautious and extrapolations to other sites and periods of time must be made tentatively, especially given the site specificity observed.

Despite all of these points, extrapolation to new contexts is a fundamental goal of ecology and of climate change research in particular. The inconsistencies in the data used here are representative of the problems in many long-term datasets, especially those from the types of highly managed systems that yield extensive data on wildlife populations. In order to make efficient use of the available resources researchers have a responsibility to use such data, albeit with as many safeguards as are feasible. Model evaluation provides one such safeguard. The best models chosen for both sites and by both modelling methods generally performed well at reproducing trends in survival over time (correlations between observations and estimates ranged from 0.55 to 0.69). Additionally, cross-validations suggested that, for the BB models, parameter estimates were robust. This consistency suggests that the results presented here can provide some insight into the drivers of roe deer survival at these sites and how they are likely to be affected by a changing climate.

Implications for the future: climate change, roe deer survival and population dynamics

The implication that indirect climatic effects via vegetation production influence roe survival in both sites highlights the need for mechanistic models of the relationship between climate and ungulate food availability. As discussed in Chapter 2, modelling net primary productivity of vegetation in response to temporal changes in climate is fraught with difficulty. Projecting net primary productivity, and thereby anticipating the effects of climate change on ungulate food availability and its ultimate impacts on roe deer populations, is an even bigger challenge. Temperatures and precipitation are expected to increase dramatically in northern Europe over the next century (Fronzek and Carter 2007, IPCC 2007). There is evidence that such climatic changes have already driven a 6% increase in global NPP (estimating using NDVI; Nemani et al. 2003). Given the relationships identified here it seems likely that climate change will have indirect positive impacts on roe deer survival through increased food availability in Bogesund and Grimsö. Similar impacts could be observed in other populations of roe deer in northern Europe.

The observed negative relationships with lynx and human harvest suggest effects on roe deer survival that could counteract increases in survival rates due to climate change. Since the end of the modelled period (2006), the lynx population in Sweden has been relatively stable (at around 250 family groups; Liljelund 2011). In the following five years (2007-2011), 50 deaths of roe deer at Grimsö were attributed to lynx predation (compared to the 56 observed during the ten years of lynx presence modelled), indicating that the impact of lynx may be growing. Additionally, wolf populations have been increasing in Sweden, growing from a national estimate of 120 wolves at the end of the study period (2006-07) to 295 in 2012 (Svensson et al. 2012). To date, wolves are believed to have killed approximately 20 marked roe deer in Grimsö. Whether or not the role of natural predation will increase will be determined by the regulation of wolves and lynx. In Sweden, the management goals for predator populations and their potential harvest is a nationally legislated issue. Meanwhile, harvest of roe deer populations is regulated on finer spatial scales from one property to the next. As evidenced by Bogesund (and years of roe deer hunting throughout Europe; Andersen et al. 1998a, Apollonio et al. 2010), roe deer populations have often been effectively manipulated through hunting. The analyses presented here imply that the choices made by wildlife managers regarding roe deer and their natural predators have great potential to impact roe deer survival and that some of the effects of climate change on these populations may be mitigated through responsible management decisions. Ultimately, however, survival rate is but one factor contributing to population growth. Models describing the drivers of other vital rates (e.g. fecundity and the early survival of young fawns) are needed in order to investigate how a changing climate will translate into the future dynamics of these populations.

Conclusion

In this chapter, I examine how roe deer survival relates to a variety of direct climatic, indirect climatic and non-climatic predictors. The survival models presented here incorporate relationships with biologically realistic predictors and perform well when replicating observed variation in roe deer survival at the two Swedish study sites. These models, in combination with models of other demographic processes (e.g. reproduction; see Ch. 4), are a key step toward the development of mechanistic simulations of roe deer population growth in response to climate change (see Ch. 5). A central outcome of these analyses is an emphasis on indirect climatic and non-climatic factors as important predictors of roe deer survival. In particular, the prevalence of positive relationships between annual vegetation production and survival suggest that climate might indirectly influence roe deer survival in both sites by driving changes in vegetation production. The direct effects of future climate change on roe deer survival are likely to be less important than indirect ones. The relationships with non-climatic predictors, namely lynx presence and human harvest, highlight differences in the ecology of the two sites (one with predators and one without) and suggest factors that might be used by managers to counteract the effects of climate change on roe deer survival. These findings demonstrate that analyses of climate change impacts can benefit substantially from a broad analytical approach in which a variety of climatic and non-climatic drivers are examined simultaneously.

Chapter 4 – Roe deer reproduction: a combination of fecundity and early fawn survival

Abstract

Anticipating the effects of climate change on wildlife populations requires disentangling its effects on the vital rates underpinning population growth. Reproduction involves a sequence of many non-independent processes (e.g. ovulation, implantation, birth and offspring survival), which together determine population recruitment. To examine the factors affecting roe deer reproduction at two study sites, Bogesund and Grimsö, I develop models of annual variation in ovulation and early fawn survival and integrate these into mechanistic simulations of per capita reproductive success. Results were consistent with site-specific expectations regarding the relative importance of climatic and non-climatic factors at each site. In Bogesund, where the climate is relatively mild, non-climatic factors were important: deer population density and fox abundance were negatively related to temporal variation in ovulation and early fawn survival, respectively. In Grimsö, ovulation was negatively related to cold winters and heavy winter precipitation and early fawn survival was positively related to spring precipitation, which might cause increased summer vegetation production. However, data constraints (e.g. small sample sizes, uneven sampling across years, and a shortage of data on related processes) limited the performance of simulations integrating ovulation and fawn survival. At both sites, the observed and simulated reproductive success of adult females was correlated (Pearson’s $r = 0.48$ across 16 years in Bogesund and 0.64 across 8 years in Grimsö), but estimates of fawns per female were associated with large uncertainty, the majority of which was attributable to the models of early fawn survival. While highlighting the considerable data requirements for mechanistic simulations of vital rates, these analyses also demonstrate how such simulations can provide insight into the role of climate in wildlife population dynamics.

Introduction

Managing wildlife populations in the face of climate change requires a thorough understanding of how population growth rates will be affected by expected climatic conditions. However, population growth, *per se,* is not driven directly by climate, but is, rather, an amalgamation of many demographic processes (Caswell 2001). Different vital rates (e.g. fecundity and survival) will be differently modified by environmental change. For example, a given change in climate could decrease survival rates, while indirectly increasing reproductive rates through a reduction in competition for food. In this situation, models of climate-driven mortality on their own would be insufficient to project changes in population growth. Mechanistic models of both reproduction and survival are necessary to underpin site-based management plans tailored to mitigate the effects of climate change.

Climate conditions affect both the fecundity and survival rates of many ungulate species (Owen-Smith 2010). In particular, juvenile (subadult) fecundity and the early survival of offspring from mothers of all ages are highly variable and responsive to environmental fluctuations (Gaillard et al. 1998a, Gaillard et al. 2000b, Gordon et al. 2004). While fecundity and survival are separate demographic processes, it is their combination that determines the per capita reproductive success (and thus the recruitment) of a population. Although small proportional changes in fecundity and offspring survival generally have little effect on the growth of ungulate populations (due to low elasticities in comparison with the high elasticity of adult survival), the high natural variability in each of these vital rates implies that the combined variation in reproductive success could play a large role in ungulate population dynamics (Gaillard et al. 1998a, Gaillard et al. 2000b). For this reason, a thorough understanding of the drivers of fecundity and offspring survival is important in order to estimate changes in ungulate reproductive success given climate change.

As with other ungulates, the reproductive success of female roe deer (*Capreolus capreolus*), defined here as the number of fawns surviving to the end of the critical pre-weaning period, has the potential to be impacted by climate at various stages. The population density, climate, and vegetation conditions in the months surrounding the time of births are important covariates of fawn growth and survival (Gaillard et al. 1996, Gaillard et al. 1997, Andersen and Linnell 1998, Kjellander et al. 2006, Mysterud and Ostbye 2006, Pettorelli et al. 2006). Modifications to the timing of spring vegetation flush, probably due to climate change, have been linked to reduced fawn survival in roe deer (Gaillard et al. 2013) and more widely among ungulates (Post and Stenseth 1999, Pettorelli et al. 2007, Post and Forchhammer 2008). Roe deer females are income breeders that invest heavily in reproduction and this investment can be subdivided into pre-natal and post-natal periods (Andersen et al. 1998b, Sempéré et al. 1998). Female roe deer ovulate in late summer and exhibit delayed implantation. A 300-day long gestation includes approximately five months of diapause before embryos are implanted in mid-winter. There is evidence that the number of eggs a female produces and the number of embryos implanted are both affected by lagged effects of food availability (an interaction between deer density and potentially climate-driven vegetation conditions) on body mass (Gaillard et al. 1992, Hewison 1996, Andersen et al. 1998b, Gaillard et al. 1998a). While nearly all females two years and older ovulate and become pregnant, the number of ovulations (typically 1-4 eggs per female; Andersen et al. 1998b) varies and can be negatively affected by high population density during the preceding year (Kjellander 2000). Some evidence suggests that heavy precipitation and cold temperatures during the winter preceding ovulation may be particularly influential (Hewison 1993, Lindström et al. 1994, Putnam et al. 1996). Subadult females (between one and two years old) also reproduce but their ovulation and implantation rates are often lower and more variable than those of mature females (Andersen et al. 1998b). Subadults tend to show a stronger response to the preceding year’s conditions than do older females (e.g. Kjellander 2000); in addition, they may be affected by density (and resulting food availability) from the time of their birth (approximately 15 months prior to ovulation; Gaillard et al. 1992, Kjellander 2000).

The births of roe deer fawns take place in late spring (typically May and June) in order to exploit the flush of new vegetation (Linnell et al. 1998b); they are highly synchronised within populations. Fawns are typically weaned at 3-4 months old (although some nursing may occur through winter; The Mammal Society 2012) and, until then, they are highly dependent on the mother for whom lactation is energetically expensive (Sempéré et al. 1998). Additionally, during the first two months of life, fawns are highly vulnerable to predation by red foxes (*Vulpes vulpes*), due to their small body size (Aanes et al. 1998). There is evidence to suggest that red foxes, which are typically generalists, are more likely to specialise on roe deer fawns in areas where a mixed forest-agriculture landscape supports high densities of both species (Panzacchi et al. 2008, Nordström et al. 2009). Liberg et al. (1993) estimated that, at a site on the Swedish mainland, predation by foxes accounted for 75% of the 33% of fawns that died during summer (i.e. foxes killed a quarter of the fawns born that year). The variability in summer survival of roe deer fawns, potentially driven by both food availability and predation pressure, can account for up to 75% of variation in population growth rates (Gaillard et al. 1998b).

In this study, I use data from two roe deer populations in south-central Sweden to investigate the role of climate conditions, plant production and other temporal covariates (density and predation pressure) as drivers of annual variation in roe deer reproductive success. Previous studies at each of the two study sites, Bogesund and Grimsö, have examined various potential drivers of ovulation rates and fawn survival individually, but have not integrated the two. In particular, at Bogesund, the higher density site, there is strong evidence of the importance of density dependence for ovulation and fawn survival (Kjellander 2000, Kjellander et al. 2006) and fox predation for fawn survival (Kjellander 2000, Kjellander et al. 2004a). Both these effects will likely impact female reproductive success simultaneously, and could do so synergistically or in a compensatory manner. At Grimsö, while there has been some indication that fox predation reduces the number of fawns per female in autumn (Lindström et al. 1994, Kjellander and Nordström 2003), the evidence for this effect has been mixed (Nordström et al. 2009). There is also some suggestion that winter conditions play a role in limiting ovulation, but this has not been investigated explicitly (Lindström et al. 1994, Kjellander and Nordström 2003). The analyses presented here build upon this research by examining climatic, vegetation, density, and predation-related drivers simultaneously, using updated datasets. Also importantly, this study mechanistically incorporates models of both ovulation and fawn survival into final estimates of per capita reproductive success.

On the basis of previous research and knowledge of the two sites, I hypothesized *a priori* that climate (particularly winter conditions) would be more important for roe deer reproductive success at Grimsö than at Bogesund; in Bogesund, a milder climate combined with higher densities of both roe deer and red foxes mean that density-dependence and predation should play a greater role in determining yearly reproductive success. The ultimate goal of these analyses is to construct models that can be used together to generate predictions of per capita reproductive success and, in doing so, to incorporate the variability and uncertainty inherent in both ovulation and fawn survival. The design of such models of reproduction is a necessary step towards the simulation of roe deer population growth in changing climatic conditions. In particular, I was interested in addressing the following questions:

1) How does climate affect variation in annual per capita reproductive success through its effects on ovulation and early fawn survival?
2) Are the available data sufficient to construct models of both ovulation and early fawn survival that together reflect the observed temporal variation in reproductive success for both subadult and adult females?
3) How much uncertainty is there in calculated estimates of reproductive success and what proportion of this uncertainty is due to each of the component models (of ovulation and early fawn survival)?

Methods

Study sites

In these analyses I used data on deer populations from two sites, Bogesund and Grimsö, in Sweden. The location, land cover, and climate of Grimsö and Bogesund are described in detail in Chapter 1, and site maps are provided in Chapter 3 (Fig. 3.1). The deer population at Bogesund has been actively managed, as described in Chapter 3 and summarised in Figure 4.1. Note that data from Bogesund used in this study come a part of the site where three-quarters of the roe deer population was culled in 1992 and then allowed to recover gradually. Management at Grimsö has been less extensive (see Ch. 3 and Fig. 4.1).

Roe deer reproduction

Age group terminology

Roe deer ovulate the year prior to that in which they give birth. This means that individuals ovulating when one year old (subadults) are two years old (technically adults) at the time they produce fawns; these younger females have more variable

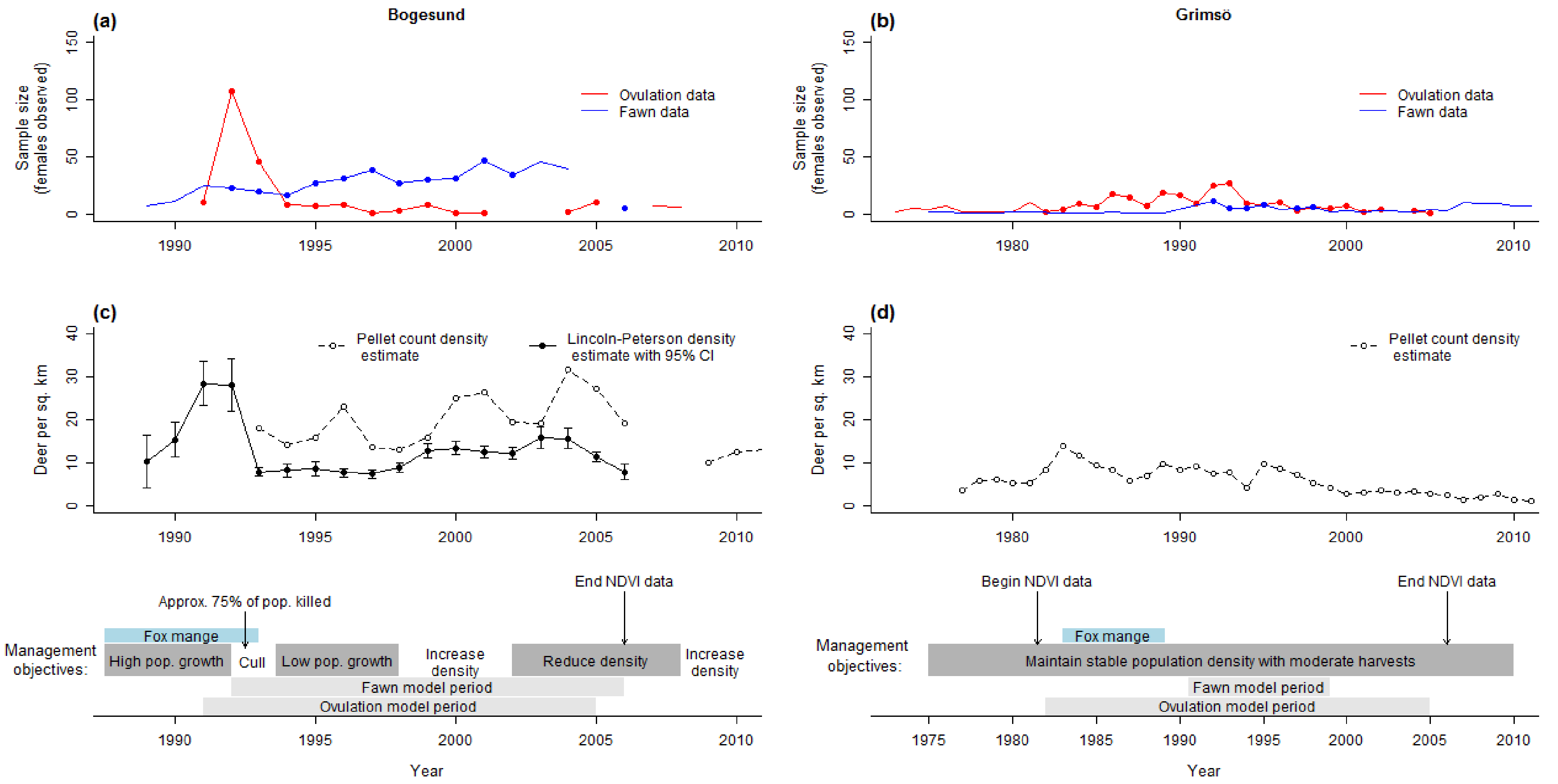

Figure 4.1: Availability of data limited the periods over which ovulation and early fawn survival could be modelled at each site. Models required data on the responses: ovulation and fawns per female (panels a & b) and the potential predictors: population density (panels c & d), NDVI (see timeline at bottom) and climate. This, in turn, constrained the overlap between the modelled periods and potentially important phases of management, density fluctuations, and periods of reduced fox densities due to outbreaks of sarcoptic mange. In panels (a) and (b), points denote the use of data in final models. In the case of fawns per female (fawn data), years in which fewer than five females were observed were excluded.

reproduction rates and are hereafter referred to as “subadult reproducers.” Females two years old or older when they ovulate (three years or older when they give birth) have more consistent rates of reproduction and, therefore, are grouped together in these analyses. These older reproducing females are hereafter referred to as “mature reproducers”. This group of “mature” females includes both the adult (2-7 years old) and senescent age classes (> 7 years old) referred to in other chapters.

Ovulation

Researchers recorded data on the number of corpora lutea observed in killed female roe deer in Bogesund from 1991 to 2008 (with the exception of 2002, 2003 and 2006) and in Grimsö from 1973 to 2005 (see Fig. 4.1 for data coverage and sample sizes). Corpora lutea are the scars left in ovaries after ovulation. The number of corpora lutea in a female’s ovaries represents the number of eggs produced during the previous mating season. Thus, the mean number of corpora lutea per female for a given autumn-winter period translates into an upper estimate of the population’s birth rate for the following spring.

The ovaries of females (marked and unmarked) hunted or killed by car within Grimsö and Bogesund study areas were stored in 70% alcohol solution, cross-sectioned and examined for corpora lutea (Stieve 1949, Borg 1970). These methods are further described by Kjellander and Nordström (2003) and Kjellander (2000). The number of corpora lutea observed in each female was recorded, along with the date and age at death (for individuals marked as fawns this was known, for other deer this was estimated based on tooth wear and eruption; Cederlund et al. 1991a).

The observed ovulation rate (O) was calculated as the mean number of corpora lutea per female. This was calculated separately for each age group (subadult and mature reproducers) and year within both Bogesund and Grimsö. Since the roe deer rut takes place in July and August and corpora lutea are visible until parturition in May and June, I used records from females examined between September 15th and April 30th in this calculation.

Implantation

Not all ovulations translate into pregnancies. Some eggs are never fertilized and some embryos fail to implant. There is evidence that, as with ovulation rates, implantation rates (I) are affected by environmental conditions (e.g. winter severity; Hewison and Gaillard 2001). Modelling this process would have been ideal, but the data necessary for this were not available for these sites. Because embryo implantation does not take place until mid-winter and the Swedish hunting season ends in February, records of embryos were only available for a small number of females (9 subadults and 78 mature females in Bogesund and 1 subadult and 30 mature females in Grimsö). Thus, only the implantation rate of mature reproducers (I_m) could be estimated directly and only as a constant. To estimate site-specific implantation rates, I divided the proportion of females that were pregnant by the proportion of females that had ovulated. Ovulation status was determined by the presence of corpora lutea in the ovaries of hunted females. Pregnancy status was determined by the presence of embryos in the uteri of hunted females. To estimate the likely implantation rate of subadult reproducers (I_s) at Bogesund and Grimsö, I used the difference between the implantation rates of subadult and mature reproducers estimated from a more extensive study of reproduction in British roe deer populations (Hewison 1996). In total, Hewison recorded the ovulation status of 511 subadults and 1850 mature female roe deer and the pregnancy status of 276 subadults and 1068 mature roe deer females. These data led to an estimated implantation rate of 0.75 for subadults (H_s) and 0.81 (H_m) for mature females (based on sample-size weighted means across nine British populations). I estimated subadult implantation rates at Bogesund and Grimsö as

$$\hat{I}_s = \hat{I}_m \cdot (H_s/H_m) \qquad \text{[Equation 4.1]}$$

These calculations led to site-specific estimates of implantation rates for subadult and mature reproducers in both Bogesund and Grimsö. These rates were assumed constant over time and used to estimate pregnancy rates used in models (detailed further below). Note that defining implantation rates as the ratio of numbers of pregnant to ovulating females (to be consistent with Hewison 1996) neglects that the ratio of counts of corpora lutea to embryos might be slightly different. However, biases will be corrected for by slightly altered estimates of the intercepts in models, and this will remove any bias in final model expectations.

Fawns per female in autumn

In both study sites, researchers recorded data on the number of fawns per female surviving through the summer pre-weaning period. Fawn per doe ratios in autumn

(September to December) have been recorded in Bogesund since 1989 (no data recorded in 2005). Researchers and hunters recorded visual observations of marked females and the number of accompanying fawns (between 0 and 4) seen within the site (while hunting, driving, conducting fieldwork etc.). Radio-collared individuals were actively “stalked”, so the females observed were not only those using open areas. Data on unmarked females (without age information) are not used here. Individual females were usually observed multiple times each autumn; if observers were not confident in their assessment, they recorded the number of fawns as unknown. If a female was observed more than once in the same year, then the maximum number of fawns she was associated with was used. Similarly, since 1975, personnel at Grimsö have reported observations of female roe deer seen by chance within the study site (Kjellander and Nordström 2003). However, in Grimsö, efforts to record fawns per marked female were less intensive than in Bogesund and sample sizes (number of unique females observed) were small. I calculated the observed fawn per female ratio (mean across known females) using observations between September and December of each year. This means that the fawn per doe estimates are timed before most of the winter mortality occurs and after the critical period when neonate fawns are most vulnerable.

Potential covariates of roe deer reproduction

Roe deer density

Researchers estimated roe deer density (Den; see Table 4.1, below, for a list of all potential predictors and abbreviations) in April of each year in both sites. In Bogesund, two methods of density estimation were used simultaneously: Lincoln-Peterson (L-P) and pellet counts (see Ch. 3 for detailed description of sampling methods). I use the Lincoln-Peterson estimates in analyses as they are available for a longer period than the pellet-based estimates (Fig. 4.1). The L-P estimates (Caughley 1977) were calculated for the 1989 to 2006 period, based on the ratio of marked to unmarked deer observed within the study area (these methods were published in Kjellander et al. 2006).

The density of the roe deer population in Grimsö has been estimated since 1977 using pellet counts. Two different sampling grids were used during this period. The original grid sampled only a 25 km^2 area (methods published by Lindström et al. 1994). Starting in 1997 a new, larger grid was used; this grid comprised clusters of 10 m^2

circular plots evenly spread throughout the Grimsö Wildlife Research Area (GWRA, Ch. 3, Fig. 3.1; Månsson et al. 2011 used a similar grid to estimate moose abundance at Grimsö). The mean number of pellets counted within each cluster was used in analyses. See Ch. 3 for further detail on these methods.

Indices of red fox abundance

The number of foxes killed each year within the county surrounding Bogesund has been recorded by the Swedish Association for Hunting and Wildlife Management, Wildlife Surveillance since 1980 (FoxHar, Table 4.1). Foxes were killed between August 1st of one year and March 15th of the next and the total fox harvest is expected to reflect the abundance of the fox population that preyed on roe deer fawns the preceding summer. The pattern shown in these county-wide records closely resembles the variation observed in the number of foxes killed each year within the Bogesund study area, which are not available for the whole study period (Kjellander 2000). Both of these records (the county fox bag, and the local one) reflect the reduction in Swedish fox populations observed from 1984 to 1993 due an epizootic outbreak of sarcoptic mange (Kjellander 2000).

The number of active fox dens (dens with litters, FoxLit) in the Grimsö study area has been recorded each spring since 1973 (Table 4.1). The presence of a litter within a den was determined by the observation of scats of young foxes and remains of fresh prey in the immediate area of the den (methods described by Kjellander and Nordström 2003). Fox kits disperse and mature during their first year, most likely impacting local adult fox abundance and predation on roe deer fawns the following summer (Kjellander and Nordström 2003). The 1980’s outbreak of sarcoptic mange (Lindström et al. 1994) is associated with a notable decrease in the number of fox litters observed during this period (Kjellander and Nordström 2003).

Climate and vegetation

I obtained observed climate data for the study period from the Climate Research Unit (CRU). The CRU 3.1 dataset provides the observed mean monthly temperature and total monthly precipitation for the entire globe at a spatial resolution of 0.5° (Mitchell et al. 2004, Mitchell and Jones 2005). Using the data from the 0.5° cell containing each study site, I calculated the mean temperature and total precipitation for

Table 4.1: Potential covariates of roe deer ovulation and fawn survival.

Metric	Abbrev.	Example dates[a]	Response modelled	Description
Response variables				
Ovulation	O_t	Aug 1995		From corpora lutea counted in dead females between Sep. of the current year (e.g. 1995) and Apr. of the next.
Fawn survival	FS_t	Jun. 1995–Aug. 1995		Estimated from fawns per female observed Sep.–Dec. compared with spring “pregnancy rate” (see text).
Climate and vegetation predictors				
Annual Integrated NDVI (INDVI)	$INDVI_t$[b]	Jan. 1995–Aug. 1995	O	Sum of bimonthly NDVI (two measures per month) from months preceding ovulation (current year).
	$INDVI_{t-1}$	Jan. 1994–Dec. 1994	O	Sum of bimonthly NDVI from full calendar year preceding ovulation.
Birth season INDVI	$BirthINDVI_t$	May 1995–Jul. 1995	FS	Sum of bimonthly NDVI at beginning of fawn survival period (surrounding period of births).
Winter temperature	$WinTmp_{t-1}$	Dec. 1994–Feb. 1995	O	Mean monthly temperature from winter preceding ovulation.
Birth season temperature	$BirthTmp_t$	May 1995–Jul. 1995	FS	Mean monthly temperature at beginning of fawn survival period.
Winter precipitation	$WinPre_{t-1}$	Dec. 1994–Feb. 1995	O	Sum of monthly precipitation from winter preceding ovulation.
Birth season precipitation	$BirthPre_t$	May 1995–Jul. 1995	FS	Sum of monthly precipitation at beginning of fawn survival period.
Snow depth	$Snow_t$	Nov. 1994–Apr. 1995	O	Mean daily snow depth in cold season preceding ovulation.
Other predictors				
Roe deer density	Den_t	Apr. 1995	O, FS	Density from April of year current to ovulation or fawn survival period.
	Den_{t-1}	Apr. 1994	O	Density from April of year prior to year of ovulation.
Fox harvest	$FoxHar_t$	Aug. 1 1995–Mar. 15 1996	FS	Foxes killed per km^2 within local county during year concurrent with fawn survival period. Bogesund only.
Fox litters	$FoxLit_{t-1}$	Spring 1994	FS	Fox litters recorded in Grimsö during spring of year preceding year of fawn survival period. Grimsö only.
Oak mast	Oak_{t-1}	Autumn 1994	FS	Whether or not year preceding fawn survival period was a mast year (binary variable on a national scale). Bogesund only.

[a] Example dates given are inclusive of entire start and end months unless stated otherwise.

[b] $INDVI_t$ is not same as $INDVI_t$ used in survival analysis (Ch. 3) which incorporated all months of current year (Jan. – Dec.).

two periods during which climate has a high potential to impact on roe deer reproductive success. Ovulation rates are related to female body mass (particularly in the case of subadult reproducers; Gaillard et al. 1992, Hewison 1996, Hewison and Gaillard 2001), which could be negatively impacted by harsh winter conditions (Putnam et al. 1996, Gaillard et al. 1998a), so I calculated mean temperature and precipitation for the winter months (December through February) preceding ovulation (WinTmp and WinPre, Table 4.1). As fawn survival and body mass have been related to climate conditions during the months surrounding births (Gaillard et al. 1996, Gaillard et al. 1997, Linnell et al. 1998b, Pettorelli et al. 2006), I calculated the mean temperature and total precipitation during the three months (May, June, and July) surrounding the time of fawn births (BirthTmp and BirthPre, Table 4.1).

Data on daily snow depth from weather stations (Ställdalen, 39 km northwest of Grimsö and Stockholm just a few kilometres south of Bogesund) near each of the study sites were obtained from the Swedish Meteorological and Hydrological Institute (1972-2009). I calculated the mean snow depth (abbreviated as Snow; Table 4.1) for each cold season using data from November through April (following Cederlund 1982).

As with previous chapters, I used Integrated NDVI (INDVI), as an index of the net primary production of vegetation over that period. Specifically, I used area-weighted means for the study sites, calculated as in Chapter 2. Given the potential lagged impacts of food availability on ovulation (via female body mass), I considered vegetation conditions from both the year of ovulation and the year prior. I summed the NDVI values across months from the year prior to the year of ovulation and across months during the current year leading up to ovulation ($\text{INDVI}_{t\text{-}1}$ and INDVI_{t}; Table 4.1). Finally, I also summed NDVI across May, June and July (BirthINDVI; Table 4.1), as the vegetation conditions in these months are potentially important to the survival of newborn fawns.

In Bogesund, oak trees (*Quercus robur*) are prevalent and years of oak mast (characterized by synchronised high acorn production) have been related to higher fawn body mass the following summer (Kjellander 2000, Kjellander et al. 2006). While mast production was not recorded in Bogesund itself, years of oak mast occurred simultaneously across Swedish oak forests during the study period. Data on whether or not a year was a “mast year” across Sweden (abbreviated as Oak, Table 4.1) were obtained from Svenska Skogsplantor AB (Hallsberg, Sweden, unpublished data). In

Grimsö, the forest is primarily coniferous and oak mast years are unlikely to impact roe deer reproduction; therefore, I did not consider oak mast as a predictor in Grimsö.

Modelling

Ovulation models

I modelled ovulation in each site (represented by 0, 1, or > 1 corpora lutea per female) assuming a multinomial distribution for the errors. Multinomial models assume that the counts in each category have a Poisson distribution, but are constrained so that the sum across all categories equals the total counts observed (in this case the number of females). Therefore, the parameters of the multinomial model describe the probability that a female, given the predictors, will have zero, one or more than one corpora lutea. By simultaneously modelling the counts in all three categories and thus accounting for the potential constraints among them, the use of the multinomial distribution reflects the discrete process of ovulation. The number of individuals observed in each year is included as a weight in the model allowing the influence of each year to scale with the sample size. Although females might produce up to four eggs at a time, grouping the females observed to have more than one corpora lutea reduced the number of responses being modelled and, thus, the number of parameters to be estimated. Preliminary analyses suggested that grouping females in this way did not change which predictors were selected in models and, furthermore, led to more parsimonious models at both sites.

I identified eight potentially important predictors of ovulation: age group (subadult or mature reproducers), INDVI_t, Den_t, $\mathrm{INDVI}_{t\text{-}1}$, $\mathrm{Den}_{t\text{-}1}$, $\mathrm{WinTmp}_{t\text{-}1}$, $\mathrm{WinPre}_{t\text{-}1}$ and $\mathrm{Snow}_{t\text{-}1}$. I tested all possible combinations of these predictors. I allowed up to three variables in a model in order to examine two-way interactions between variables. Specifically, I allowed for interactions between variables from the same time period (e.g. Den_t and INDVI_t; $\mathrm{Den}_{t\text{-}1}$ and $\mathrm{INDVI}_{t\text{-}1}$, $\mathrm{WinTmp}_{t\text{-}1}$ and $\mathrm{WinPre}_{t\text{-}1}$; and, finally, the winter variables and $\mathrm{Den}_{t\text{-}1}$) and between age group and any of the seven temporal predictors. As in previous analyses (see Ch. 2 and Ch. 3), I ranked candidate models using Akaike's Information Criterion (AIC) and model weights (Anderson et al. 2000, Burnham and Anderson 2002). I removed nested models, and selected models with Δ AIC ≤ 6 for consideration in the top model set (Richards 2008). Finally, I examined correlations amongst candidate predictors across the modelled years. Any models of ovulation including combinations of predictors that were strongly correlated (Pearson's $r > 0.4$; c.f. Freckleton 2011) with each other were removed from the final model set.

The multinomial models describe the probabilities of three non-independent responses (0, 1, or > 1 corpora lutea) and, therefore, the sign (positive or negative) of a single coefficient does not directly indicate the direction of a predictor's effect on mean fecundity. For example, winter precipitation could increase the probability of having > 1 corpora lutea vs. no corpora lutea (and have a positive coefficient for this effect) and could simultaneously increase the probability of only one corpora lutea at a greater rate (another positive coefficient); this combination could result in a larger proportion of females having 1 vs. > 1 corpora lutea (but fewer with 0) and consequently a decline in the mean number of corpora lutea per female with increasing precipitation. Additionally, the combination of a predictor's effects on the probabilities of having 0, 1, and > 1 corpora lutea can result in non-linear relationships between a predictor and mean fecundity which would not be apparent from any one model parameter. For ease of interpretation, the fitted values from the multinomial models are considered in terms of mean ovulation rates (mean number of corpora lutea per female; see Equation 4.2, below) for each of the two age groups. Likewise, instead of presenting single coefficients, the relationship between predictors and associated mean ovulation rates are plotted in order to visualise these effects. The estimated mean ovulation rate ($\hat{O}$) given predictors was calculated as:

$$\hat{O} = P_1 + (P_{>1} \cdot C_{>1}) \qquad \text{[Equation 4.2]}$$

Where P_1 is the probability of one corpora lutea, $P_{>1}$ is the probability of more than one corpora lutea, and $C_{>1}$ is the mean number of corpora lutea above one calculated from the data. $C_{>1}$ was an age-group and site-specific constant. I calculated $C_{>1}$ separately for subadults and mature females in each site using all possible records from that site and age group (across all years). Confidence intervals were generated using a parametric bootstrap (Gelman and Hill 2006) with 1000 iterations. At each iteration, a new set of coefficients was generated by sampling from a multivariate normal distribution defined by the coefficients and variance-covariance matrix extracted from the fitted model. The simulated coefficients were then used to produce estimates of mean ovulation rates (see Equation 4.2) given predictor values over the modelled period. The 0.025 and 0.975

quantiles of those estimates were taken as the 95% confidence interval surrounding the model estimates.

The years over which ovulation was modelled differed between the two study sites according to data availability. Ovulation data were available for 15 years at the Bogesund site, but two of those years (2007 and 2008) were not used in models due to lack of data for the potential predictors, NDVI and deer density (Fig. 4.1). Ovulation data were available for 31 years from 1973 until 2005 in Grimsö; however, due to the availability of NDVI data (1982-2006) only 23 years of data were used in model fitting.

Fawn survival models

I modelled the number of fawns per female in autumn at each site assuming a lognormal distribution of errors. These models included an estimate of “pregnancy rate” as an offset term to control for the observed variation in ovulation across years. I calculated the pregnancy rate as the observed ovulation rate (O, corpora lutea per female) multiplied by the estimated age-specific implantation rate ($\hat{I}_s$ or $\hat{I}_m$; see Equation 4.1). I calculated this pregnancy rate separately for the mature and subadult reproducers to allow for different ovulation and implantation rates in the two groups. The mean pregnancy rate across all females was then calculated as a weighted mean of the subadult and mature females, with the weights equal to the number of subadults and mature females examined for corpora lutea that year. The pregnancy rate, incorporates the processes of ovulation and implantation, but does not consider potential abortions. It therefore represents an estimate of the maximum number of fawns born per female in spring, typically in May and June in both Bogesund and Grimsö (pers. comm., Kjellander 2012). By including the expected pregnancy rate as an offset term in these models, I accounted for yearly variation in the number of potential births so that residual variation in number of fawns per female will represent variation in early fawn survival (and potentially abortions). This residual variation can then be related to potential predictors.

Years in which there were fewer than five females observed (for fawn presence) were excluded from this analysis because the fawn survival models do not account for variation in sample size across years. The number of females observed in autumn was generally low in both sites. This, in combination with the limited temporal extent of other data, meant that only a limited number of years could be used in models. In

Bogesund, sufficient data on the number of fawns per female were available for 17 years from 1989 to 2006 but five of those years could not be used in models due to lack of ovulation data from the preceding year or lack of NDVI data (Fig. 4.1). In Grimsö, the number females observed per year was extremely low (mean females observed = 3.9 ± 3.13 [SD]). Due to the exclusion of years with fewer than 5 females observed and the limited temporal extent of the ovulation data (Fig. 4.1), only six years of data from 1992 to 1998 could be used in models of fawn survival at this site.

Due to these data limitations, I only considered models based on a single predictor. I considered five potential predictors (see Table 4.1) likely to affect early fawn survival: indices of fox abundance (FoxHar_t in Bogesund, and $\text{FoxLit}_{t\text{-}1}$ in Grimsö), Den_{t} (surveyed in April in both sites), BirthPre_t, BirthINDVI_t, and $\text{Oak}_{t\text{-}1}$ (Bogesund only). I examined inter-annual correlations between pairs of candidate predictors, across modelled years, to understand relationships among the temporal predictors better. Preliminary analysis of data from Bogesund suggested that maternal age group (subadults at ovulation vs. mature females that were two or older at ovulation) was not an important predictor of early fawn survival in that site. In Grimsö, there were not enough two-year-old females (subadult reproducers) observed during surveys to consider maternal age as a predictor. Therefore, maternal age was not considered further in these models. Finally, I used the same model ranking procedure as with the ovulation models and selected models with Δ AIC ≤ 6.

Model cross-validation

Predictive abilities of the AIC best ovulation and fawn survival models (one of each for Bogesund and for Grimsö) were evaluated by examining the correlation between the observed and estimated rates of ovulation and numbers of fawns per female in autumn. To evaluate the ovulation data and estimates of the multinomial models, I used a weighted correlation coefficient (Bland and Altman 1995) where the weights were the number of females observed each year. To evaluate the correlation between observed fawns per female and the estimates produced by the fawn survival models, I used Pearson’s correlation coefficient (r). I did this for the complete datasets, using the best models (fitted with all possible data), and for years of data excluded from model-fitting during a cross-validation procedure. This procedure was repeated for both the ovulation and fawn survival models at each study site separately (four times in all).

Years of data were chosen at random and excluded from the relevant dataset. The selected best model was then re-fitted using the reduced dataset and the newly estimated model parameters were used to reproduce the omitted years of data. This was repeated once per year in the dataset excluding one year at a time and 1000 times each excluding between 2 and 5 years at a time. In the case of the Grimsö fawn survival models, which included only six years of data in the complete dataset, I left out only 1-3 years of data at a time because there would be insufficient data to estimate the model's parameters if more data were excluded. In order to investigate the effects of sample size and potential outliers on parameter estimates, I recorded the parameter estimates from each model fit. I then compared the median and 95% quantiles of parameters (i.e. 95% confidence intervals across iterations) estimated using models fitted with 1-5 years excluded from the dataset.

Simulations of reproductive success

The cross-validation analysis, described above, evaluates the individual models of ovulation and fawn survival separately. When estimating overall reproductive success, errors are likely to propagate across the two individual models. To examine the ability of the ovulation and fawn survival models to estimate reproductive success, and evaluate the joint uncertainty associated with modelling these two processes, I used a simulation-based approach (a parametric bootstrap with 1000 iterations). I combined estimates from the best ovulation models and best fawn survival models (one of each for each site) to simulate reproductive success across years in each site. At each iteration, the ovulation rate was simulated, with error, from the ovulation model; the fawn survival model was then used to simulate fawn per female rates, once again with error. Instead of incorporating observed ovulation rates in the offset term, the fawn survival models in these simulations used the simulated ovulation rates from the ovulation models. All models of ovulation included age group as a predictor and, thus, produced separate estimates of ovulation rates for subadult and mature reproducers. These rates were multiplied by age-group specific implantation rates to produce estimates of the pregnancy rates of mature and subadult reproducers for each year. These pregnancy rates were included as an offset term in the fawn survival models. This allowed the calculation of separate estimates of fawns per female for subadult and mature reproducers, which assumed equal rates of fawn survival but incorporated the distinct ovulation rates of the maternal age groups. It also allowed simulation of fawns per female in years for which observed ovulation data were unavailable.

Simulations were run for the entire time period for which a) predictors included in top models were available and b) observations of at least one component of reproductive success (either ovulation or fawns per female) were available. This meant including years which had previously been excluded due to the lack of observed ovulation data (used to fit the fawn survival models) or due to the temporal extent of candidate predictors (e.g. NDVI, available only from 1982-2006, limited the Grimsö ovulation models). To evaluate the combined ability of the selected ovulation and fawn survival models to simulate reproductive success, I examined the correlations between all available ovulation and fawn data, and the median estimates (across within-year iterations) of ovulation and fawns per female based on the simulations. I did this separately for each study site and maternal age group. The calculation of age-group specific correlations, and inclusion of additional data not used to fit the original models, meant that these correlations differ from the correlations involved in the cross-validation procedure described above and provide one further test of model predictive ability.

Variation in the estimates of reproductive success is due to a combination of measurement errors and uncertainty from both the component processes of ovulation and early fawn survival. To quantify the relative contributions of these sources of variation to the overall uncertainty in estimates of fawns per female, I simulated fawn per female data under three different scenarios. In the first, the simulations from the ovulation models included error but the simulations of fawn survival did not (i.e. the maximum likelihood estimate of the linear predictor was used). In the second scenario, the simulations of fawn survival included error but the simulations of ovulation did not. In the third, and final, scenario both the simulations of ovulation and the simulations of fawn survival included error. I then calculated the variance among simulated values under all three scenarios. The variance from the first scenario (sampling ovulation parameters) divided by the variance from the third scenario (sampling both ovulation and fawn survival parameters) estimates the proportion of the total variation due to uncertainty in modelling ovulation. Similarly, the variance from the second scenario (sampling fawn survival parameters) divided by the variance in the third scenario estimates the proportion of the total variance explained by uncertainty in modelling fawn survival.

All data preparation and statistical analyses were performed in program R 2.13.0 (R Core Development Team 2011).

Results

Models of ovulation in Bogesund

In the thirteen years for which ovulation data were available between 1991 and 2005, the ovaries of 213 females were examined for corpora lutea; nearly all of these females had been hunted (188 deaths) or killed in traffic accidents (22 deaths). Thirty-two of these females were subadults; records of subadults were only available for six of the years modelled. Most of the ovulation data came from the large harvests during the two years of high density: 107 and 46 females were killed and examined in 1992 and 1993, respectively. An average of 5.5 ± 0.82 [SD] females per year were examined across the remaining 10 years. On average, mature reproducers had 1.8 ± 0.18 corpora lutea (mean ± SD across 12 years) and subadult reproducers had 1.0 ± 0.46 (across 6 years). Several pairs of the predictors considered in these models had reasonably strong correlations (Pearson's *r* between 0.4 and 0.55; Appendix 4, Table A4.1).

In Bogesund, age group was strongly related to the number of corpora lutea observed. While more than 80% of mature reproducers had more than one corpora lutea, this was the case for less than 30% of subadults (Fig. 4.2). All the models with Δ AIC ≤ 6 included age group as a predictor (Appendix 4, Table A4.2). Among age groups, individuals with more than one corpora lutea had similar ovulation rates (subadults: mean corpora lutea when > 1 is observed, $C_{>1} = 2$, no variance; adults: $C_{>1} = 2.1 \pm 0.31$ [SD]).

The best performing ovulation model in Bogesund (with the lowest AIC) had a weight (ω_i) = 0.76 and included only one temporal predictor (Appendix 4, Table A4.2): the current year's density (Den_t). In this model, density had a negative effect on the probability of females having > 1 corpora lutea. Increasing density was associated with a decline in the fecundity of both mature and subadult reproducers; the slope of this

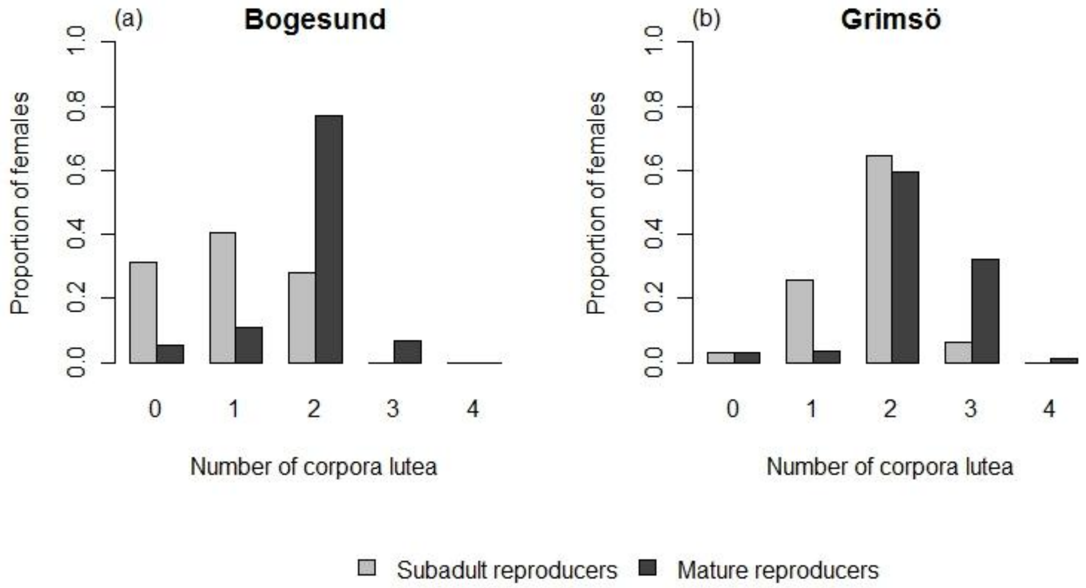

Figure 4.2: The number of corpora lutea (an indicator of egg production) of killed female roe deer from Bogesund (panel a: n = 32 subadults, n = 181 mature reproducers) and Grimsö (panel b: 31 subadults, n = 186 mature reproducers).

decline is slightly steeper for subadults than for mature reproducers (Fig. 4.3). There were three other models with Δ AIC ≤ 6 in the ovulation model set; one of these included only age group and no temporal predictors (Δ AIC = 5.37). Other models in the set included weak effects of the previous winter's temperature (negatively related to fecundity of subadults only) and the previous year's density (weak negative association with the fecundity of both age groups).

The best ovulation model (including an effect of Den_t) reproduced the observed ovulation data well (Appendix 4, Fig. A4.1a and b). The correlation between observed mean fecundity and that estimated by the model was high (weighted correlation = 0.88, $P < 0.001$, n = 18). The cross-validation analysis of the model suggests that parameter estimates would be affected by decreases in sample size (Fig. A4.1c). Additionally, there was evidence of a decline in predictive ability with smaller sample sizes; the correlation between estimated and observed fecundity (for the years excluded during model-fitting) was generally high but decreased from 0.86 when one year was excluded at time to 0.71 when 5 years were excluded with each iteration. This is principally because detecting the effects of density is highly reliant on data from 1992 and 1993 (the high density years).

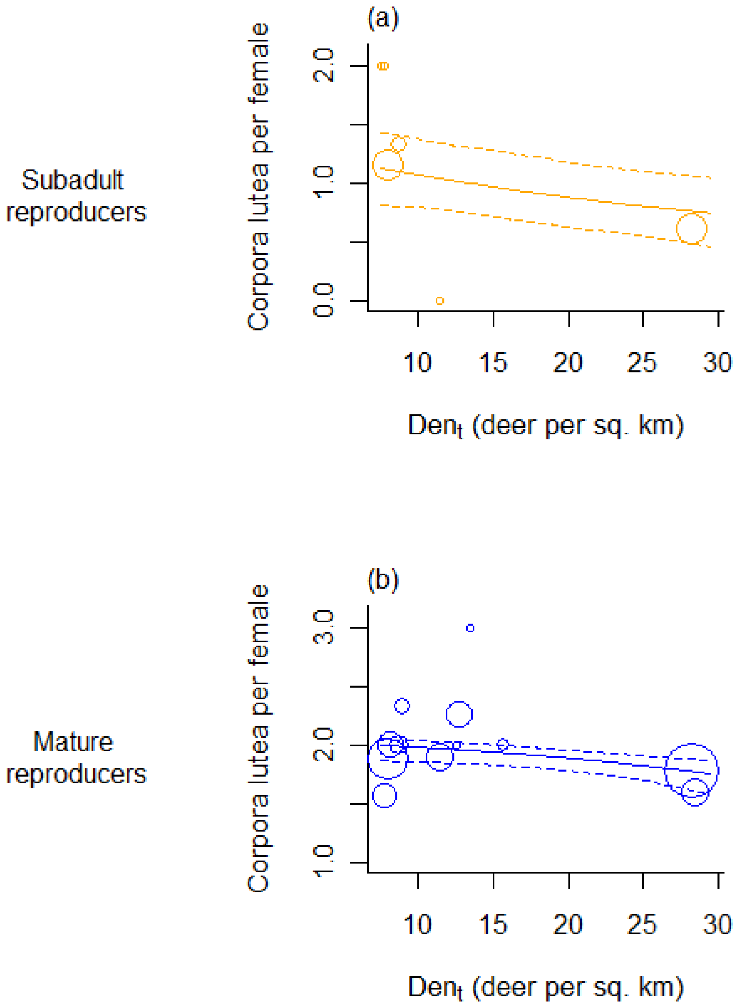

Figure 4.3: The relationships between the current year's density (Den$_t$) and ovulation rates (corpora lutea per female) based on the Bogesund ovulation model (solid lines) with 95% confidence intervals (dashed lines). Deer were divided into subadult reproducers (panel a) and mature reproducers (panel b). Point size is proportional to the sample size (number of females observed) within a given year and the relative weight of that data point within the model.

Models of fawn survival in Bogesund

Over the twelve years modelled, 332 females were observed (27.7 ± 10.84 [SD] per year); forty-seven of these females were 2 years old and would have been subadults at ovulation (i.e. were subadult reproducers). The mean early survival of fawns was 0.44 ± 0.188 (mean ± SD across 12 years). There were few strong correlations among the candidate predictors of fawn survival (Appendix 4, Table A4.3). All fawn survival models included an offset term equal to the estimated pregnancy rate for a given year. This pregnancy rate incorporated age-specific estimates of implantation rates (assumed constant over time, see Equation 4.1). These were estimated as 91% for subadults and 99% for adults at Bogesund (i.e. $\hat{\text{I}}_{s} = 0.91$ and $\hat{\text{I}}_{m} = 0.99$).

Three models of fawn survival in Bogesund had a Δ AIC ≤ 6 (Appendix 4, Table A4.4). The best AIC model of fawn survival ($\omega_i = 0.76$) included a strong negative relationship with the following autumn's fox harvest, an index of fox abundance ($\beta_{\mathrm{FoxHar}(t)} = -28.4 \pm 9.35$; Fig. 4.4). The second best model (Δ AIC = 3.23) included a positive effect of INDVI from the months surrounding fawn births but 95% confidence intervals surrounding this effect were wide and overlapped zero. The null model was ranked third.

While estimates of fawns per female produced by the best AIC model of fawn survival captured some of the inter-annual variation in fawns per female at Bogesund, the predictive ability of this model was relatively poor (Appendix 4, Fig. A4.1d and e). The correlation between estimates and observations of fawns per female across years was low (Pearson's $r = 0.43$, $P = 0.17$) and cross-validation exposed a lack of robustness of the fitted model to variations in the available data (Fig. A4.1f). Pearson's r ranged from 0.15 to 0.08 across iterations when 1-5 years were excluded at time in cross-validation.

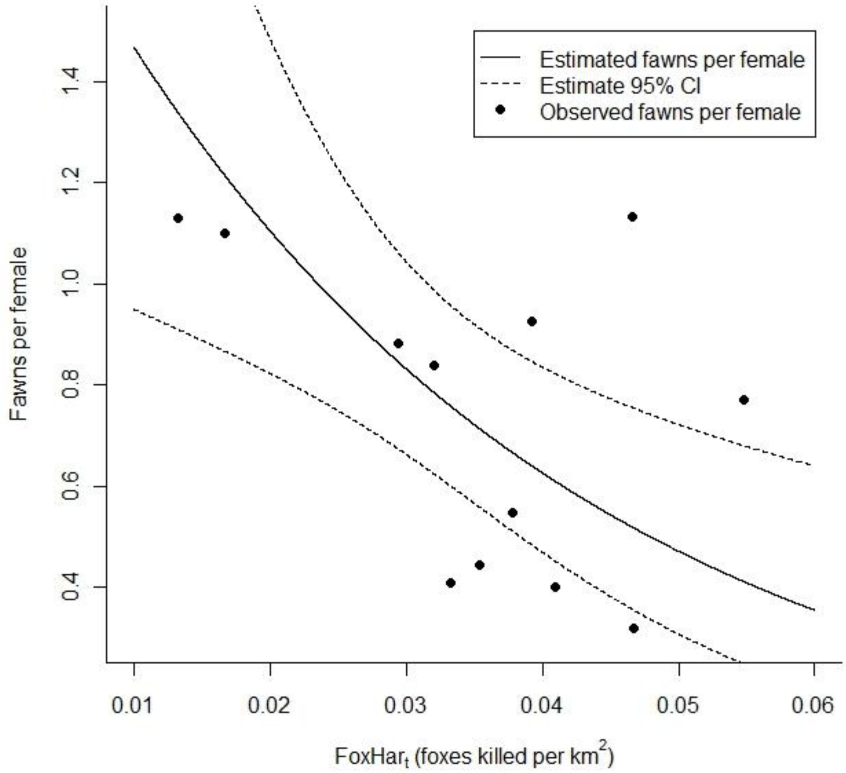

Figure 4.4: The relationship between annual fox harvests (FoxHar$_t$, an index of fox abundance) and fawns per female based on the AIC best model of early fawn survival in Bogesund. Displayed estimates of fawns per female were calculated assuming a constant pregnancy rate (equal to the mean pregnancy rate from the modelled period, 1.9 ± 0.41 embryos per female). Model performance is examined further in Appendix 4, Fig. A4.1.

Simulations of reproductive success in Bogesund

In Bogesund, ovulation was simulated between 1989 and 2006 and fawn survival, which incorporated the previous year's ovulation estimate, was simulated from 1990-2007 (Fig. 4.5). Simulations included estimates of fawns per female for four years (1990, 1991, 2003, 2004) with observed fawn data that were not included during the original model fitting process due to lack of ovulation data from the prior year (see points in Fig. 4.1a for years used in original model fitting).

The simulations, which combined the best model of ovulation (Den_t) and fawn survival (FoxHar_t), indicated that final estimates of reproductive success (as measured by fawns per female in autumn) were associated with a high degree of uncertainty and did not reflect the observed inter-annual variation in final reproductive success well (Fig. 4.5). Only 24% of the total variation in surviving fawns per female was due to uncertainty associated with the ovulation models, while 76% of the total variation was due to the uncertainty associated with the fawn survival models.

The correlation between estimated and observed ovulation rates was reasonably good for subadults (weighted correlation = 0.74; $P < 0.1$, n = 6; Fig. 4.5a), but low for mature females (weighted correlation = 0.48; $P < 0.2$, n = 12; Fig. 4.5b). Much of the variation in ovulation that was explained by the model was related to the age of females (see Appendix 4, Fig. A4.1b) not to inter-annual variation which could be explained by the temporal predictor. The correlations between the simulated fawns per female (mean across 1000 iterations) and observed fawns per female were low for both age groups (Pearson's $r = 0.48$, $P < 0.1$, n = 14 for subadult reproducers; $r = 0.48$, $P < 0.1$, n = 16 for mature reproducers). The number of fawns observed per subadult reproducer appears to have been underestimated in nearly all cases (Fig. 4.5c). Estimates of fawns per female observed with mature reproducers often fell within the confidence intervals, but those CIs were wide; the simulated values do not reflect well the observed changes in reproductive success from one year to the next (Fig. 4.5f). The wide bootstrapped CI surrounding simulated estimates of fawns per female indicate the high uncertainty in both underlying processes.

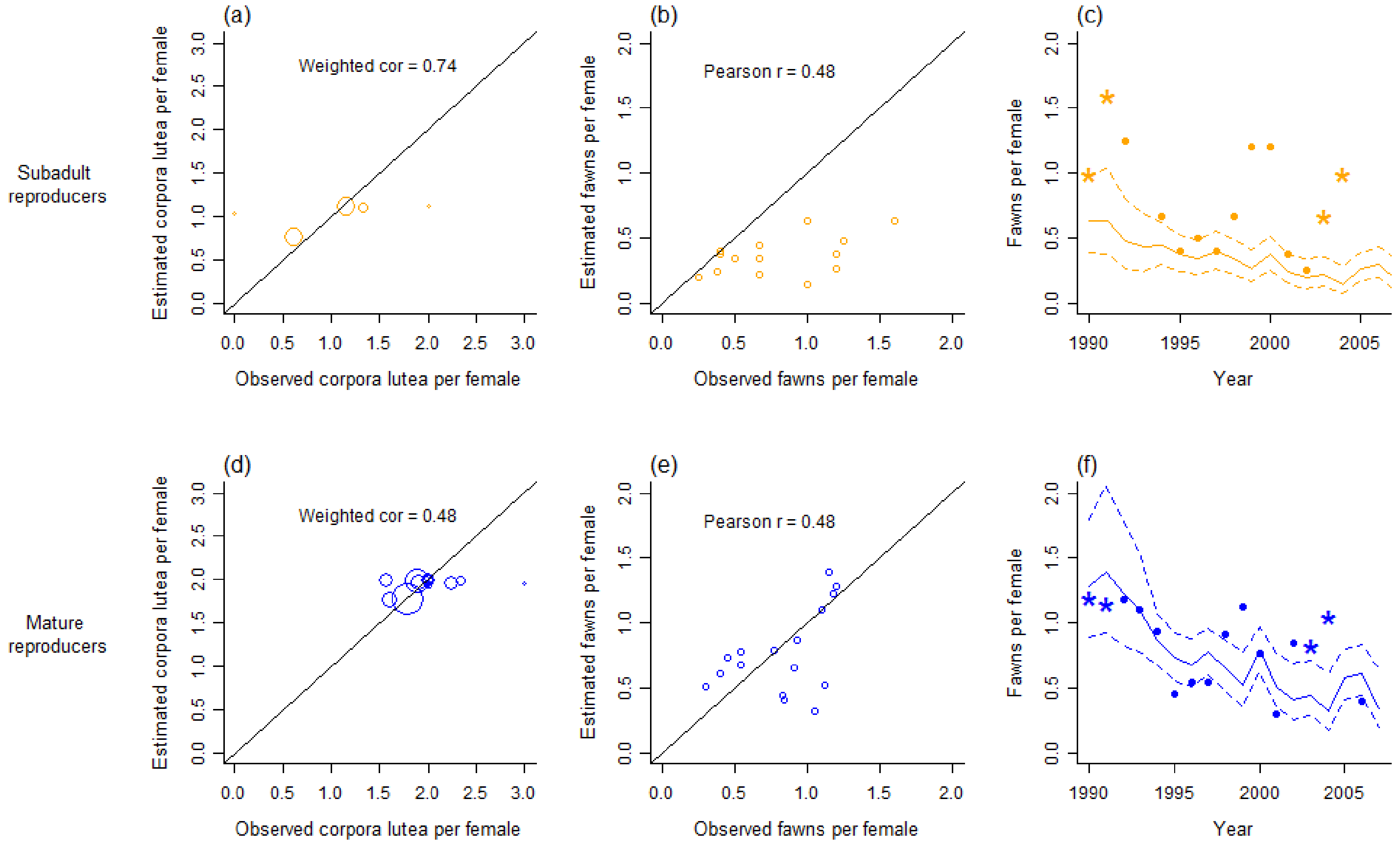

Figure 4.5: Simulations of the reproductive success of subadult (top row of panels) and mature reproducers (bottom row) in Bogesund against observed ovulation rates and numbers of fawns per female. Panels (a) and (d) show correlations between estimated and observed ovulation from the AIC best model of ovulation (see text), including sample-size weighted correlation coefficients (point size is proportional to sample size). Panels (b) and (e) show estimated versus observed fawns per female from the AIC best model of early fawn survival (including Pearson's correlation coefficient). The simulated per capita reproductive success (solid line, measured in terms of fawns per female in autumn) across years is shown in panels (c) and (f) (with 95% CI, dashed lines). In these panels, points represent observed values from years used in model fitting and asterisks represent years that were not used to fit the fawn survival model (see text).

Models of ovulation in Grimsö

Across the 23 years modelled, 186 mature reproducers and 31 subadult reproducers were examined for corpora lutea, resulting in an average sample size of 9.4 ± 7.35 [SD] females per year. All but one of these females died due to harvest, traffic accidents or other human-related causes (the one remaining female was killed by a lynx). On average, mature reproducers had 2.2 ± 0.21 corpora lutea (mean ± SD across 21 years) and subadult reproducers had 1.7 ± 0.44 (across 14 years). There were several strong correlations (Pearson's $r > 0.6$) between candidate predictors in this dataset; in particular, the current year's INDVI and the preceding winter's temperature and snow depth were all highly correlated (Appendix 4, Table A4.1).

As in Bogesund, age group was an important predictor of ovulation in Grimsö and was included in all models with Δ AIC ≤ 6 (Appendix 4, Table A4.5). More than 90% of mature reproducers examined had more than one corpora lutea, but only 71% of subadults did (Fig. 4.2). When more than one corpora lutea was counted, mature females averaged 2.4 ± 0.51 corpora lutea [$C_{>1}$ ± SD] and subadults averaged 2.1 ± 0.27 corpora lutea.

The four ovulation models in the Grimsö model set (with a Δ AIC ≤ 6) all included the preceding winter's precipitation ($\text{WinPre}_{t\text{-}1}$) as a predictor (Appendix 4, Table A4.5). The AIC best model had high weight within the model set ($\omega_i = 0.56$). According to this model, increasing $\text{WinPre}_{t\text{-}1}$ above 100 mm in a given winter was associated with a strong decrease in subadult fecundity (Fig. 4.6a). The relationship of $\text{WinPre}_{t\text{-}1}$ with the fecundity of mature reproducers is much weaker (implying little decrease in ovulation rate until $\text{WinPre}_{t\text{-}1}$ >150 mm; Fig. 4.6c). This model also included an effect of the previous winter's temperature ($\text{WinTmp}_{t\text{-}1}$) on ovulation: the fecundity of subadults was generally positively related to $\text{WinTmp}_{t\text{-}1}$ but, again, the effect was much weaker for mature reproducers (Fig. 4.6d). The second best model was also well-supported (Δ AIC = 1.24, $\omega_i = 0.30$). This model suggested a negative impact of mean snow depth from the preceding cold season ($\text{Snow}_{\text{t-1}}$) on subadult fecundity with, again, limited impacts on mature reproducers. The age-only and null models performed relatively poorly, with Δ AIC > 17.

The best ovulation model, including WinPre$_{t\text{-}1}$ and WinTmp$_{t\text{-}1}$, was moderately good at explaining variation amongst subadult reproducers, but performed less well when reproducing the fecundity rates of the mature reproducer age group (Appendix 4, Fig. A4.2b). The correlation between estimated and observed rates of ovulation (r = 0.64, weighted correlation coefficient, $P < 0.001$, n = 36) was primarily because the model explained inter-annual variation in subadult ovulation and the difference in ovulation between the two age groups. The model captured inter-annual variation in adult ovulation poorly. Cross-validation analysis for this top model showed that parameters associated with WinPre$_{t\text{-}1}$ and WinTmp$_{t\text{-}1}$ were robust to the availability of data (Appendix 4, Fig. A4.2 c and d). There was a small but steady decline in the model's predictive ability as years were excluded in the cross-validation analysis (Pearson's r ranged 0.71-0.64 when 1-5 years were left out of model-fitting).

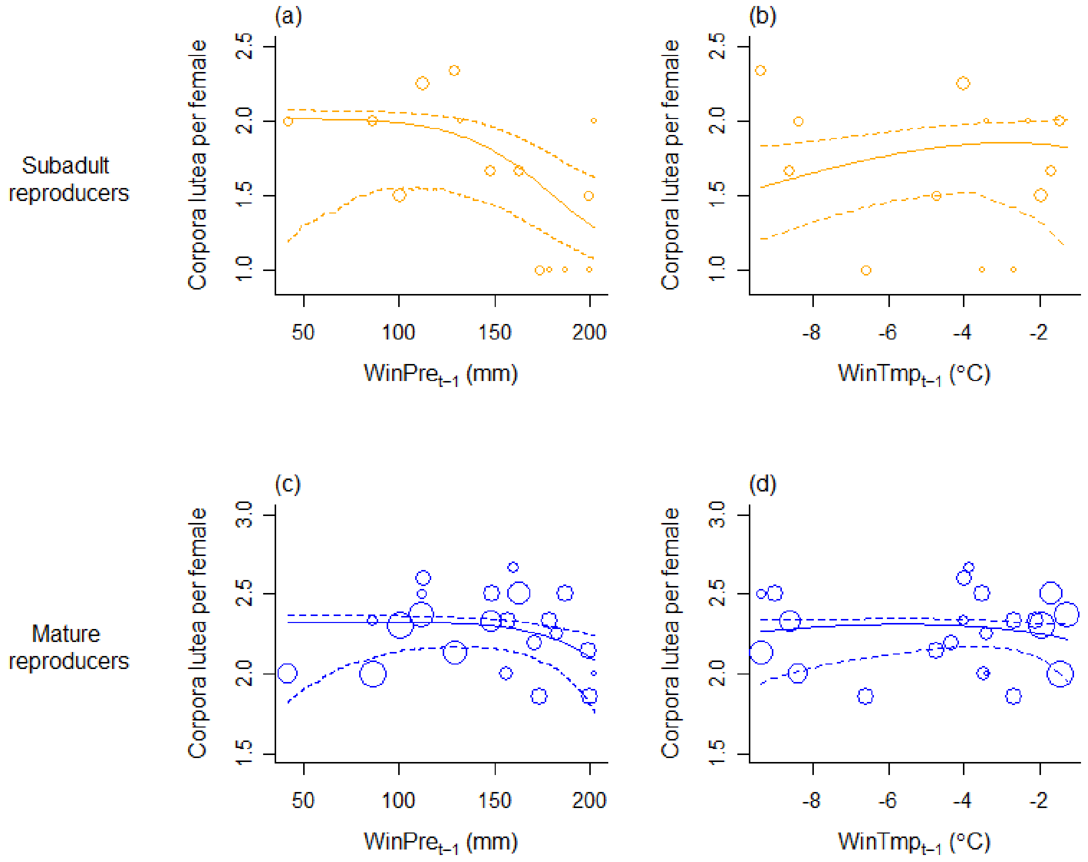

Figure 4.6: The relationships between temporal predictors and ovulation rates (corpora lutea per female) based on the Grimsö ovulation model (solid lines) with 95% confidence intervals (dashed lines). When calculating estimates of corpora lutea per female given WinPre$_{t\text{-}1}$ (panels a & c), WinTmp$_{t\text{-}1}$ was held constant at its mean (-4.4 ± 2.70 °C across the modelled period). Likewise, when estimating ovulation given WinTmp$_{t\text{-}1}$ (panels b & d), WinPre$_{t\text{-}1}$ was held constant at its mean (145 ± 42.2 mm). Deer were divided into two age groups: subadult reproducers (panels a & b) and mature reproducers (panels c & d). Point size reflects the sample size (number of females observed) within a given year and the relative weight of that data point within the model.

Models of fawn survival in Grimsö

Over the six years included in the Grimsö fawn survival models, 41 females were observed (mean sample size = 6.8 ± 2.79 [SD] per year), including 2 subadult reproducers and 39 mature reproducers. The mean early survival of fawns was 0.26 ± 0.113 (mean ± SD across 6 years). In this site, many of the candidate predictors for fawn survival were strongly correlated over the years modelled, including INDVI, precipitation and temperature from the months surrounding fawn births (Appendix 4, Table A4.3). The offset terms in these models included estimated implantation rates of 0.93 for subadults ($\hat{I}_s$) and 1.0 for mature reproducers ($\hat{I}_m$).

Three models of fawn survival in Grimsö had Δ AIC ≤ 6 (Appendix 4, Table A4.6). The best performing model had a high weight within the model set ($\omega_i = 0.86$) and included a positive effect of BirthPre_t on fawn survival ($\beta_{\text{BirthPre}(t)} = 0.007 \pm 0.0019$ [SE]; Fig 4.7). Because the other models in the set had Δ AIC > 4.5 and contained biologically implausible relationships, they were not considered further. The null model performed relatively poorly (Δ AIC = 9.49).

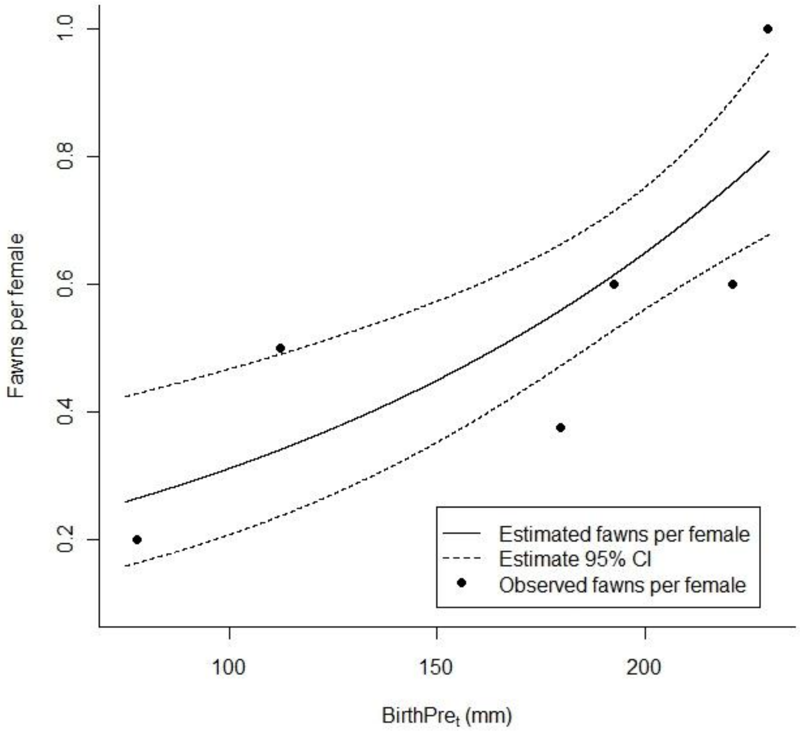

Figure 4.7: The relationship between precipitation during May, June and July (BirthPre_t) and fawns per female in Grimsö. Fawns per female was estimated based on the best AIC model of early fawn survival at this site. Displayed estimates of fawns per female were calculated assuming a constant pregnancy rate (equal to the mean pregnancy rate from the modelled period, 2.1 ± 0.27 embryos per female). Model performance is examined further in Appendix 4, Fig. A4.2.

The AIC best model reproduced well the number of fawns per female observed (Appendix 4, Fig A4.2e and f). The correlation between estimated and observed fawns per female was high (Pearson’s $r = 0.94$, $P < 0.01$). Cross-validation analysis suggested that parameter estimates were vulnerable to sample size reductions but this is unsurprising, given the sparse data. The model’s predictive ability remained high when data were excluded (Pearson’s r ranged 0.79-0.78 when 1-3 years were excluded).

Simulations of reproductive success in Grimsö

In Grimsö, ovulation data were recorded from 1973 and climate data were available until 2009; hence, ovulation was simulated from 1973-2008 and fawn survival from 1974-2009 (Fig. 4.8). Simulations included estimated ovulation for seven years that were not included in model fitting because of missing ovulation observations. Similarly, the simulations included estimates of fawns per female surviving until autumn for three years with observed fawn data that were not included in model fitting. Separating the limited fawn per female data according to maternal age group meant that there were only eight years for which an estimate of fawns per female (requiring observations on at least five females; see Methods) could be calculated for mature reproducers; unfortunately, there were no years in which sufficient fawn per female data existed for subadult reproducers. The observations of fourteen subadults over the entire study period yielded an average of 0.73 ± 0.199 [SE] fawns per subadult reproducer (sample size weighted mean across 10 years; grey line in Fig. 4.8b).

Simulations of reproductive success in Grimsö combined the best model of ovulation including WinPre_{t-1} and WinTmp_{t-1} and the best model of fawn survival including BirthPre_{t}. While the ability of these models to reproduce temporal patterns of ovulation and, ultimately, fawns per female appears to have been mediocre, the narrow CIs suggest low levels of uncertainty inherent in the parameterisation of the component models (Fig. 4.8b and e). Approximately 36% of the total variation among simulations was due to uncertainty in the ovulation models, while the remaining 64% was attributed to uncertainty in the fawn survival model. The correlation between the estimated and observed ovulation rates was reasonably good for subadult reproducers (weighted correlation = 0.63, $P < 0.01$, n = 18; Fig. 4.8a), but was approximately zero for adults (weighted correlation = -0.03, $P > 0.2$, n = 30; Fig. 4.8c). The fawn survival model appears to have performed moderately well at reproducing observed numbers of fawns

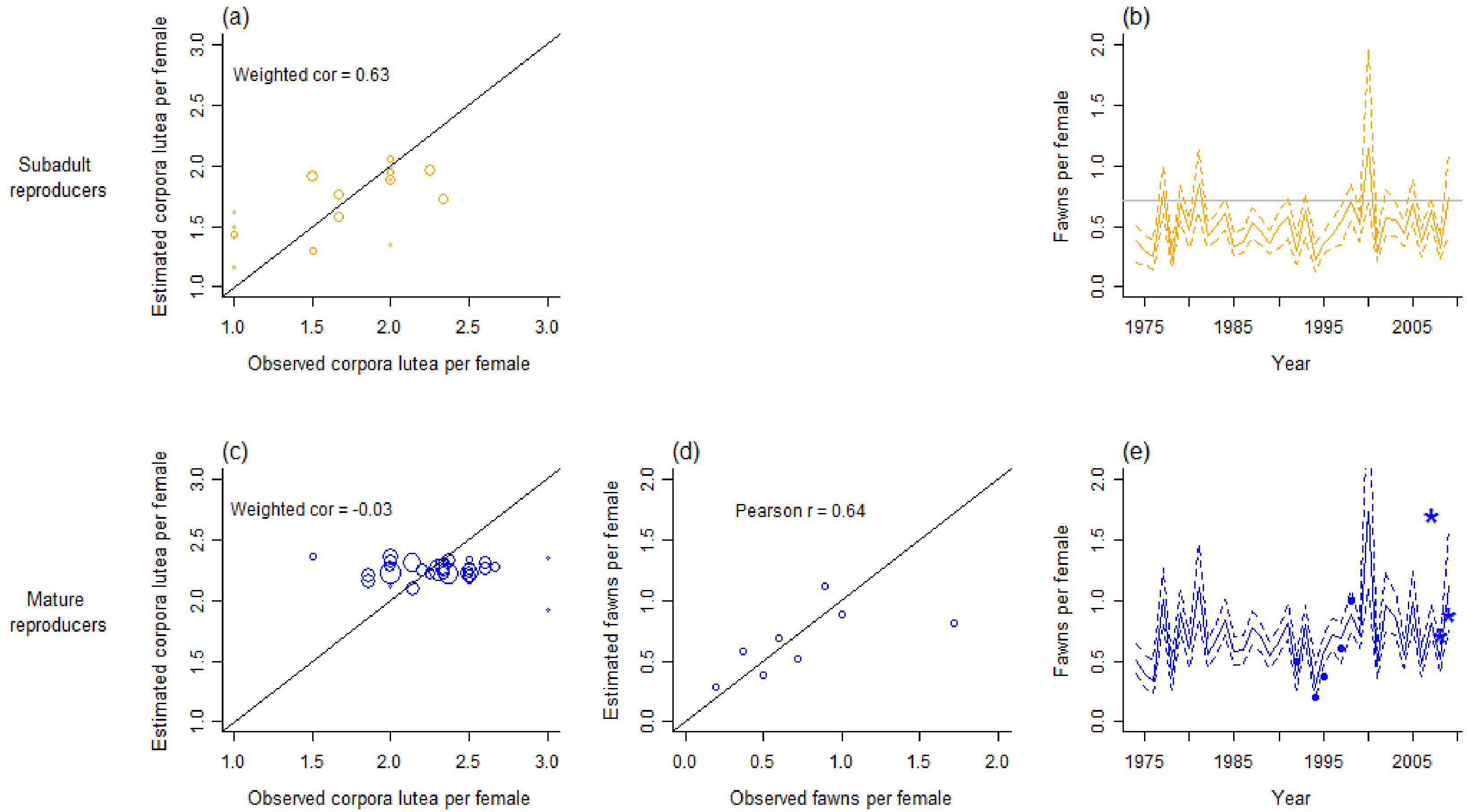

Figure 4.8: Simulated reproductive success of subadult (top row) and mature reproducers (bottom row) in Grimsö against observed ovulation and fawns per female in autumn. Panels (a) and (c) show correlations between estimated and observed ovulation from the AIC best model, including sample-size weighted correlation coefficients (point size proportional to sample size). Panel (d) shows the correlation between simulated and observed fawns per female for mature females (including Pearson’s correlation). Lack of years with > 5 subadult reproducers observed for fawns precluded examination of model fit for this group. Panels (b) and (e) show simulated reproductive success (solid line) across years (with 95% CI, dashed lines). In (b), the grey line is the mean fawns per subadult reproducer observed across years. In panel (e), points are observed values used to fit models and asterisks are years not used to fit the fawn survival model (see text).

per female for mature females (Fig. 4.8d), despite incorporating the estimates of ovulation, which explained little variation within the age group. Ultimately, the simulations succeeded in capturing the direction of inter-annual changes in the number of fawns per female reasonably well, but failed to replicate the magnitude of those changes (Fig. 4.8e). There were insufficient data on subadult reproducers to examine the performance of the fawn survival model in this way. The observed mean number of fawns per subadult reproducer suggests that the simulations generally underestimate the reproductive success of this group (Fig. 4.8b).

Discussion

Modelling vital rates, such as reproductive success, in response to a changing climate requires a detailed understanding of component processes and how they are driven by both climatic and non-climatic environmental conditions. The reproduction of roe deer, like that of other ungulates, may be impacted by climate at several stages because it is controlled by a sequence of many non-independent processes (e.g. ovulation, fertilization, implantation, birth, and offspring survival). The simulations presented here provide a first mechanistic integration of ovulation and early fawn survival in roe deer. Achieving a mechanistic understanding of such a complex pathway requires large amounts of data and presents a substantial challenge, even with modern statistical tools. Given this complexity, the models of ovulation and fawn survival presented here are relatively simple (containing ≤ 2 temporal predictors), but still highlight relationships with environmental conditions that are consistent with the existing literature on roe deer reproduction.

The models support the *a priori* hypothesis that climatic factors would influence roe deer reproduction more in Grimsö than at Bogesund. In Bogesund, where deer densities are high and the climate is relatively mild, deer density and fox predation (non-climatic factors) were identified as important predictors of ovulation and fawn survival, respectively. In Grimsö, where deer densities are low and the climate is harsher, the emphasis was on climatic factors; in particular, precipitation was identified as an important driver of both ovulation and fawn survival. These results are consistent with results from previous studies of roe deer at these and other sites in Europe (mainly in France and Scandinavia; Gaillard et al. 1992, Lindström et al. 1994, Gaillard et al.

1996, Gaillard et al. 1997, Linnell et al. 1998b, Focardi et al. 2002, Kjellander et al. 2004a, Kjellander et al. 2006, Pettorelli et al. 2006, Panzacchi et al. 2008).

While the models of ovulation and fawn survival appear biologically reasonable, the sparse nature of the data used to fit them limits the number of possible parameters, the predictive ability of the models, their robustness to decreases in the underlying data, and the precision with which reproductive success can be predicted. The parameters included in models indicate which predictors of reproduction are most important, without providing a complete explanation of variation in reproductive success. The data used in this study were not collected with these analyses in mind. They were often collected for shorter-term intensive studies of single aspects of roe deer ecology (e.g. density dependence; Kjellander 2000) or for more general management purposes. Consequently, sample sizes within years were often small, not all data were available in every year (limiting the temporal extent of models), and sufficient data on some key processes (e.g. pregnancy and birth rates) were not available. Despite some uncertainty in model selection, however, there is moderate to good support for the selected best AIC models (weights of these models ranged 0.56 to 0.86). Therefore, the analyses presented here demonstrate what can be learned through the cautious use of available data. Simultaneously, however, these analyses highlight a need for more extensive data in order to build models that can estimate the response of roe deer reproduction to climate change with the accuracy and precision necessary to inform management decisions.

Ovulation

The ovulation rates observed at both sites are consistent with those observed by other studies, with most mature females producing two or more corpora lutea and subadults showing lower and more variable ovulation (Appendix 1, Table A1.1; Gaillard et al. 1992, Andersen et al. 1998b). In Bogesund, the ovulation models including only roe deer density and age group outperformed models based on climatic conditions while, in Grimsö, winter climate conditions were consistently highlighted as important. This reflects differences in the ecology of the two sites and the overlap between the modelled period and an experiment on density dependence in Bogesund. The negative relationship between density and fecundity that was included in the best AIC model of ovulation in Bogesund is consistent with previous studies at this site and others which provide evidence of density dependence (via effects on food availability and body mass) in roe deer reproductive rates (Gaillard et al. 1992, Hewison 1996, Putnam et al. 1996, Andersen et al. 1998b, Kjellander 2000). This association appears to have been driven primarily by two years in which the deer density at this site was manipulated to test for density dependence in roe deer dynamics (Kjellander 2000). Density was allowed to increase to more than twice that of other years and then was drastically reduced through an organised cull. More than half the ovulation data came from this experimental period. As a result, the power to detect an association with density in Bogesund was greater than for other temporal variables.

None of the selected models of ovulation in Grimsö included density as a predictor but all of them included a negative relationship between winter precipitation and mean fecundity (especially that of subadult reproducers). This is consistent with the assertion of Mysterud and Ostbye (2006) that the combination of low roe deer densities and harsh winter conditions found in inland Scandinavia mean that winter rather than density dependence limits roe deer population growth. The negative association of ovulation with winter precipitation and the relatively weak positive association of subadult ovulation with winter temperatures included in the best model could indicate effects of snow on roe deer ovulation rates via food availability and body mass (deep snow has been associated with starvation due to reduced mobility and access to ground vegetation; Cederlund 1982, Fruzinski and Labudzki 1982, Mysterud et al. 1997, Mysterud and Ostbye 2006). Support for a negative effect of harsh winters is consistent with Hewison’s (1993) study that found correlations between winter conditions and various reproductive rates (pertaining to ovulation and pregnancy) among populations (distributed throughout Britain) as well as across years within particular populations. The association between winter precipitation and ovulation in Grimsö also helps explain the results of past studies of fawns per female in this site. Lindström et al. (1994) found a negative relationship between fawns per female (observed in Autumn) and the snow depth from the winter a year and a half earlier; while Lindström et al. (1994) did not analyse ovulation data directly, they speculated that this relationship was due to a delay in the reproduction of subadults that experienced a harsh first winter as fawns. Subsequently, Kjellander et al. (2003) found that fawns per female was unrelated to winter conditions when ovulation was accounted for in models.

It is well recognised that population age-structure can play an important role in ungulate population dynamics (Gaillard et al. 1998a, Gaillard et al. 2000b, Clutton-Brock and Coulson 2002, Festa-Bianchet et al. 2003, Gordon et al. 2004, Ezard et al. 2010) and the ovulation models presented here reflect this. Age group was included in all selected models at both sites. In fact, in Bogesund, the model including only age group (and no temporal variables) was part of the top model set, implying limited explanatory power of temporal predictors (even density) at this site. In both Grimsö and Bogesund, models explained much more of the variation in subadult ovulation rates than in the ovulation rates of mature reproducers, reflecting the greater variability of subadult ovulation (Hewison 1996, Andersen et al. 1998b) and its greater vulnerability to environmental conditions (Putnam et al. 1996, Gaillard et al. 2000b).

Fawn survival

In both Bogesund and Grimsö, rates of early fawn survival were low, and highly variable among years as has been observed in other studies (Appendix 1, Table A1.1; Gaillard et al. 1997, Gaillard et al. 1998b). My analyses highlight ecologically reasonable drivers of fawn survival. The number of foxes killed each year (an index of fox abundance in the area), was identified as the best predictor of fawn survival in Bogesund. This is expected, given that fox predation has previously been identified as an important source of fawn mortality (Aanes et al. 1998) and other studies have found associations between fox indices and the number of fawns per female at Bogesund (Kjellander 2000, Kjellander et al. 2004a). In Grimsö, the available index of fox abundance, the number of fox litters in the area, was not negatively associated with fawn survival. This is consistent with the growing consensus (Jarnemo and Liberg 2005, Panzacchi et al. 2008, Nordström et al. 2009) that fox predation is more likely to be an important driver of fawn survival in agricultural sites which support high population densities of both foxes and roe deer (such as Bogesund). However, owing to differences in the periods of data availability at the two sites (in particular, the overlap with the period when fox populations were recovering from an outbreak of sarcoptic mange), it is impossible to rule this out as the ultimate explanation for differences between models of fawn survival at the two sites.

In Grimsö, early fawn survival was best explained by a positive relationship with precipitation during the months surrounding fawn births (May, June and July).

This is consistent with rain during this period promoting vegetation growth and, thereby, positively affecting fawn body mass and survival (Gaillard et al. 1996, Gaillard et al. 1997, Linnell et al. 1998b). That the second best model included a negative relationship between fawn survival and INDVI from May, June and July is puzzling and somewhat undermines confidence in the model. However, it is established that bodies of water can lower INDVI values (Pettorelli et al. 2005c) and this provides a possible explanation for the negative association between spring INDVI and spring precipitation (see Appendix 4, Table A4.3), and consequently between spring INDVI and fawn survival. Precipitation often creates temporary, but large, vernal ponds in Grimsö (pers. comm., Kjellander 2013); this could result in lower INDVI measures for the area, which do not reflect current vegetation production. However, caution should be used with such *post hoc* interpretations, particularly given the very sparse dataset.

Simulating reproductive success

The simulations of reproduction presented in this chapter mechanistically incorporate the processes of both ovulation and early fawn survival into estimates of reproductive success. While several studies have examined roe deer fecundity and fawn survival individually, to my knowledge this is the first integrated quantitative approach. Even single components of reproductive success can account for the majority of variation in population growth rates (e.g. fawn survival can account for as much as 75% of the variation; Gaillard 1998). These individual components feed into each other to determine overall reproductive success, and their combined influence on population growth rates are likely to be large. For this reason, combining the processes involved in reproductive success is vital: these simulations make progress toward this goal. The ability of the simulations to reproduce observed patterns of reproductive success in both sites was modest (Pearson’s correlations between observed and estimated reproductive success ranged 0.48 – 0.64 across sites and age groups), which is, perhaps, unsurprising given the complexity of the processes involved and the limited data.

In both sites, there was much unexplained variation in, and a tendency to underestimate, reproductive success. The majority of the uncertainty in the simulations is associated with the fawn survival models (the fawn survival model accounted for 76% of the total variation in reproductive success in Bogesund and 64% in Grimsö). This could result from limitations on the available data and consequent limitations on the fitted models. In addition, the fawn survival models are reliant on age-group specific implantation rates which were assumed to be constant over time and were derived, in part, using published data from roe deer populations in other areas (Hewison 1996). The resulting estimates of implantation rates at both Bogesund and Grimsö (90-100%), are close to those observed at other Scandinavian sites (Borg 1970 and Strandgaard 1972 report implantation rates of 91% and 96% respectively). More site-specific data on pregnancy rates (which would account for the failure of embryos to implant) and birth rates (which would account for abortions) might improve model predictive ability. Also, covariance among the individual processes (i.e. years resulting in low ovulation rates could also result in low implantation rates) would result in larger variability in reproductive success than estimated by the models. This extra variation could explain the disparity between simulated and observed reproductive success and, in particular, the underestimation of variance in reproductive success at Grimsö.

Climate implications and considerations for future research

The models presented here add to the understanding of the climatic and non-climatic factors driving roe deer reproductive success, but that understanding remains far from complete. Part of the goal of these analyses was to understand how climate change might impact roe deer reproduction and, thus, population growth. It is possible to draw some cautious conclusions regarding the effects of climate change but those must be considered in light of a few recommendations which may improve future studies. These are discussed below.

This study suggests three general lessons regarding the data requirements of studies that explore environmentally driven variation in wildlife populations. Firstly, long-term data are critical to longitudinal analyses such as these. The models presented here are sensitive to reductions in the number of years used in model-fitting. It is difficult to obtain sufficient funding for consistent long-term data collection; however, studies which are relatively short in duration (only a few years) and focus on only one or two aspects of a species’ ecology are unlikely to provide the data necessary to thoroughly investigate drivers of temporal variation in the vital rates of long-lived species (such as ungulates). Secondly, if only one variable of interest is manipulated or varies dramatically (as in a natural “experiment”) during the study period, then the analyses may be pre-disposed toward detecting relationships with this variable and the influence of other important factors may be overlooked. Effort should be made to achieve a reasonably “balanced design”, either through manipulating several potential drivers or, in the case of observational studies, by continuing the study for long enough that sufficient variation in other factors of interest is encompassed. Finally, data on additional processes are necessary to completely understand the mechanisms that ultimately determine reproductive success in roe deer. For example, reduced implantation rates have been linked to harsh winters in Britain (Hewison and Gaillard 2001), but a lack of data from Bogesund and Grimsö prevents explicit incorporation of this process in the models presented here. Whether incorporating further stages of the reproductive process will affect the results of mechanistic simulations remains a question for further research.

Climate change could impact roe deer reproduction directly, as shown in the results of this chapter, or indirectly by influencing other vital rates. Density was negatively related to ovulation at Bogesund, so while no direct effect of climate was identified, any climate-driven variation in other vital rates which affect density may influence reproductive rates. For example, survival in Bogesund was positively related to INDVI (see Ch. 3), which is influenced by climate (see Ch. 2). In Grimsö, climate change could impact roe deer reproduction more directly because projections of increasing precipitation in Sweden (Christensen et al. 2007) could translate into decreased ovulation rates and increased fawn survival. However, projecting the impact of winter precipitation is particularly complex due to the effect of temperature changes on the nature of precipitation (whether snow or rainfall). Also, the net impact of precipitation changes on reproductive success will depend on the relative changes in both ovulation and early fawn survival rates, which could respond to precipitation in opposite directions. Such interplay among vital rates complicates projections and demonstrates that an integrated approach, incorporating multiple population processes, is instrumental to understanding how climate change will influence wildlife population dynamics.

Conclusion

The simulations of roe deer reproductive success that are presented here demonstrate how an important demographic process (reproduction) that is a combination of separate vital rates (including ovulation and early fawn survival) can be modelled mechanistically as a response to a range of environmental drivers including climate. The predictors of roe deer ovulation and fawn survival identified in these analyses indicate relationships with biologically realistic drivers that are consistent with prior research on roe deer, but differ greatly between the two study sites. This site-specificity is reflective of the ecological conditions at each site. Relationships between ovulation and winter climate and between fawn survival and spring precipitation emphasize the importance of climate conditions at the more northern site, Grimsö. By contrast, in Bogesund, where the climate is milder, there is more support for non-climatic drivers including density as a predictor of ovulation and predator abundance as a predictor of fawn survival. When models of ovulation and fawn survival were combined, the resulting simulations demonstrated a modest ability to estimate observed inter-annual variation in roe deer reproduction. An analysis of the uncertainty surrounding the simulations of reproductive success indicates a need to prioritise research on early fawn survival and its drivers. These results demonstrate the considerable data requirements associated with modelling complex demographic processes like reproduction, while also providing insight into the climatic and non-climatic factors influencing roe deer ovulation and early fawn survival.

Chapter 5 – The response of roe deer populations to climate change: the use of mechanistic simulations with trophic interactions

Abstract

Climate change impact research has focused on projecting future changes in geographic ranges. Such analyses often overlook the population dynamics and trophic interactions generating these distributions. Here I investigate the effects of climate and trophic interactions on two populations of roe deer in Sweden, at Bogesund and Grimsö. I use age-structured matrix models to simulate roe deer population dynamics for the study sites. Site-specific models of vegetation production and deer vital rates incorporate the effects of climate, vegetation, predation and harvest conditions. The correlation between the simulated and observed population densities was high in Bogesund (Pearson's r = 0.86), but negative in Grimsö (Pearson's r = -0.72). Population dynamics of roe deer in Bogesund, under three greenhouse gas emission scenarios indicated high population growth rates (averaging 2-3% per year), driven by increased vegetation productivity and roe deer survival. However, large confidence intervals indicated a need for cautious interpretation. An investigation of harvest, predation and deer population growth in Bogesund under current climate conditions suggested that increased predation would allow for little harvest by humans without causing the population to decline. In the future, by contrast, climate change and associated increases in roe deer survival could necessitate unrealistically high annual harvests (amounting to ~20-50% of the population to prevent population growth), unless there is a commensurate increase in predation. This study is one of the first to explore the potential effects of climate change on roe deer population dynamics and demonstrates the management value of mechanistic population models that incorporate the effects of both climate and trophic interactions.

Introduction

The potential impacts of expected climate change on biodiversity are vast: one estimate suggests that more than one third of the world's species might be at risk of extinction due to climate change within the 21st Century (Thomas et al. 2004). However, many such studies of the impacts of climate change have been criticised for projecting species' geographic ranges into the future without accounting for the interactions among species and the population dynamics which drive changes in abundance within a geographic range (Parmesan 2006, Barnard and Thuiller 2008, Van der Putten et al. 2010, Walther 2010, Pagel and Schurr 2012). Ideally, models of temporal population dynamics should be explicitly incorporated into large-scale geographic models for many species (Huntley et al. 2010). These models could include mechanistic relationships between a species' vital rates and their drivers, thus accounting for interactions across trophic levels. By simulating expected changes in population growth across space and time, and by providing estimates of associated uncertainty, these "integrated dynamic species distribution models" could provide invaluable information to wildlife managers around the globe.

While the data necessary to build integrated models are unlikely to be available for many species (Bellard et al. 2012), a growing number of such models are being published (e.g. Keith et al. 2008, Anderson et al. 2009, for additional exceptions see Ch. 1). These ground-breaking models highlight the importance of integrating population dynamics into species distribution models. However, they are still relatively simple: they do not explicitly incorporate trophic interactions (i.e. changes in food availability or predation) and they assume that the factors affecting vital rates over time are similar among sites and, sometimes, among related species. Similarly, a number of studies have examined the impacts of climate change on species interactions including those across trophic levels, but many of these studies concentrate on invertebrates, with few on mammals and even fewer which investigate the implications for a species' population dynamics (for reviews and exceptions see Parmesan 2006, Traill et al. 2010). Studies of mammalian systems have suggested that climate change is causing mismatches in phenology (Post and Stenseth 1999, Inouye et al. 2000, Gaillard et al. 2013), limiting herbivore food availability (Pettorelli et al. 2005d) and influencing predation (Post et al. 1999). The potential combined influence of these changes on the population growth of a species is very difficult to determine. Studies, many on hypothetical model systems, suggest that while climate change may cause increased fluctuations in the population growth of many species, predation has a stabilising effect on that growth, and therefore, predators could play an important role in mitigating the ecological effects of climate change (Gilg et al. 2003, Wilmers and Getz 2005, Wilmers et al. 2006, Wilmers et al. 2007a, Wilmers et al. 2007b). Integrating the effects of predators into models of population dynamics could facilitate better management of herbivore populations in the face of climate change. Given the on-going recovery of large predator populations in many parts of Eurasia and North America (Linnell et al. 2000, Mech and Boitani 2003, Beschta and Ripple 2009), this possibility warrants further consideration.

In many ways, large herbivore populations provide ideal systems for examining the indirect impacts of climate and trophic interactions on population dynamics. Many ungulate species are considered economically valuable due to their status as game species and, therefore, their populations are relatively well-monitored. Temporal variation in ungulate population growth is often strongly influenced by trophic interactions, through vegetation production (food availability) and predation or harvest-related mortality (Gaillard et al. 2000b). Research on large herbivores has documented relationships between climate and ungulate food resources (Post and Stenseth 1999, Post and Forchhammer 2008) and between climate and predation (Post et al. 1999, Hebblewhite 2005). However, these relationships are complex and there is evidence that the knock-on effects of climate change for ungulate population growth will not be consistent across wide geographic areas. Many studies have found that the importance of climate and vegetation-related drivers, and the strength of their relationships with ungulate vital rates, varies among and within species (Loe et al. 2005, Månsson and Lundberg 2006, Weladji and Holand 2006, Martinez-Jauregui et al. 2009). Furthermore, predation patterns also vary among sites and are influenced by a range of factors including (but not limited to) climate, habitat productivity, prey community composition and prey density (Sinclair and Krebs 2002; see Ch. 6 for an investigation into one area of uncertainty surrounding predation patterns). This suggests that models of ungulate population dynamics in response to climate change may need to be developed on a site-by-site basis. Constructing such models is likely to be a challenge but is an important step towards enabling the future management of herbivore populations.

While many studies have investigated the effects of climatic drivers on the vital rates of ungulates, many have concentrated on only a small number predictors and have not simultaneously considered the impacts of climate alongside those of lower (e.g. vegetation production) and upper (e.g. predation) trophic levels (see Ch. 3 and 4 for a review). In fact, many studies of ungulates come from sites without natural predators (Gaillard et al. 2000b, Nilsen et al. 2009a) and, therefore, are of limited applicability at a time when predators are making a recovery and have been highlighted as having potentially stabilising effects on prey populations. Additionally, few studies have integrated models of vital rates into mechanistic population models and simulated the potential response of an ungulate population to climate change (see Wang et al.'s, 2002, study of elk, *Cervus elaphus*, in Colorado for a notable exception).

Here I use matrix population models to simulate the population dynamics of roe deer (*Capreolus capreolus*) at two sites in Sweden, and to project roe deer population growth under scenarios of climate change. Previous studies have related roe deer population dynamics to a variety of factors (Gaillard et al. 1998b) and have identified interactions between the driving effects of climate, vegetation productivity and predation pressure across wide geographic areas (Melis et al. 2009, Melis et al. 2010). Generally, roe deer abundance is expected to increase with rises in mean temperatures throughout Europe, as longer growing seasons drive increases in vegetation production (Melis et al. 2009), but negative effects of climate change have also been documented (Gaillard et al. 2013).

The roe deer populations at the study sites, Bogesund and Grimsö, have been monitored for more than twenty years, to inform population management through annual harvests. Previous analyses presented in this thesis have developed models of vegetation productivity, roe deer survival and reproduction at each of these sites (see Ch. 2, 3, and 4 respectively). These models have incorporated not only direct climatic drivers, but also indirect relationships with climate through vegetation, and the impacts of predation and deer harvest. Integrating these separate models into age-structured population simulations will allow estimates of population growth that not only account for changing climatic conditions, but also the impacts of lower and upper trophic levels on roe deer vital rates. If simulated changes in population density reflect the observed changes in densities at the study sites well, these models may provide valuable insight into the manner in which climate change, predation, and harvest may interact to alter roe deer populations in the future. If, conversely, trends in roe deer abundance are poorly represented, this may reflect data limitations in model parameterisations, even with a species as widespread and relatively well-studied as the roe deer. The main goals of these analyses are to answer the following questions:

1) Is the understanding of roe deer ecology which has been gained from the long-term monitoring programs in Bogesund and Grimsö, sufficient to simulate inter-annual changes in roe deer population density, as a response to the observed climate, harvest and predation conditions at each study site?
2) How much uncertainty surrounds the densities estimated from these models, how much of this is due to each of the component processes (and associated models) and where should future research efforts be focused in order to increase the precision of those estimates?
3) Given expected climate change for the 21st Century what, if anything, can be concluded about the future trajectory of roe deer abundance at Bogesund and Grimsö?
4) What levels of harvest might be necessary to maintain relatively stable roe deer populations at the study sites in the future?

Methods

Study sites

The two study sites have contrasting winter severity, landscape, management regimes and predation pressure. Bogesund has a relatively mild climate and higher vegetation productivity (see Ch. 1 for details on site location, land cover, and climate). The deer population has been heavily managed through annual autumn harvests (see Ch. 3 and Fig. 3.2 for more detail on site management). The only natural predators of roe deer in Bogesund are red foxes (*Vulpes vulpes*). Grimsö experiences much harsher winter conditions and contains less productive habitat (see Ch. 1). The Grimsö roe deer population has been managed loosely with the goal of maintaining a stable population size and annual harvests have been relatively small (see Fig. 3.2). There are currently three natural predators of roe deer in Grimsö: the lynx (*Lynx lynx*), the red fox, and the wolf (*Canis lupus*).

Component models

Models of INDVI (an index of vegetation production; Ch. 2), deer survival (including all deer > 3 months old; Ch. 3), ovulation (Ch. 4), and early fawn survival (including fawns ≤ 3 months old; Ch. 4) were used to estimate the annual survival and reproduction of deer in Bogesund and Grimsö, resulting in four "component models" for each site (Table 5.1).

Vegetation production was modelled using the monthly sums of bimonthly NDVI (normalized difference vegetation index) measures, which were then summed within years to yield annual integrated NDVI (INDVI), an index of net primary productivity (NPP). In both sites, the best models of INDVI indicated positive relationships between NPP and temperature-related predictors (either temperature or growing degree days) and negative relationships with measures of dryness from the current and previous months (see Table 5.1 and Ch. 2 for more detail).

In the survival models (see binomial and beta-binomial models in Ch. 3), deer were classed by sex and were separated into three age groups: fawns (> 3 months and < 1 year old), subadults and adults (1 to 7 years old), and senescents (> 7 years old). The selected model of survival in Bogesund included a negative relationship between survival and per capita harvest (Harvest_t) and a positive relationship between survival and the previous year's INDVI ($\text{INDVI}_{t\text{-}1}$). The best model of survival in Grimsö included a positive relationship between survival and the current year's INDVI (INDVI_t) and a negative relationship with lynx presence at the site (LynxPres_t). Details on the specifications and performance of the survival models can be found in Ch. 3 (also in Table 5.1 below).

Reproductive output was estimated using models of ovulation and early fawn survival (from birth through 3 months of age) detailed in Ch. 4. Roe deer ovulation takes place during late summer of the year preceding fawn births. Ovulation was measured as the number of corpora lutea observed in the ovaries of examined females.

Table 5.1: Site-specific models of INDVI, deer survival, ovulation and early fawn survival used in simulations of roe deer population densities in Bogesund and Grimsö.

Study site and model [a]	Model type	Selected model predictors [c]	Weight, ω_i, within model set [d]	Correlation between estimates and observations [e]
Bogesund				
INDVI [b]	Auto-regressive GLS	Tmp$_m$, Dry$_m$, Tmp$_{m-1}$, Tmp$_{m-2}$, Gdd$_{m-2}$, Month	0.36	0.55
Survival	Beta-binomial	Age [d], Sex, Harvest$_t$, INDVI$_{t-1}$	0.88	0.69
Ovulation	Multinomial	Age [c], Den$_t$	0.76	0.88
Early fawn survival	Lognormal	FoxHar$_t$	0.76	0.43
Grimsö				
INDVI	Auto-regressive GLS	Tmp$_m$, Dry$_m$, Tmp$_{m-1}$ * Dry$_{m-1}$, Month	0.93	0.60
Survival	Binomial	Age, Sex, LynxPres$_t$, INDVI$_t$	0.34	0.69
Ovulation	Multinomial	Age, WinPre$_{t-1}$, WinTmp$_{t-1}$	0.56	0.64
Early fawn survival	Lognormal	BirthPre$_t$	0.86	0.94

[a] For details of modelling methods, see relevant chapters for models associated with INDVI (Ch. 2), survival (Ch. 3), and ovulation (Ch. 4) and early fawn survival (Ch. 4).

[b] Logit-transformed integrated NDVI (an index of vegetation production) was modelled on a monthly scale (see Ch. 2). Monthly integrated NDVI (INDVI$_m$) was then summed across months to yield estimates of annual integrated NDVI (INDVI; which were then used as predictors in survival models).

[c] Predictors include: age-group (Age), Sex, Month, annual integrated NDVI (INDVI), temperature (Tmp), dryness (Dry), growing degree days (Gdd), winter precipitation (WinPre), winter temperature (WinTmp), precipitation from the months surrounding fawn births (BirthPre), per capita harvest rate (Harvest), fox harvest (FoxHar), roe deer density (Den), and lynx presence (LynxPres). Subscripts indicate annual time period (t) or month (m). The age groups used as predictors differed between the models of survival and ovulation (see text for detail).

[d] Model weights are indicative of the relative support for a model within its model set. Weights were calculated within site-specific model sets (including all models with Δ AIC ≤ 6) for each analysis; see relevant chapters for more detail.

[e] The correlation between model estimates and observed data was used as a indicator of model performance in each analysis. For the INDVI, survival and early fawn survival models Pearson's correlation coefficient (r) was used to measure the correlation between model estimates and observed values. In the case of the ovulation models a weighted correlation coefficient was used (see Ch. 4 for detail).

In ovulation models, reproducing females were divided into two age groups: subadult reproducers (1 year old at ovulation, 2 years old when giving birth) and mature reproducers (> 1 year old at ovulation, > 2 years old when giving birth). The best model of ovulation in Bogesund included a negative relationship between ovulation and the density observed the previous spring (Den_t; Table 5.1). The best model of ovulation in Grimsö included a negative effect of the previous winter's precipitation and a positive effect of the previous winter's temperatures (WinPre_{t-1} and WinTmp_{t-1}; Table 5.1). The output from the ovulation models (mean corpora lutea per female) was multiplied by implantation rates and used to estimate the pregnancy rate (and maximum possible birth rate) for the following year. The fawn survival models incorporated the estimated pregnancy rates and estimated the number of fawns per female surviving from birth (in June) until autumn. In Bogesund, variation in fawn survival was best explained by a negative relationship with the annually recorded regional fox harvest (FoxHar_t; an index of fox abundance; Table 5.1). In Grimsö, fawn survival was best estimated by a positive relationship with the precipitation from the months surrounding fawn births: May, June and July (BirthPre_t; Table 5.1).

Density simulations

The density of roe deer has been estimated each April since 1989 in Bogesund and 1977 in Grimsö. In Bogesund, Lincoln-Peterson estimates of density (Caughley 1977) were calculated based on the ratio of marked to unmarked deer observed within the study area (See Ch. 3 and Kjellander et al. 2006 for more detail). In Grimsö, density was estimated using pellet counts; the format of the grid used to sample pellet densities changed in 1997 (methods described in Ch. 3). Due to data availability, roe deer population dynamics were simulated from 1991 to 2007 in Bogesund and from 1982 to 2006 in Grimsö. The change in roe deer density from one year to the next was simulated using a series of age-structured transition matrices which incorporated the estimates of INDVI and vital rates calculated using the component models of INDVI, survival (which used INDVI as a predictor), ovulation, and fawn survival. The predictors included in these models meant that observed climate conditions (necessary to estimate INDVI for both sites and ovulation and fawn survival in Grimsö), per capita harvest rates (Bogesund only) and observed levels of predation pressure (red fox harvest in Bogesund and lynx presence in Grimsö) were used as the driving "environmental" conditions in simulations. In addition, at Bogesund, the preceding year's estimated roe deer density was included as a predictor (see density variable in Bogesund's ovulation model, Table 5.1).

In Grimsö, the observed density from 1981 was used as the starting density for the simulation. In Bogesund, two years of density observations were necessary to start simulations: one to estimate initial ovulation (1989; n.b. ovulation takes place the year prior to fawn births) and one as the starting density (1990; see Fig. 5.2 and Fig. 5.3 in Results for starting densities in each site). Only the female portion of the population was modelled. Following Nilsen et al. (2009a), I assumed an equal sex ratio. I considered nine age classes: fawns (< 1 year old), subadults (1 year old), six annual adult classes (individuals 2-7 years old), and a senescent age class (deer > 7 years old). Data on the initial age distribution of the roe deer populations were not available. To estimate an age distribution to initialize the simulations in each site, I ran the simulation (described below) for 500 years, having fixed the environmental conditions to those recorded in the years just prior to the starting period in each site (see Appendix 5, Table A5.1). Changes in the initial age distribution had very little effect on the resulting simulations.

To begin each multi-year simulation the initial density estimate for the relevant study site was multiplied by the starting age distribution and by 0.5 to represent the female portion of the population. After that the resulting female density and associated age structure from the previous year's simulation was used to begin the next year's simulation. Each simulated year extended from one April to the next and was divided into sub-annual periods based on the timing of density estimates, the roe deer reproductive cycle, the component models (e.g. survival rates were estimated one February to the next), and the harvest season (see Fig. 5.1 for an illustration of this annual cycle). Six corresponding transition matrices incorporated the relevant age-group specific vital rates and were used to progress the population through the simulated year (Appendix 5, Fig. A5.1). Natural, non-harvest related mortality was distributed according to the observed mean proportion of the total natural mortality occurring during each sub-annual period (calculated given all mortality data available for each site; see Appendix, Table A5.2). Mortality due to harvest (estimated in Bogesund only) was incorporated during the autumn harvest season. Roe deer births took place in June, but new fawns were not added to the population until September. This allowed the estimates of ovulation and early fawn survival to be incorporated in one step; it also ensured that when a female died over the summer, her fawns were assumed to have died as well. At the end of each simulated year the total population density (female density multiplied by 2) was recorded.

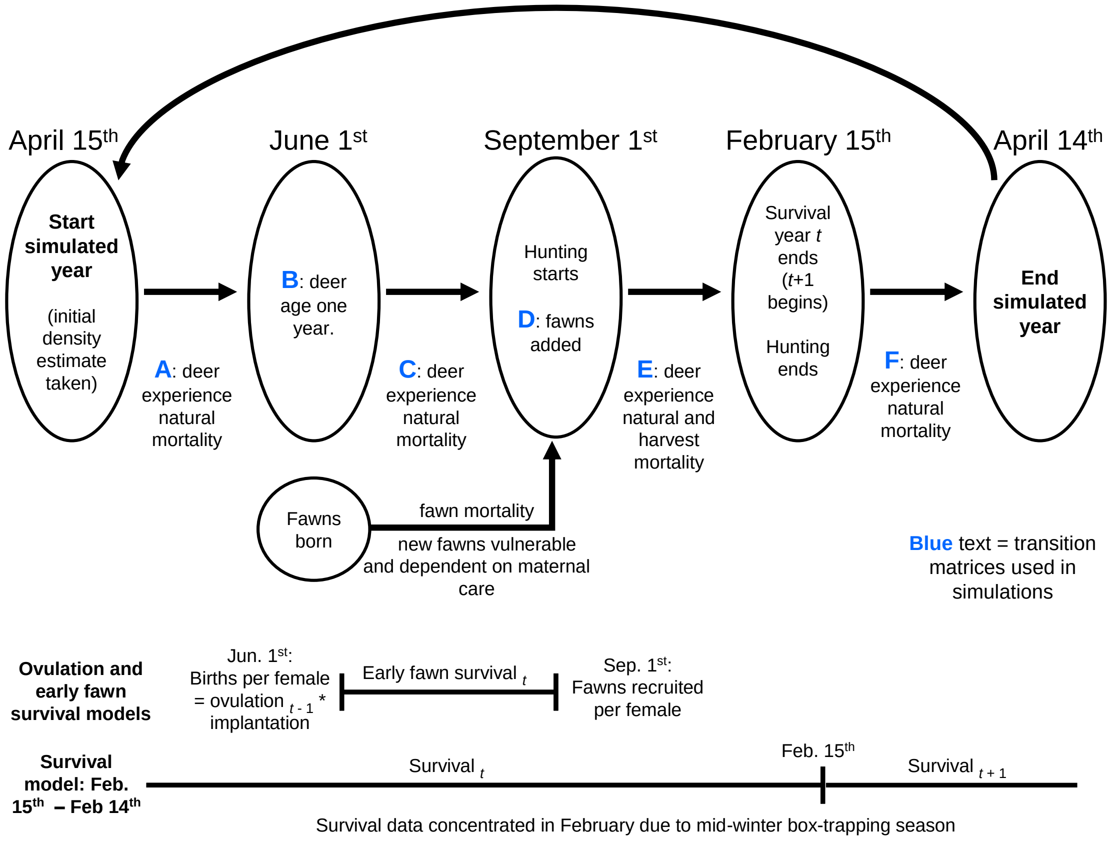

Figure 5.1: The annual cycle used in simulations of roe deer population dynamics was divided into sub-annual periods associated with six age-structured transition matrices, which described survival and reproduction from one period to the next (matrices are indicated by the blue text; matrix structures are illustrated in Appendix 5, Fig. A5.1). Because survival was estimated from one February to the next, two different survival estimates were associated with the simulated April to April year (Survival$_t$ and Survival$_{t+1}$; see survival model timeline at bottom of figure). See Table 5.1 for description of vital rate models and predictors.

Projections of roe deer density given climate change

Due to poor performance of the simulations for the observed period in Grimsö (simulated densities did not reflect observed densities; see Results), I focused only on Bogesund for future projections. I used climate projections to simulate roe deer population dynamics and project roe deer density for three climate change scenarios for the 2007-2101 period. Projected climate conditions using the HADCM3 climate model (http://www.alarmproject.net/alarm/; Mitchell et al. 2004, Spangenberg 2007) were available on a monthly time-scale for three greenhouse gas emission scenarios (A1FI, A2, and B1; Nakicenovic et al. 2000 table SPM-3a) (see further in Chapter 2).

Using the projected climate conditions for Bogesund, I created projections of INDVI for each of the three scenarios (see Ch. 2 and Fig 2.8 for methods and resulting projections of INDVI). Projected INDVI values were then used to project roe deer survival rates given climate change. I assumed a constant per capita harvest of 5.7% (mean harvest from 1989-2006, excluding 1992 and 1993 when there was an experimental cull). Observed roe deer density from 2006 (7.94 deer per km^2) was used as the starting density for the projection; the density from 2005 (11.42 deer per km^2) was used to estimate initial ovulation rates (following which simulated density values were used). I estimated fawn survival during this period by assuming that the future fox harvests (an index of fox abundance) would follow a log-normal distribution with the same mean and standard deviations as observed in the 1994-2006 period (0.43 ± 0.097 [SD] fox killed per km^2; years prior to 1994 were excluded due to an outbreak of sarcoptic mange). To calculate a starting age distribution, I ran the simulation for 500 years using the mean observed environmental conditions from 1989 through 2006 (Bogesund only; see Appendix, Table A5.1). This was the observed period that was originally simulated at this site and was also the period for which data on all the environmental drivers were available.

Uncertainty analysis

I incorporated uncertainty from each of the component models into the density simulations, described above, by randomly sampling the posterior distributions of the model parameters (Gelman and Hill 2006). To quantify the relative contributions of these uncertainties to the final uncertainty in estimates of roe deer density, I ran the simulations under five different uncertainty “scenarios”. Each scenario involved a different combination of the sources of uncertainty. There was one scenario in which parameters from all models were sampled and four scenarios (corresponding to the models of INDVI, survival, ovulation and fawn survival) in which the parameters from one of the models were fixed at their maximum likelihood estimates. I calculated the variance of the logged density estimates for each year across the 1000 iterations and summed these variances across all years as a measure of the total uncertainty in the simulated densities. I also calculated the 95% quantiles surrounding density estimates for a given year in each scenario to determine the 95% confidence intervals. Comparing the range of these 95% confidence intervals and the summed variance from the scenario including all the sources of uncertainty to the outcome from scenarios in which a given source of uncertainty was omitted, provides an indication of each model's contribution to overall uncertainty in density estimates. The median was extracted as the estimate of density for a given year.

When using the simulations to project roe deer population dynamics given climate change in Bogesund, all sources of uncertainty were included. As with the simulations of roe deer density for the observed period, the median and 95% confidence intervals of the density estimates for a given year (across 1000 iterations) were used as indicators of the projected density and of the uncertainty surrounding that projection.

Assessing management actions

To explore the roles of predation and human harvest in limiting the population growth rate of roe deer, I identified combinations of harvest and predator pressure that would maintain a constant population size (i.e. produce zero population growth) under different climate conditions. Lynx are not currently resident in Bogesund and it is unlikely that lynx will have a major impact there in the near future as the area is isolated by the Baltic Sea to the East, the city of Stockholm to the South and West, and a fenced highway in the North. Additionally, the Bogesund peninsula is small relative to lynx home range sizes (Linnell et al. 2001). Nevertheless, lynx are spreading southward throughout Sweden and the arrival of lynx is likely to impact the survival, growth rates, and management (through harvest) of many roe deer populations. I explored the impact of varying fox abundance and including hypothetical lynx predation pressure on roe deer at Bogesund. I used the estimated effect of lynx presence on roe deer survival rates in Grimsö ($\beta_{LynxPres}$ = -0.576, 95% confidence interval = -0.851 to -0.301), as a guide to their likely impacts.

Transition matrices were constructed as before (including 9 age classes) but with three alterations: the year was not separated into sub-annual periods (one matrix summarised the total reproduction and survival for a year given specified conditions), the year was designated from February to February (to avoid the use of more than one year's survival rate; see Fig. 5.1), and in the survival model I incorporated an effect of lynx. I allowed the magnitude of the effect of lynx presence to range from 0 (indicative of no effect or lynx absence) to -0.851 (the lower confidence limit of $\beta_{LynxPres}$ from Grimsö, indicating a large negative effect of lynx presence) in increments of 0.005. Given mean observed INDVI and harvest conditions at Bogesund, this effect translates to a decrease in adult female survival from 0.85 when lynx are absent, to 0.72 when lynx are present with a strong negative effect on survival (see Table 5.2 for more detail).

Table 5.2: Expected survival of deer in Bogesund rates given different hypothetical effects of lynx presence[a].

Hypothetical effect of lynx[b]	Fawn survival	Subadult and adult survival	Senescent survival
None	0.83	0.85	0.66
Weak	0.78	0.81	0.59
Moderate	0.73	0.77	0.52
Strong	0.68	0.72	0.46

[a] Survival of deer in Bogesund was modelled using a beta-binomial model (see text and Ch. 3 for more detail). Survival rates shown were calculated given an INDVI of 10.00 (mean INDVI from 1982-2006) and per capita harvest of 0.057 (mean from 1989-2006 excluding 1992 and 1993; see text for more detail).

[b] Lynx were absent in Bogesund throughout the observed period. Hypothetical effects of lynx presence on survival were parameterised based on estimated negative effect of lynx presence in Grimsö. A weak lynx effect was equal to the upper confidence limit of the effect of lynx presence in the Grimsö survival model ($\beta_{LynxPres}$ = -0.301). A moderate lynx effect is equal to the point estimate of the effect of lynx presence in Grimsö ($\beta_{LynxPres}$ = -0.576). A strong lynx effect is equal to the lower confidence limit of the effect of lynx presence in Grimsö ($\beta_{LynxPres}$ = -0.851).

When estimating the ovulation rate of each maternal age group, I assumed a desired roe deer density of 12.5 deer per km^2 (pers. comm., Kjellander 2013). I considered two levels of fox abundance (low and high) to estimate fawn survival. Fawn survival given low fox predation was estimated assuming the observed mean fox harvest of 0.13 fox per km^2 from 1989 to 1993, during an outbreak of sarcoptic mange (see Table 5.3 for associated fawn survival and reproductive rates). Fawn survival given high fox abundance was estimated using a fox harvest level of 0.43 (mean observed from 1994 to 2006 after the mange outbreak; Table 5.3). When estimating "baseline survival rates", due to mortality unrelated to predation or harvest, I used mean levels of INDVI under seven sets of climate conditions (see Ch. 2, Table 2.4 for exact INDVI values). I used the observed mean INDVI from 1982 to 2006 to estimate the baseline survival given climate for the observed period. I then used the mean projected INDVI for the 2001-2050 and 2051-2100 periods under the A1FI, A2, and B1 climate scenarios to estimate baseline survival given climate change.

Table 5.3: Expected reproductive rates of deer in Bogesund given different levels of fox abundance.

Fox conditions	Age Group	Ovulation rate (corpora lutea per female)[a]	Pregnancy rate	Early fawn survival[b]	Fawns per female in autumn
Low abundance due to mange outbreak (1989-1993: mean fox bag = 0.134 per km^2)	Subadult reproducers	1.02	0.93	0.70	0.65
	Mature reproducers	1.96	1.93		1.34
High abundance (1994-2006: mean fox bag = 0.426 per km^2)	Subadults reproducers	1.02	0.93	0.30	0.28
	Mature reproducers	1.96	1.93		0.59

[a] Ovulation was modelled using a multinomial model with density and age group as predictors. Reproductive rates shown were calculated assuming a roe deer density of 12.5 deer per km^2 in this model. Pregnancy rates were calculated as the ovulation rate multiplied by an age-group specific implantation rate (see text and Ch. 4 for more detail).

[b] The number of fawns per female in autumn was modelled using a generalised linear model with a log-link; this model incorporated fox bag (an index of fox abundance) as a predictor. Age-group specific pregnancy rates were included as an offset in this model so that age-group specific estimates of fawns surviving until autumn could be calculated. Early fawn survival is equal to the number of fawns per female in autumn divided by the associated pregnancy rate.

For each combination of fox and climate (INDVI) conditions (14 in total), I estimated roe deer survival at Bogesund given different levels of lynx predation (see above) and human harvest, varying the per capita harvest rate from 0 to 0.6 in increments of 0.001. The combination of lynx effects and per capita harvest rates resulted in 102,771 population transition matrices for each of the 14 combinations of climate (INDVI) and fox conditions. I calculated lambda (λ) as the dominant eigenvalue of each matrix (Caswell 2001). Then, for each combination of fox abundance, climate conditions, and lynx predation pressure, I identified the per capita harvest rate that resulted in zero population growth ($\lambda = 1$). Under high predation pressure (due to high fox abundance or strong effects of lynx presence) and low vegetation productivity (indicated by low INDVI) the harvest rate which results in zero population growth should be relatively low. Under contrasting conditions, such as increased vegetation production (as is expected with climate change), the harvest necessary to yield zero population growth is expected to be higher. All data preparation and statistical analyses were conducted using program R 2.13.0 (R Core Development Team 2011).

Results

Simulations of density during the observed period

Changes in roe deer density were simulated for 17 years in Bogesund (from 1991 to 2007; Fig. 5.2) and for 24 years in Grimsö (from 1983 to 2006; Fig. 5.3). The estimated starting age distributions indicated populations with high proportions of fawns (31% and 29% of the population in Bogesund and Grimsö respectively) and subadults (21% in both sites), and very few senescent individuals (< 5% in both sites).

The simulations in Bogesund reproduced the observed changes in roe deer vital rates (see Appendix 5, Fig. A5.2) and population densities (Fig. 5.2) well. The correlation between simulated and observed densities was high (Pearson's $r = 0.86$, $P < 0.001$, n = 16, Fig. 5.2f; note that in 2007 there was no observed density estimate with which to compare the simulated density). However, the simulated magnitude of the population peak and subsequent decline from 1991-1993, was less than that implied by observed densities. It seems likely that this mismatch is due to the fact that estimated ovulation fluctuations were small compared to those observed (Appendix 5, Fig. A5.2). The 95% confidence intervals (CI) of density estimates were wide, indicating large uncertainty (Fig. 5.2a). The models of the survival of older deer and of young fawns accounted for most of this uncertainty. When the uncertainty surrounding estimates of survival and fawn survival was omitted, the sum of the variances surrounding density estimates dropped by 50% and 38% respectively and the CI surrounding density estimates were narrower (Fig. 5.2c and e). Omitting uncertainty in estimates of INDVI and ovulation reduced the variation surrounding density estimates by only 13% and 2% respectively.

The simulations in Grimsö did not replicate the trajectory of the pellet counts in that area well. Despite the moderately good performance of the component models when estimating observed vital rates (see Appendix 5, Fig. A5.3), there was a negative correlation between the simulated densities and those observed (Pearson's $r = -0.72$, $P < 0.001$, n = 24; Fig. 5.3f). The uncertainty surrounding density estimates was large (Fig. 5.3a) and most of it was due to the models of survival (of older deer) and early fawn survival (Fig. 5.3c and e); omitting these sources decreased the variance surrounding simulated densities by 54% and 39% respectively. The uncertainty

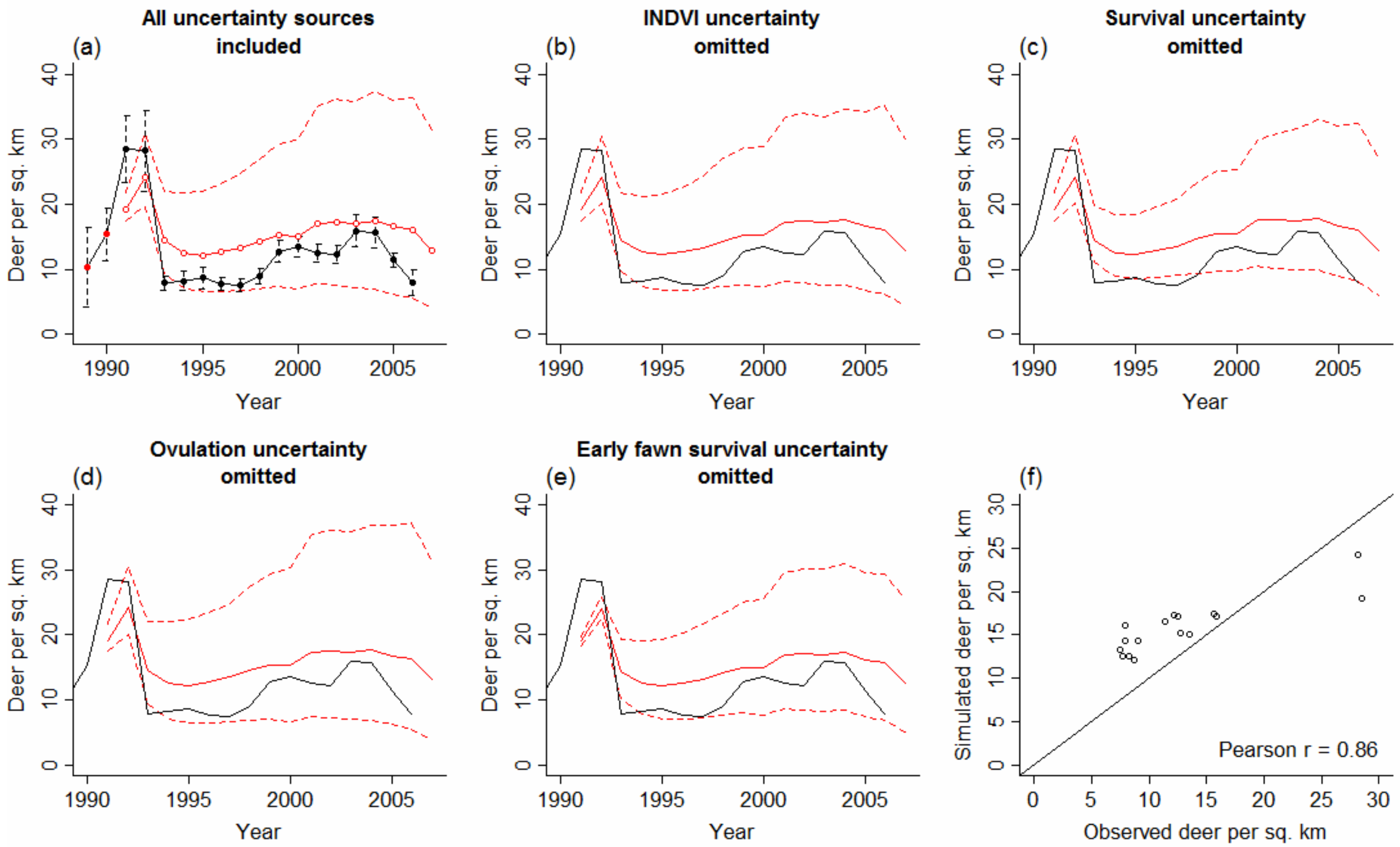

Figure 5.2: Roe deer density in Bogesund was simulated from 1991 until 2007 using the NDVI, survival, ovulation and fawn survival models developed in previous analyses (see text for more detail). Red lines (and red hollow points) represent median (50% quantile) simulated densities, while black lines (and black solid points) represent observed densities from each year. Observed densities were estimated each April using a Lincoln-Peterson estimator. In panel (a), red solid points represent the observed densities used as starting values for the density simulation. Uncertainty due to each of the modelled processes was incorporated in simulations (see text for more detail). Dashed red lines represent the upper and lower 95% confidence intervals for the simulated densities across 1000 iterations. The proportion of variation surrounding simulated density estimates was evaluated by including all sources of uncertainty simultaneously (panel a) and then omitting each source of uncertainty in turn (panels b-e) and comparing the variation in simulated densities across iterations. The correlation between simulated the observed densities and the median simulated density estimate across years is shown in panel (f).

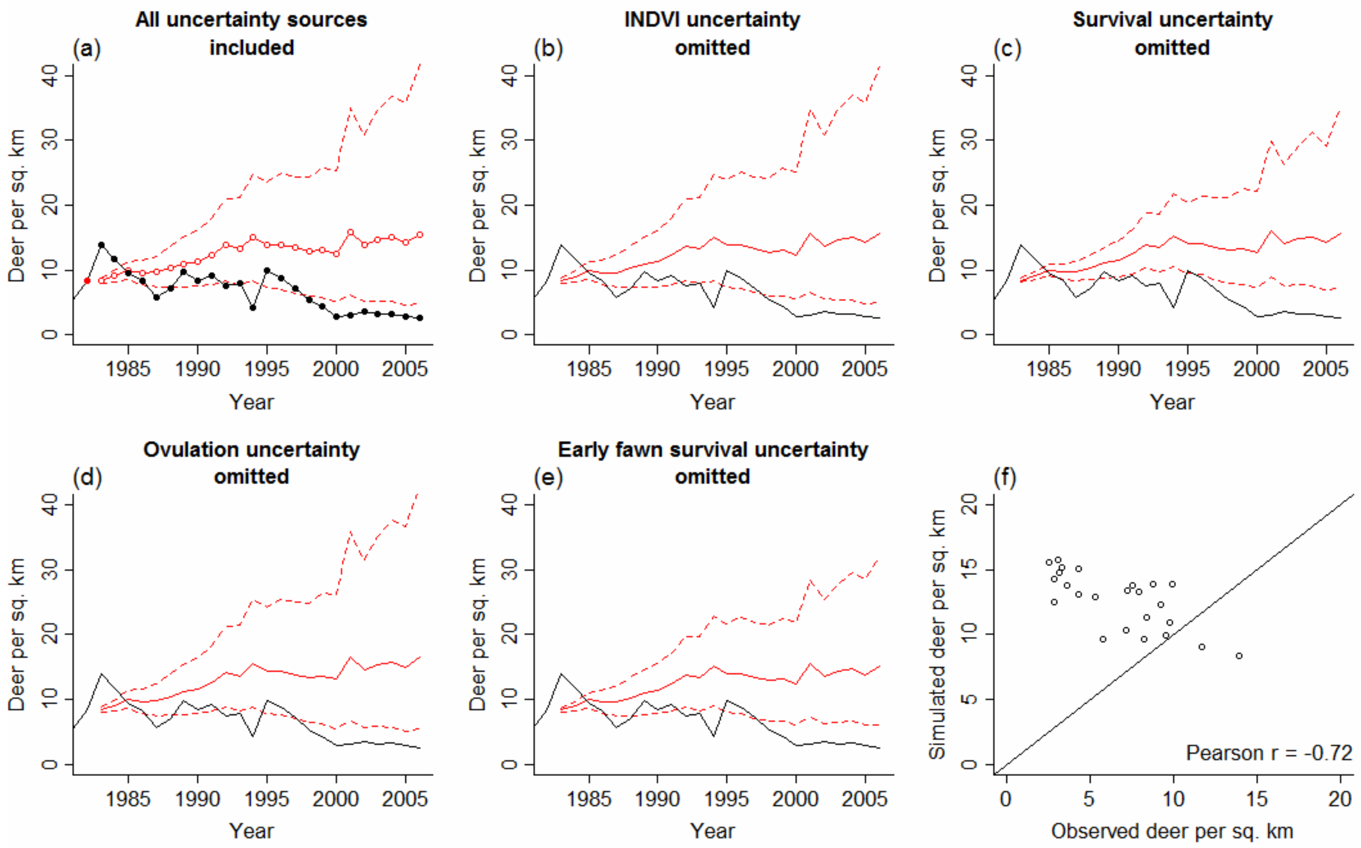

Figure 5.3: Roe deer density in Grimsö was simulated from 1983 until 2006 using the NDVI, survival, ovulation and fawn survival models developed in previous analyses (see text for more detail). Red lines (and red hollow points) represent median (50% quantile) simulated densities, while black lines (and black solid points) represent observed densities from each year. Observed densities were estimated each April using pellet counts. In panel (a), the red solid point represents the observed density used as a starting values for the density simulation. Uncertainty due to each of the modelled processes was incorporated in simulations (see text for more detail). Dashed red lines represent the upper and lower 95% confidence intervals for the simulated densities across 1000 iterations. The proportion of variation surrounding simulated density estimates was evaluated by including all sources of uncertainty simultaneously (panel a) and then omitting each source of uncertainty in turn (panels b-e) and comparing the variation in simulated densities across iterations. The correlation between simulated the observed densities and the median simulated density estimate across years is shown in panel (f).

attributable to the estimation of NDVI and ovulation was small and their omission reduced variation by < 10% in both cases.

Projections of roe deer density in Bogesund

Projections of roe deer population dynamics in Bogesund implied a large increase in roe deer density in all climate scenarios although the estimates were surrounded by wide confidence intervals (Fig. 5.4). The densities simulated by the scenarios are similar until approximately 2060, when they diverge. In the most extreme emissions scenario examined, the A1FI scenario, the population was projected to increase by almost 3% per year (mean λ across years = 1.029 ± 0.0497 [SD]). Even in the B1 scenario, the least extreme scenario examined, the population grew by approximately 2.4% per year ($\lambda = 1.024 \pm 0.0530$). In all scenarios, the rate of population growth meant that the simulated population density (median across 1000 iterations) exceeded 29 deer per km^2 (the maximum density observed in 1992) by the year 2046. This increase appears to be driven by a gradual increase in estimated roe deer survival (Fig. 5.5b), which is positively related to the increases in INDVI projected with climate change (Fig. 5.5a; see also Ch. 2, Fig. 2.7). Ovulation rates during this period were projected to decrease dramatically due to the increasing population density (Fig 5.5c). The uncertainty surrounding projected densities is large and increases toward the end of the 21st Century (Fig. 5.4).

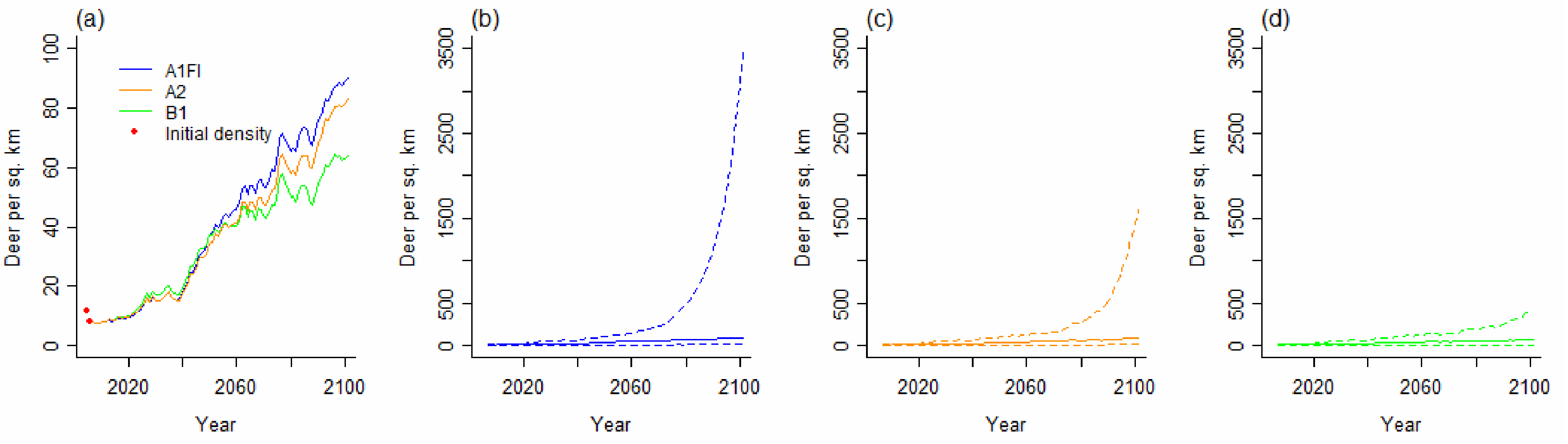

Figure 5.4: The density (number of deer per km^2) of the Bogesund roe deer population projected under future climate projections. Three different IPCC emissions scenarios are examined: the A1FI scenario (blue lines, panels a and b), A2 scenario (orange lines, panels a & c) and B1 scenario (green lines, panels a & d). Uncertainty due to each of the component models of NDVI, survival, ovulation and early fawn survival was incorporated into the simulations which were run for 1000 iterations (see text for more detail). Solid lines represent the median of the simulated densities across iterations. Dashed lines represent the upper and lower 95% confidence intervals. Note that at the beginning of the 21st Century the lines representing different scenarios are difficult to distinguish because they are nearly overlapping.

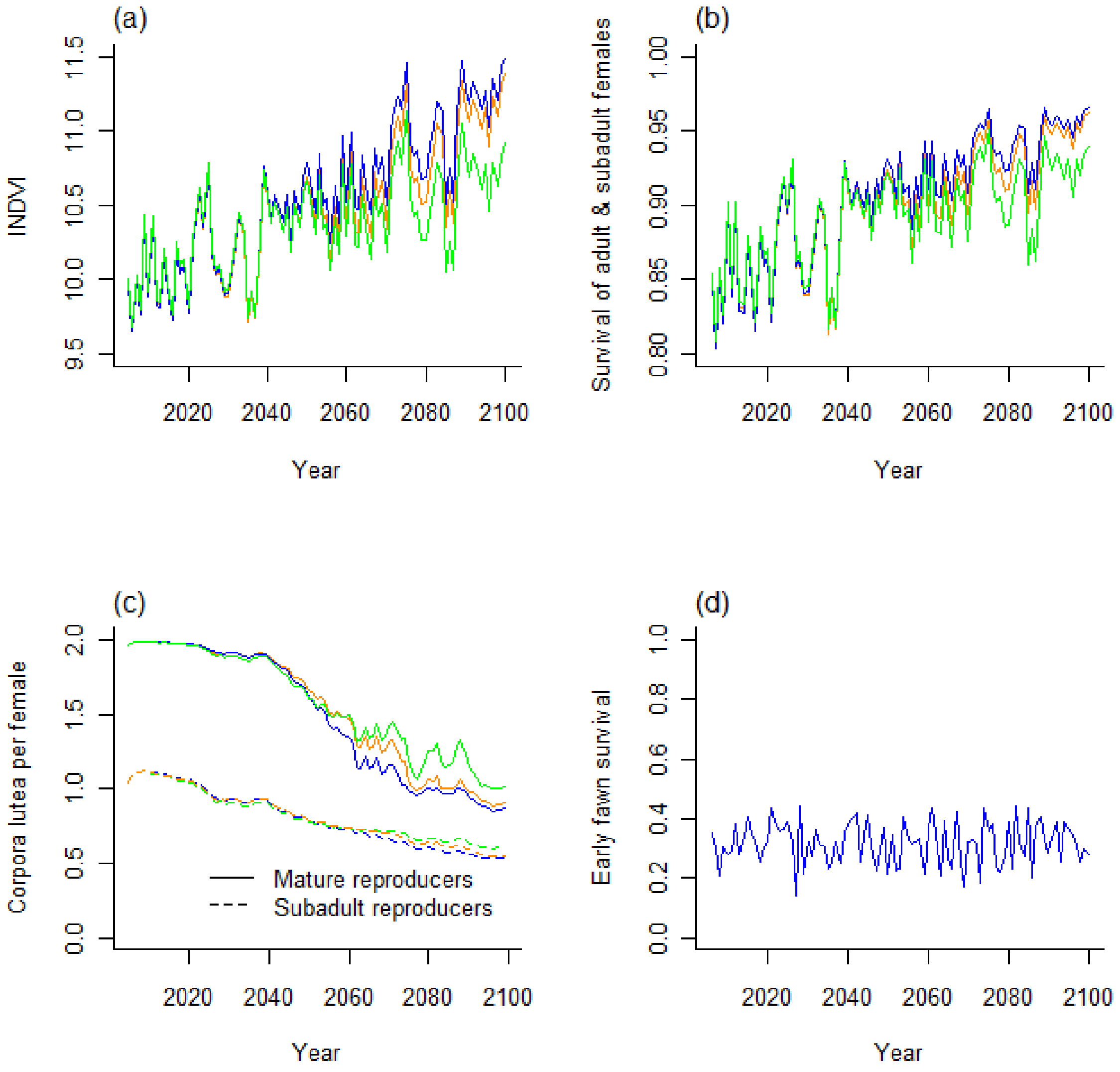

Figure 5.5: The vegetation productivity (indicated by INDVI, panel a) and vital rates of roe deer (survival, panel b; ovulation, panel c; early fawn survival, panel d) within Bogesund was projected given future climate conditions from the HadCM3 General Circulation Model under three different IPCC emissions scenarios: the A1FI scenario (blue lines), A2 scenario (orange lines) and B1 scenario (green lines). The survival rates shown are those of adult and subadult females (panel b). For more detail on models, simulations and predictors involved see Table 5.1 and text. Note that at the beginning of the 21st Century there is little difference among emission scenarios and, thus, the lines representing the scenarios are nearly overlapping in panels (a), (b), and (c). In panel (d), the lines representing fawn survival overlap completely, because the same sequence of FoxHar$_t$ was used as a predictor of fawn survival in all three scenarios (see Methods for details).

Management under a changing climate

The sustainable per capita harvest of the Bogesund roe deer population is projected to decrease with increasing predation pressure (due to fox or lynx) and increase with climate change (which was associated with higher INDVI) (Fig. 5.6). Given high fox abundance and consequent lower rates of fawn survival (similar to current conditions; Table 5.3), adult female roe deer need to have an annual survival of 0.85 or greater for the population to be viable (with $\lambda \geq 1$). During years of low fox abundance, a survival rate of 0.73 would maintain a stable population. All else being equal, this means that the deer harvest rate would almost have to double to suppress population growth when fox predation pressure is low (due to low fox abundance, corresponding to a fox harvest rate of 0.134 per ha).

Because lynx predation and harvest were assumed to have additive negative effects on roe deer survival, there was a direct trade-off between the levels of harvest and lynx predation that could be supported. Under the observed recent climate (linked to survival through INDVI), high fox abundance, and lynx absence, the estimated maximum harvest rate that could be supported (without causing population declines) was 5.9% (this is similar to the mean harvest rate observed, 5.7%, excluding the cull of 1992 and 1993). When lynx predation is included, an impact of lynx stronger than $\beta_{LynxPres} = -0.24$, which is approximately half the magnitude of the effect observed in Grimsö ($\beta_{LynxPres} = -0.576$; Table 5.2), would result in population declines without any harvest (Fig. 5.6b).

When projected future climate and INDVI are used to estimate survival, the capacity of the population to withstand lynx predation and human harvest (and still show positive growth) was increased. During the first half of the 21st Century, survival under the three IPCC scenarios is very similar. If lynx had a “weak” to “moderate” effect on deer ($\beta_{LynxPres} > -0.43$, implying a < 5% decrease in adult survival with lynx presence; Fig. 5.6), moderate harvest (≤ 0.11 deer killed per capita) would result in a stable deer population. Toward the end of the 21st Century, and with increasing climate change, higher levels of harvests would be necessary to maintain population stability. The level of harvest needed to prevent the growth of the roe deer population under the A1FI, A2, and B1 scenarios was determined by the level of predation pressure. When fox abundance was low and lynx were absent, very high rates of harvest (up to 50% of the population depending on the scenario) were required to suppress population growth.

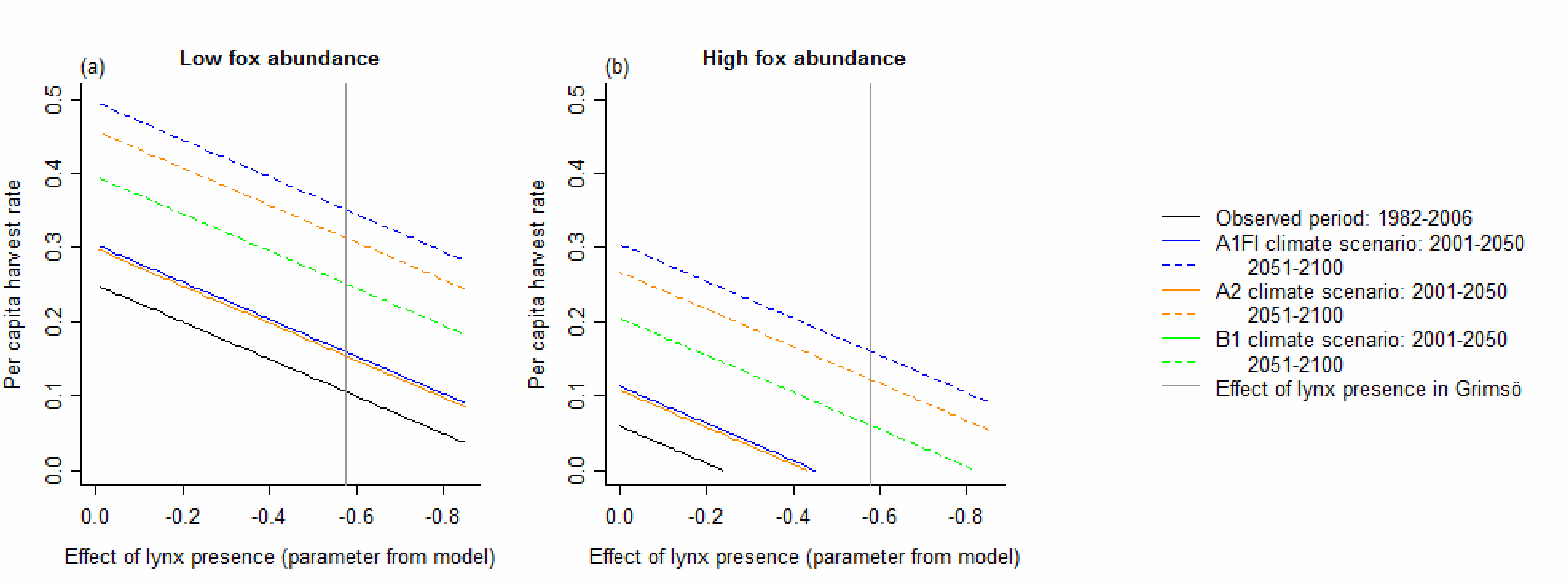

Figure 5.6: The per capita harvest rate necessary to produce zero growth (λ = 1) for the Bogesund deer population is shown for different levels of fox abundance, hypothetical effects of lynx presence (lynx were functionally absent from Bogesund throughout the study period), and climate scenarios. Conditions given low and high fox abundance are shown in panels (a) and (b), respectively. Zero growth isolines are shown by the black, blue, orange and green lines for the observed period, A1FI, A2, and B1 climate scenarios respectively. For the future climate scenarios (A1FI, A2, and B1), solid lines represent the zero growth isolines for the 2001-2050 period and dashed lines represent zero growth isolines for the 2051-2100 period. Areas below lines indicate combinations of harvest and predation conditions which result positive growth (i.e. λ > 1); areas above lines indicate conditions which result in negative growth (λ < 1). The lines for the A1FI and B1 climate scenarios are overlapping for the 2001-2050 period.

Discussion

Climate change will impact not only the geographic extent of a species' range but also the growth of populations within that range (Shoo et al. 2005). For this reason, there have been numerous calls for demographically explicit models in response to climate (Guisan and Thuiller 2005, Thuiller et al. 2008, Huntley et al. 2010, Pagel and Schurr 2012), but few studies have met this challenge. In this chapter, I use models of roe deer vital rates and their drivers to build mechanistic simulations of population growth, which incorporate trophic interactions in addition to the effects of climate. While the component models were site-specific, the resulting simulations were similar both in structure and in the incorporation of effects from both lower and upper trophic levels. At Bogesund and Grimsö, the effects of climate on roe deer survival were manifested through climatically driven changes in vegetation productivity (indexed by INDVI). Similarly, at both sites, simulations incorporated the impacts of human harvest or predation; models in Bogesund included the effects of harvest and fox abundance, and models in Grimsö included an effect of lynx presence. The ability of the simulations to reproduce observed changes in population density at each site differed strikingly. While the simulations of the Bogesund roe deer population were good, the simulations of the Grimsö population were very poor. In both sites, wide confidence intervals surrounded simulated densities, mainly due to uncertainties in the survival rates of deer of all ages. To improve the simulations and their utility for wildlife management purposes, a greater understanding of roe deer ecology at these sites is necessary. I discuss these findings in light of three main issues: simulation performance and uncertainty; projections of roe deer population dynamics under climate change; and the future management of roe deer subject to natural predation.

Simulation performance

The ability of the simulations to reproduce observed roe deer densities differed greatly between sites. This is surprising because the support for component models and the ability of those models to reproduce the observed response values were generally similar between sites (see model weights and correlations in Table 5.1). The high correlation between simulated and observed densities in Bogesund provides some support for the assertion that the simulation structure and the component models of vital rates are biologically reasonable. Roe deer in Bogesund have been relatively well-studied (Liberg et al. 1994, Kjellander 2000, Kjellander et al. 2004a, Kjellander et al. 2004b, Kjellander et al. 2006, Gaillard et al. 2008) and throughout previous analyses (see Ch. 2, 3, and 4), selected models have consistently reflected expectations regarding ecology in the area.

The mismatch between the simulated and observed densities in Grimsö could be caused by errors in the component models underlying the simulation, errors in the observed density measures (estimated using pellet counts), or both. Data availability limited inferences: the data used to fit the models of vital rates (survival, ovulation, and fawn survival) were sparsely spread across years (see Ch. 3 and 4 for more detail) and, in particular, only six years of data could be used to fit the model of fawn survival at this site. It is likely that these limitations were exacerbated by the free emigration and immigration of the Grimsö deer (which contrasts with Bogesund). Also, Grimsö supports multiple predator species including lynx, red foxes, and, most recently, wolves; in Bogesund, the only natural predator of roe deer is the fox. Therefore, the relatively simple models supported by the data may be inadequate to describe roe deer dynamics in Grimsö. An additional possibility is that pellet counts, the accuracy of which is debated (Fuller 1991, 1992, White 1992) do not reflect the true density of roe deer at Grimsö. This method assumes constant rates of pellet production (roe deer defecation) and detection and that pellets decompose between surveys. Pellet decomposition and production are likely to be affected by weather conditions and vegetation production (which impacts roe deer foraging). Additional data on vital rates and deer density at Grimsö would be necessary to determine which of these potential sources of error contributes most to the mismatch between the simulated and observed density estimates.

Simulations for both Bogesund and Grimsö are associated with substantial uncertainty. Although the point estimates of the simulated densities in Bogesund closely match the observed densities at this site, the 95% confidence intervals surrounding these estimates encompass two-fold differences in either direction (i.e. the density could be half or twice the point estimate). In Grimsö, simulations cannot confidently discriminate between population decreases or increases during the observed period. This lack of precision limits the utility of the simulations for wildlife management and is discouraging considering the effort that has gone into long-term monitoring programs at both sites (since 1972 in Grimsö and 1989 in Bogesund). By omitting each source of uncertainty in turn, it is possible to infer that the precision of the density simulations could be most improved by reducing the uncertainty surrounding estimates of survival, especially early fawn survival. Future research efforts at Bogesund and Grimsö should focus on these processes. Wildlife managers in many areas may be limited by the understanding of a few ecological processes. Extrapolating from knowledge of other sites is one possible solution; however, the literature suggests that ungulate population dynamics are often site-specific (Loe et al. 2005, Månsson and Lundberg 2006, Weladji and Holand 2006, Martinez-Jauregui et al. 2009, Nilsen et al. 2009a, Johnson et al. 2010). My findings are in keeping with this assertion: extrapolation among sites should be pursued with great caution.

Projections of roe deer density given climate change

Substantial increases in the density of roe deer at Bogesund were projected under all three climate change scenarios. The projected increase in roe deer density at Bogesund is consistent with the assertion that climate-driven increases in environmental productivity are likely to result in a widespread increase in roe deer abundance (Melis et al. 2009). In contrast, Gaillard et al. (2013) found that earlier springs were related to decreased population growth of roe deer in France due to a mismatch between the spring flush and fawn births. In more Northern sites, it seems possible that such a phenological mismatch could be less detrimental to population growth as its negative effects are offset by the positive impact of a longer growing season on roe deer survival. Moreover, mismatches are likely to be subject to strong selection (Moyes et al. 2011, Reed et al. 2013) and, thus, unlikely to persist in the face of increasing shifts in spring. The projected rise in simulated roe deer densities at Bogesund was driven by the effect of climate on vegetation productivity, which increased roe deer survival rates. The potential for vegetation to impact roe deer population dynamics in this manner highlights the importance of accounting for the indirect effects of climate on wildlife. While I chose not to project roe deer density in Grimsö, it is interesting that the model of roe deer survival in Grimsö included a similar positive effect of vegetation productivity to the effect specified in the Bogesund survival model (see Table 5.1 and Figure 3.4 in Ch. 3). For this reason, it seems likely that climate change will also have a positive effect on roe deer population growth in Grimsö.

My inferences must be considered in light of the extensive uncertainty surrounding the simulated densities in Bogesund. The combination of uncertainty from the component models meant that projections for the later half of the 21st Century ranged from stasis to unrealistic increases (see Fig. 5.4). In the A1FI scenario, the median projection of density for the year 2100 was three times the highest roe deer density that has been observed at the site. Therefore, the projections presented here represent a starting point for further analyses but should be interpreted with caution. One potential limitation of the models presented is the form of density dependence. The only vital rate apparently affected by density was ovulation and that effect was linear. Many of the effects of density on vital rates, including ovulation, are likely to be mediated by food availability (McShea et al. 1997). Higher density populations are likely to reduce vegetation through foraging and, therefore, could affect multiple vital rates (e.g. survival was related to NDVI in this analysis). However, no effects of density on vegetation were included in these simulations. Additionally, density dependence is often non-linear: as densities continue to rise, the negative effect of density on vital rates is likely to become stronger and density may impact other vital rates (Eberhardt 1977, Gaillard et al. 2000b, Sinclair and Krebs 2002). Unfortunately, the power of the models to parameterise such indirect and non-linear relationships was limited by the relatively narrow range of roe deer densities in this study. These constraints probably downplay the role of density dependence in limiting population growth.

Accounting for uncertainty in future conditions is an important part of all climate impact research. In these analyses, I considered this type of uncertainty by examining three alternate climate change scenarios. These scenarios assume that environmental factors other than climate, such as harvest and community composition, will remain the same. This is unlikely. Ideally, harvest rates will be adapted on an annual basis in response to observed roe deer densities. Community composition is also unlikely to remain the same. Fox ranges have expanded over the 20th Century and it is unclear whether climate is driving increases in their abundance (Hersteinsson and Macdonald 1992, Barton and Zalewski 2007, Gallant et al. 2012). While large predators are not resident in Bogesund, lynx are moving southward throughout Sweden and have occasionally been observed in the area (pers. comm., Kjellander 2013). Wolf populations are also increasing in Sweden (Liljelund 2011) and this is also likely to impact roe deer populations (wolf predation on roe deer in Grimsö has resulted in approximately 20 mortalities of radio-collared animals since 2006). Such changes in Swedish forest ecosystems make any extrapolations to the future more complex. A challenge for future studies would be to consider a wider range of future scenarios, which incorporate adaptive management regimes and changes in community composition, in addition to changes in climate.

The role of predation and implications for future management

My preliminary analyses of the effects of predation on roe deer dynamics provide some insight into the potential ramifications of predation for the management of this popular game species in south-central Sweden. I used the observed effect of lynx presence in Grimsö and of fox abundance (indicated by regional fox harvests) in Bogesund to infer the per capita harvest rates that could be supported by the Bogesund roe deer population given different levels of predation pressure and different climatic conditions (associated with vegetation productivity). The results of this analysis suggest that given current levels of productivity (under observed 1982-2006 climate), increased predation pressure (due to high fox abundance and lynx presence) could reduce roe deer survival rates to such an extent that very little harvest could be supported without causing population decline. This result is consistent with a recent study, which found that the combination of mortality from hunters and lynx was associated with declining roe deer abundance across 144 sites in Norway (Melis et al. 2010).

Over the next century, however, climate change could increase the resilience of roe deer populations to predation and hunting. As shown by the projections, increasing vegetation productivity is likely to increase roe deer survival rates at Bogesund. Due to this change, the future roe deer population could support higher levels of mortality caused by a combination of harvest and predation. In fact, my results imply that increased predation pressure could aid wildlife managers by reducing the harvest necessary to maintain the desired population density (12.5 deer per km^2 in this case). Without increased predation pressure, a per capita harvest rate of ~20-50% might be required to prevent population growth; such high rates of harvest would be very difficult to achieve. While tentative, these results suggest that predation might aid managers in the mitigation of climate change impacts on roe deer at this site and, perhaps, at others like it. This is consistent with research on predator mitigation of some of the destabilising effects of climate change (Gilg et al. 2003, Wilmers et al. 2007a).

The possibility that predators could aid managers to maintain stable ungulate populations is an interesting outcome of the simulations presented here. However, the parameterisations of predation effects were relatively simplistic, with predation included in models as an additive linear effect. This is probably unrealistic: the impact of predators on their prey is dependent on many factors (Sinclair and Krebs 2002), most notably including prey and predator densities (Holling 1965, Vucetich et al. 2002) and prey community composition (Okarma 1995, Garrott et al. 2007). These factors were not included in my models and are likely to affect the impacts of predation. For example, wild boar (*Sus scrofa*) are spreading northward through Sweden and have recently become resident in the Grimsö study area (Kjellander pers comm. 2013). While lynx do not often prey on boar (Okarma et al. 1997), wolves do and it seems likely that boar presence in the area could indirectly influence predation on roe deer (see Ch. 6 for an investigation of wolf predation patterns at a site containing both wild boar and roe deer populations). Also, it is important to point out that while predation can be similar to human harvest in terms of its direct effects on prey (they both reduce prey survival); predation is likely to have many indirect effects on communities that human harvest does not (see review by Kuijper 2011). The models used here imply that the effects of predation and harvest on roe deer survival are mechanistically similar; however, it would be naïve to conclude that their effects on the overall ecology of a system are interchangeable.

Conclusion

In this chapter, I assessed the feasibility of building mechanistic simulations of population dynamics in response to climate, while simultaneously accounting for trophic interactions. Despite the challenges involving data limitations and associated uncertainties, the simulations provided useful insight into roe deer population dynamics. The close correspondence of the simulated and observed densities at Bogesund provide additional support for the ecological validity of the component models of vital rates and vegetation developed in this thesis, allowing roe deer density at this site to be projected into the future. Poorer model performance at Grimsö, however, emphasises limitations arising from sparse data within complex ecosystems.

With increased precision, the potential usefulness of simulations such as these for wildlife management is very high. My projections suggest that future climate change could drive the growth of roe deer populations in northern Europe. This growth could be controlled by a combination of human harvest rates and heightened predation pressure by either fox or lynx. The combined influences of global climate change and increased predation pressure could have important ramifications for the future management of this widespread ungulate. If large predators continue to expand their ranges southward through Sweden, simulations such as these could provide valuable insight into how prey populations will be simultaneously impacted by climate change and increased predation pressure. These findings emphasise the need to move beyond simple projections of changes in species range. Future research would benefit from explicitly considering the mechanistic drivers of species population dynamics, including trophic interactions, in order to understand how species will respond to future climate change.

Chapter 6 – Prey selection by an apex predator: the importance of sampling uncertainty[‡]

Abstract

The impact of predation on prey populations has long been a focus of ecologists, but a firm understanding of the factors influencing prey selection, a key predictor of that impact, remains elusive. High levels of variability observed in prey selection may reflect true differences in the ecology of different communities but might also reflect a failure to deal adequately with uncertainties in the underlying data. Indeed, a review shows that less than 10% of studies of European wolf predation accounted for sampling uncertainty. Here, I relate annual variability in wolf diet to prey availability and examine temporal patterns in prey selection within a community including both roe deer and wild boar. In particular, I identify how considering uncertainty can alter conclusions regarding prey selection. I also consider how fluctuations in relative prey availability, driven primarily by changes in the abundance of one prey species, can impact predation on other prey.

Over nine years, researchers in Catenaia collected 1,974 wolf scats and conducted drive censuses of ungulates in the site. I bootstrapped these scat and census data within years to construct confidence intervals around estimates of prey use, availability and selection. Wolf diet was dominated by boar (61.5 ± 3.90 [SE] % of biomass eaten) and roe deer (33.7 ± 3.61%). Temporal patterns of prey densities revealed that the proportion of roe deer in wolf diet peaked when boar densities were low, not when roe deer densities were highest. Considering only the two dominant prey types, Manly's standardised selection index using all data across years indicated selection for boar (mean = 0.73 ± 0.023). However, sampling error resulted in wide confidence intervals around estimates of prey selection. Thus, despite considerable variation in yearly estimates, confidence intervals for all years overlapped. Failing to

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[‡] The material in this chapter has been published in Davis, M. L., P. A. Stephens, S. G. Willis, E. Bassi, A. Marcon, E. Donaggio, C. Capitani, and M. Apollonio. 2012. Prey Selection by an Apex Predator: The Importance of Sampling Uncertainty. PLoS One **7**: e47894.

consider such uncertainty could lead erroneously to the assumption of differences in prey selection among years. This analysis highlights the importance of considering the relative availability of prey species and of accounting for sampling uncertainty when interpreting the results of dietary studies.

Introduction

Predator populations that have long been subjected to persecution are receiving increased conservation attention and are recovering in both North America and Europe (Linnell et al. 2000, Boitani and Mech 2003, Beschta and Ripple 2009). Predicting the impact of changing predator numbers on prey species is important for managing populations of both predators and their prey (Schmidt 2005, Wilmers et al. 2007a, Berger et al. 2008). Accurate predictions require a thorough understanding of predator diets and prey selection, which can be affected by a multitude of factors including: prey and predator densities (Vucetich et al. 2002); the functional and numerical responses of predators to changes in prey density (Messier 1994, Messier 1995); community composition (particularly the presence of alternative prey; Okarma 1995, Garrott et al. 2007); climatic conditions (Post et al. 1999); seasonal cycles (Jedrzejewski et al. 2000, Barja 2009, Mejlgaard et al. 2013); vegetation productivity (Denno et al. 2005, Melis et al. 2009); and landscape heterogeneity (Kauffman et al. 2007). These drivers can result in considerable temporal and spatial variation in patterns of predation. For this reason, studies of predation often require large sample sizes and high quality data to overcome uncertainty. However, because large predators are generally elusive and exist at low densities, they are expensive and time-consuming to study, meaning that large sample sizes are rare and results must usually be interpreted with caution. Failure to describe adequately the uncertainty in a dataset can promote misleading conclusions about predator feeding habits.

In Europe, the wolf (*Canis lupus*) is recovering from centuries of persecution. The expansion of wolf populations in many European countries (Boitani and Mech 2003) has the potential to change fundamentally the ecology of communities by exposing large ungulates to natural predation after decades (and in some cases, centuries) of predator absence. In North America, wolves limit ungulates in some areas (Messier 1994, Mech et al. 2003) and predation by recovering wolf populations has triggered complex trophic cascades, altering prey distribution and plant recruitment (Fortin et al. 2005, Beschta and Ripple 2009). Studies of ungulate dynamics and distributions in Europe indirectly suggest that wolves might play a similar role by limiting prey (Okarma 1995, Jedrzejewski et al. 2000, Melis et al. 2009) but the intricacies of wolf-prey relationships and the potential for trophic cascades in European communities is poorly understood (Aanes et al. 1998, Jedrzejewska et al. 2005).

Dietary studies that accurately describe wolf prey selection are a necessary first step toward understanding the impacts of wolf predation on European wildlife.

Over the past three decades, scat analysis has been used to describe the dietary composition and prey selection of wolves, and to estimate their potential impact on prey communities (Macdonald et al. 1980, Salvador and Abad 1987, Meriggi et al. 1996, Jedrzejewski et al. 2000, Capitani et al. 2004, Mattioli et al. 2004, Gazzola et al. 2007, Barja 2009). Scat-based dietary studies in Europe have highlighted the flexibility of the wolf as a predator. This variability is especially evident from reports of wild boar (*Sus scrofa*) utilisation among sites. Based on a review of results from the Bialowieza Primeval Forest (BPF), Poland, and other literature, Okarma (1995) concluded that wild boar are generally avoided, while red deer (*Cervus elaphus*) are the prey of choice. However, BPF has a diverse ungulate community comprising 5 species (*Cervus elaphus*, *Sus scrofa*, *Capreolus capreolus*, *Alces alces*, *Bison bonasus*), some of which are no longer common elsewhere in modern-day Europe. By contrast, studies in southern and Mediterranean areas of Europe indicate that boar are sometimes preferred as prey (Mattioli et al. 1995, Meriggi et al. 1996, Capitani et al. 2004, Barja 2009, Mattioli et al. 2011).

Some of these southern sites are dominated by only two species, roe deer (*Capreolus capreolus*) and wild boar, and could be considered more representative of communities throughout much of Europe (Apollonio et al. 2010). Over the last century roe deer populations have grown substantially (recovering from a bottleneck in the 1800’s) and roe deer are now the most common ungulate in Europe (Andersen et al. 1998a, Apollonio et al. 2010). Similarly, wild boar populations are expanding northward in Russia and Scandinavia (Welander 2000, Melis et al. 2006). As a result there are likely to be a growing number of sites (especially in northern Europe) where these two ungulates co-exist. In these sites, the impact of wolf predation on each species will be determined, in part, by wolf preferences. Selection between these two prey appears to vary both among and within sites. This has been attributed to a variety factors including differences in community composition and in the vulnerability of individuals (as influenced by age, body size, grouping behaviour and season); unfortunately, the data required to distinguish between these alternatives are lacking (Cuesta et al. 1991, Mattioli et al. 1995, Capitani et al. 2004, Barja 2009).

Some of the apparent variability in wolf diet may be a result of the scat analysis methods that are widely used to determine diet. Several papers have highlighted potential pitfalls in the scat analysis process, including those which may arise from the analysis of small datasets (Reynolds and Aebischer 1991, Weaver 1993, Ciucci et al. 1996, Trites and Joy 2005, Marucco et al. 2008). The potential for sampling error to arise is particularly high when the number of scats collected is small relative to the number produced by the study population. Such samples might not be representative and can lead to incorrect conclusions about diet, especially when the uncertainty in estimates based on small samples is not reported. Reynolds and Aebischer (1991) advocated the use of re-sampling techniques (e.g. bootstrapping) to produce confidence intervals around estimates of dietary composition. While some recent studies (e.g. Marucco et al. 2008) have used re-sampling techniques, much of the existing literature on European wolf diet does not account for uncertainty due to sampling error in results (20 out of 22 studies examined; Appendix 6, Text A6.1 and Table A6.1). In addition, studies of prey selection require estimates of prey availability, which are themselves subject to error. Failure to consider uncertainty in both prey use and prey availability can result in inappropriate conclusions.

Predation patterns may be further obscured by neglecting variation in prey selection among years, within a site. Many studies of wolf diet are either relatively short or pool scat samples across years (to increase sample size), thereby obscuring inter-annual variation (Appendix 6, Text A6.1 and Table A6.1). Mattioli et al. (2011) found that prey use can vary substantially among years and that much of this variation is unaccounted for by the changing abundance of prey. Environmental factors affecting prey vulnerability (e.g. weather conditions, land use) may vary substantially from one year to the next, creating variability that could underlie some of the inconsistencies observed in wolf predation among sites. Long-term studies that explicitly incorporate this variability will facilitate comparisons of wolf diet among sites and enable the identification of potential drivers of predation patterns across the continent.

In this study, I combine re-sampling techniques with nine years' scat sampling and drive census data to address the following questions regarding the dietary habits of wolves in Alpe di Catenaia:

1) Do the wolves select for either of the two main prey species available, roe deer and wild boar?

2) How might an explicit consideration of uncertainty affect conclusions about wolf dietary selection?

3) How does wolf diet relate to the relative availability of prey species in the area?

Methods

Study site

This study focuses on the Alpe di Catenaia (hereafter referred to as Catenaia) study area in the Apennine Mountains (Arezzo province, Italy). There is a 27 km^2 protected area where hunting is banned, located in the centre of the larger 120 km^2 site (Fig. 6.1). The deciduous hardwood forest in the site is dominated by oak (Quercus *spp.*), chestnut (*Castanea sativa*) and beech (*Fagus sylvatica*). The climate in Catenaia is temperate and seasonal. Snowfall usually starts in October and may continue through April. There are a number of farms surrounding the study area which raise livestock (mostly sheep) that are a potential additional source of prey for wolves. Further detail on the location, climate, and land cover of Catenaia is provided in Ch. 1.

Prey density and biomass estimation

The wild ungulate community included only wild boar and roe deer for the first seven years of the study; red deer have been occasionally recorded in the study area since 2007. Densities of wild boar and roe deer were estimated from drive censuses completed every May (2000 – 2005, and 2007 – 2008; method also described by Mattioli et al. 1995) by the Provincial Administration of Arezzo; the 2006 census excluded a large portion of the study area, so was excluded from the analyses. Censuses took place in both the protected and non-protected parts of the study area each year, encompassing about 80% wooded area and 20% other cover types. Government employees, researchers, and volunteers encircled an area of forest (each 0.14-0.52 km^2 in size) then moved inwards and counted wild boar and roe deer observed in the contained area. Between 9 and 15 such forest blocks were sampled each year. The average density of observers during these surveys was approximately 110 persons per km^2 (Mattioli et al. 2004). In order to extrapolate from the surveyed areas to estimates of overall density at the site, researchers in Catenaia corrected for the differences in

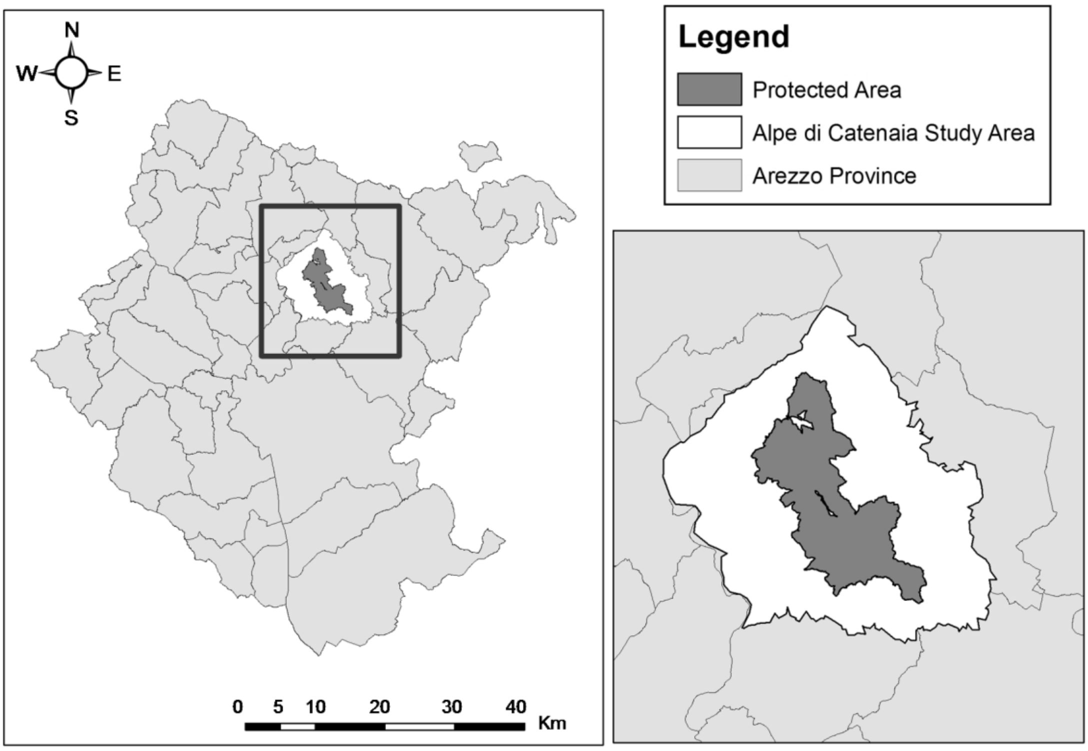

Figure 6.1: The Alpe di Catenaia study site (a.k.a. Catenaia) is located in the Arezzo province in Northern Tuscany, Italy. The study site includes a central protected area, where hunting is prohibited.

block area and the forest cover surrounding each block. The latter is necessary because wooded areas surrounded by more open habitat could appear to have higher densities of animals because during drives animals congregate in the more sheltered, forested areas (Mayle and Staines 1998). The percentage area covered by forest within a 1 km buffer surrounding each forest block was extracted using GIS (ArcGIS version 10; ESRI 2011). The corrected density of animals within each surveyed block was thus calculated as number of individuals counted divided by block area and multiplied by percentage forest cover of the surrounding area (median value 81%, range 41-96.1% across blocks). The overall density of wild boar and roe deer at the site was then estimated as the mean across the different blocks. Drive censuses are a widely used technique and, while some animals are not seen during a census, it has been found that such drive census generally give higher density estimates than alternative methods (Bongi et al. 2009). To convert densities to biomass densities (kg per km^2) I used the average body mass of boar (43.2 ± 0.33 [SE] kg, n = 5003) and roe deer (21.1 ± 0.12 [SE] kg, n = 2355) hunted in the districts that immediately surround the protected area (all age classes included).

Scat collection and assessment of wolf diet

During the study period the area supported a single wolf pack which contained 3-6 individuals. This was confirmed using genetic analysis of scats (unpublished data), snow-tracking (Jedrzejewski et al. 2000) and wolf-howling surveys (Gazzola et al. 2002). Wolf scats were collected monthly between May 2000 and April 2009 from seven transects distributed throughout the study area (total length: 73 km per month). Years were defined as extending from May to the following April (i.e. scats collected between May 2000 and April 2001 were assigned to the year 2000). Scats were washed and the recovered prey remains were oven-dried at 68°C for 24 hours. Prey categories included wild boar, roe deer, red deer, hare (*Lepus europaeus*), small rodents, goats, sheep and cattle. Prey remains were identified through comparison to a reference collection of mammal hair, bones, and teeth collected from within the study area. Specimens were identified to species and age class (for ungulates only) when possible. This identification was based on the macroscopic characteristics of hairs and bones following Mattioli et al. (1995, 2011). Boar remains were divided into three age-weight classes: newborn piglet (< 10 kg), piglet (10-35 kg), and adult (> 35 kg). Roe deer remains were classified into two classes: fawn (< 1 year) and adult (> 1 year, including the subadult, adult and senescent age groups distinguished in other chapters). The ability of researchers to discriminate among samples from different species and age classes was verified by means of a blind test using artificial “scat samples” containing prey remains from a variety of species and age classes. A total of 200 samples were stored in plastic bags, each consisting of remains from one potential prey item. All potential prey in the area were represented in these samples, including hair samples from animals during both summer and winter. Each researcher was assigned 50 of these bags, chosen at random, and was assessed on their ability to correctly identify the age class and species represented by the sample. Ability to discriminate among wild boar weight classes was additionally assessed using a further 25 samples per researcher. Only researchers who correctly identified all test samples went on to analyse true scat samples.

Most scats were entirely composed of just one prey item; the relative volume of these scats amounted to 100% of the same prey type. When more than one prey type was evident in a single scat, the relative volume of each was estimated as approximately 25, 50 or 75% of the scat’s total volume. When the age class of ungulate remains could not be identified, the relative volume of the unidentified material was redistributed according to the proportions of the age classes observed among other scats collected during the relevant period. The biomass of prey consumed to produce the collected scats was estimated using Weaver's biomass model (Weaver 1993). In this model the live weight (w_i) of an individual of prey type i is converted into c, an estimate of the biomass (kg) of that prey type that must have been consumed to produce one scat, according to the following equation:

$$c = 0.439 + 0.008 \cdot w_i \qquad \text{[Equation 6.1]}$$

Multiplying c by the summed relative volumes of scats attributable to each prey species gave the inferred total biomass of each prey species consumed (hereafter, the "biomass consumed"), as indicated by the sample of scats collected. The weights of different age classes (obtained from data on hunted individuals in each age class) were accounted for in this calculation. The general composition of wolf diet each year was described as the percentage of total biomass consumed attributable to each prey group. These calculations were completed for the entire set of scat samples collected each year.

Wolf dietary response and prey selection within the main, two-ungulate community

Wild boar and roe deer dominated the prey community in Catenaia and were the main prey items of importance. To estimate selection by wolves, I focused on boar but, because two species form the predominant part of wolf diet at this site, the complement of the estimated parameters applies to roe deer. Based on the scat analysis, I inferred the biomass consumed of boar (C_B) and roe deer (C_R), calculating the relative use of boar as $U_B = C_B / (C_B + C_R)$. U_B was calculated for each of the nine years and is hereafter referred to simply as boar use. The relative availability of wild boar for eight years of the study (the 2006 census was excluded, see above) was given by $A_B = B_B / (B_B + B_R)$, where B_B and B_R are, respectively, the biomass densities of boar and roe deer in the area.

I used linear regression to model relative boar use as a function of boar availability. Consistency with the assumptions of linear regression was checked using diagnostic plots. Several studies have found seasonal differences in the absolute consumption of wild boar (percent of diet) by wolves (Jedrzejewski et al. 2000, Capitani et al. 2004, Ansorge et al. 2006, Barja 2009), so I initially developed models that included a seasonal component. However, season was not significant in these models so was not considered further (Appendix 6, Text A6.2 and Table A6.2).

Wolf selection for wild boar (within the wild boar-roe deer community) was assessed using Manly's standardised selection ratio, α (Manly et al. 1972, Manly et al. 2002):

$$\alpha = \frac{U_B / A_B}{(U_B / A_B) + ((1 - U_B)/(1 - A_B))} \qquad \text{[Equation 6.2]}$$

Here, α is the probability that wild boar would be selected when offered in equal biomass to roe deer. An estimate of $\alpha_i \approx 0.5$ indicates use of boar in proportion to boar availability. $\alpha_i > 0.5$ indicates selection for wild boar, while $\alpha_i < 0.5$ indicates selection against boar. I calculated Manly's selectivity index for boar for all eight years with availability estimates.

Uncertainty estimation

Uncertainty in the estimates of wild boar use, availability, and selection by wolves within years was determined by bootstrapping (Efron 2000). For estimating boar use, all scat samples for a year were randomly sampled with replacement to produce a new estimate of the biomass consumed of both wild boar and roe deer. Similarly, for estimating boar availability, densities based on drives in separate areas of the study site were randomly sampled with replacement to produce a new estimate of density for both ungulate species. As drives in some areas each year failed to find any individuals of a given species (resulting in a density of 0 for that drive) the possibility existed for bootstrap estimates of site densities to be zero (causing analytical problems when dividing use by availability); I controlled for this by assuming a minimum possible density equal to the total number of individuals observed divided by the total area sampled that year in all drives. I used this approach to generate 4,000 bootstrap samples within each year. The relative use and relative availability of wild boar and Manly's selectivity ratio were calculated for each bootstrap sample, using the 2.5% and 97.5% quantiles to construct 95% confidence intervals around yearly estimates for each year. All analyses presented here were performed in R 2.13.0 (R Core Development Team 2011).

Results

Ungulate community composition

Wild boar density estimates ranged from 4.7 to 26 per km^2 during the nine-year study period (mean = 14.3 ± 2.57). Roe deer density was less variable than boar density and ranged from 32.8 to 47.7 deer per km^2 (mean = 39.6 ± 1.64; Fig. 6.2). Confidence intervals, representing the uncertainty surrounding yearly density estimates due to potential sampling error, were wide for both species and made it difficult to say with confidence that densities differed among years. In fact, only the low boar density observed in 2004-05 was significantly different from other years, with 95% confidence limits that excluded the mean density observed across years. Bootstrapping simulations resulted in an exceptionally wide confidence interval for the boar density estimate for 2007 (Fig. 6.2), which reflects the high variation observed among different drives in that year (boar densities ranged from 0 to 304 per km^2 across the 15 areas surveyed). Due to the combined uncertainty surrounding density estimates of both species, the confidence intervals surrounding the estimates of the relative availability of wild boar (based on biomass density) within this two-species community were also wide and overlapped among years (Fig. 6.3a further below).

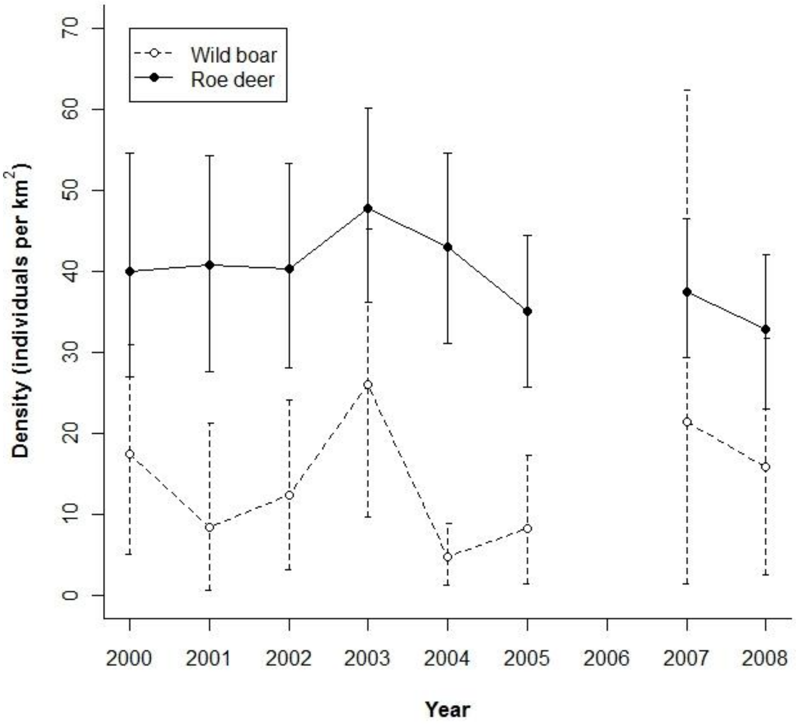

Figure 6.2: The densities of the two main wolf prey items, wild boar (open circles) and roe deer (solid circles), from drive counts conducted each Catenaia. Error bars represent bootstrapped 95% confidence intervals. Density estimates for the year 2006 were unavailable.

Wolf diet and relative use of wild boar

A total of 1,974 wolf scats were collected and analysed during the study. The diet of wolves in Catenaia was consistently dominated by the consumption of wild boar and roe deer, which together made up 95.2 ± 1.29% of the annual diet (Appendix 6, Table A6.3). Wild boar was the primary prey, being found in the majority of scats collected, and accounting for 61.5 ± 3.90% of biomass eaten. Roe deer, the second most prevalent prey species, accounted for 33.7 ± 3.61% of total prey biomass. Other prey, including livestock, represented only a very small proportion of the diet (Appendix 6, Table A6.3).

Although boar and roe deer consistently accounted for over 90% of biomass eaten, the percent of diet individually attributable to either species was variable across the nine year study period (Appendix 6, Table A6.3); this is reflected in the estimates of boar use by wolves (Fig. 6.3a). Boar use (mean over the entire period: 0.615 ± 0.0390; Fig. 6.3a) was generally higher than that of roe deer and, for five of the years analysed, the percent of wolf diet made up of wild boar was more than twice that of roe deer.

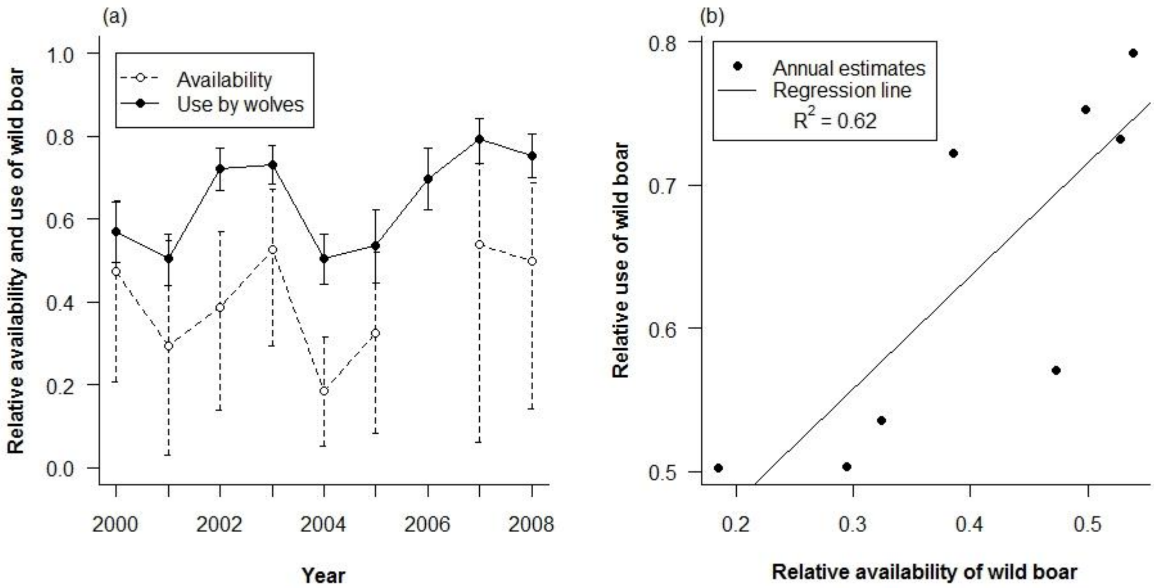

Figure 6.3: The relationship between the availability and use of boar (relative to ungulate community including wild boar and roe deer only). Panel (a) shows the relative availability (grey dashed line, open circles) and relative use (black solid line, solid circles) estimated annually from 2000 to 2008 (excluding 2006 in the case of availability, see text). Error bars represent bootstrapped 95% confidence intervals around estimates. Panel (b) shows the relationship between the relative availability and use of wild boar (observed values, solid circles) estimated using linear regression (black line, $y = 0.323 + 0.784x$, $R^2 = 0.621$, $P = 0.0124$).

Confidence intervals surrounding estimates of boar use were narrow in comparison to those calculated for boar availability (Fig. 6.3a), reflecting the large number of scats collected each year (> 140 scats each year compared to only 9-15 drives per year that were used to estimate availability).

Inter-annual fluctuations in boar use, the proportional biomass of wild boar in wolf diet relative to that of roe deer and wild boar combined, reflected changes in the proportional availability of wild boar as a prey item. Based on the regression of boar use as a function of availability, boar availability accounted for 62% of the variation in boar use across years ($\beta_{BA} = 0.784 \pm 0.2222$, $R^2 = 0.621$, $t_6 = 3.529$, $P = 0.012$; Fig. 6.3b). The years of comparably low boar use (2001, 2004, and 2005; Fig. 6.3a) coincided with years of low boar density, rather than years of high roe deer density (Fig 6.2).

Prey Selection

Estimates of Manly's selectivity index ranged between 0.60 and 0.82 across eight years with a mean of 0.73 ± 0.023 indicating a strong tendency for selection for boar and against roe deer by the wolves in Catenaia (Fig. 6.4, also Appendix 6, Table A6.4). Estimates of Manly's index indicated selection for boar ($\alpha_{Boar} > 0.5$) in five out of the eight years examined. This reflects the fact that boar use was generally high relative to its availability (Fig. 6.3a). The confidence intervals for the yearly estimates of Manly's index were wide, representing a high level of uncertainty due to sampling variation among scats and drive censuses. The overlap of confidence intervals among years cautions against the temptation to infer variation in selection for boar during the study period (Fig. 6.4).

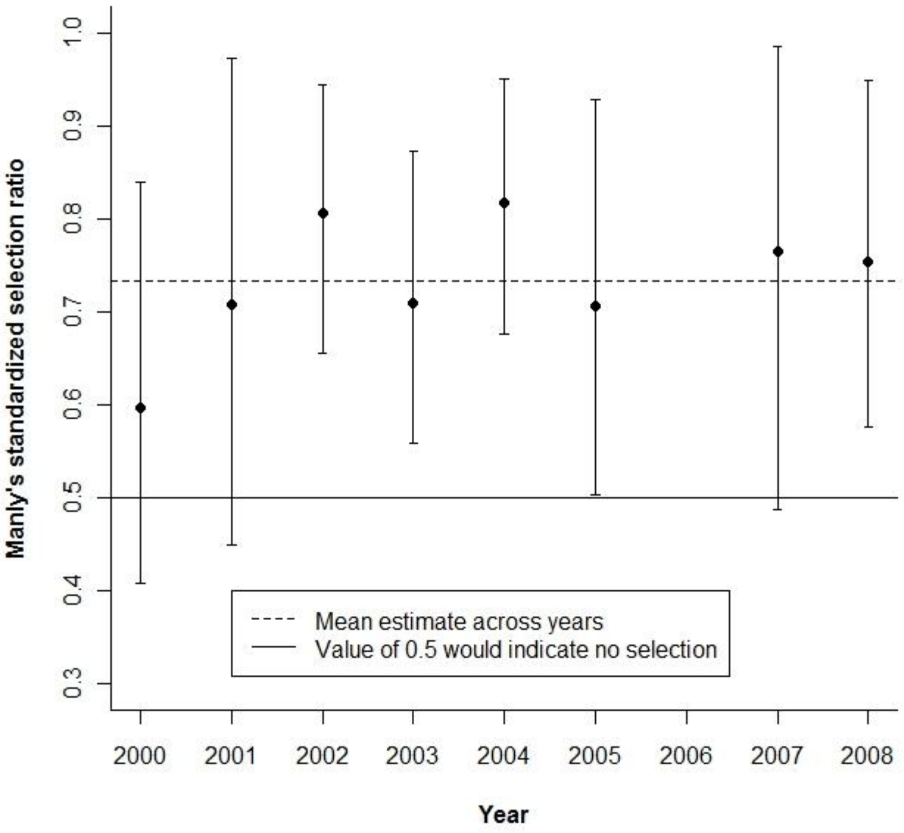

Figure 6.4: The uncertainty and inter-annual variation in the selection of wild boar (relative to that of roe deer) was examined. Manly's standardised selection ratio was calculated based on the relative availability and use of boar within the main two-prey community composed only of wild boar and roe deer. Error bars represent bootstrapped 95% confidence intervals. Values approximately equal to 0.5 (black line) indicate prey use in proportion to availability in a two-prey system while selection for and against wild boar are indicated by higher and lower values respectively. The mean value of Manly's selection ratio for boar during the study period was 0.73 ± 0.023 (dashed line).

Discussion

In Catenaia, the consumption of wild boar dominated wolf diet and the use of boar as prey (relative to the use of roe deer) was strongly related to the relative availability of wild boar across years. This finding implies that wolf predation on a particular prey species can be affected by changes in the community composition which are not determined by the abundance of one prey item alone. Wolves in the area selected wild boar over roe deer as prey and there is little evidence of variation in the strength of this selection among years. Had the uncertainty inherent in the data not been recognised, I may have erroneously interpreted variation in the estimates of prey selection as indicative of differential selection among years. The length of the study combined with the large sample size of scats (1,974 over the nine-year study period) allowed not only the examination of inter-annual variation in wolf predation, but also the consideration of the potential impacts of sampling error on results. The amalgamation of uncertainty from multiple sources (i.e. the estimation of both prey availability and use) means that the uncertainty surrounding final estimates of prey selection is very large. Accounting for this uncertainty limits the conclusions that can be made but ensures that the interpretation of inter-annual variability in prey selection by wolves in Catenaia is fully supported by the data.

Wolf diet in Alpe di Catenaia

As in other areas with an abundance of wild prey (Mattioli et al. 1995, Okarma 1995, Meriggi et al. 1996, Jedrzejewski et al. 2000, Meriggi et al. 2011), the wolves inhabiting the Catenaia site subsist mainly on wild ungulates, with a very low frequency of livestock predation. It is the selection of prey species within the wild ungulate community that appears somewhat unusual. In contrast to wolves in other parts of Europe which often avoid boar as prey (Okarma 1995), wolves in Catenaia appear to rely heavily on wild boar. Despite the wide confidence intervals surrounding annual estimates of boar selection, there is evidence that boar were selected (over roe deer) in five of the eight years examined. Boar made up the majority of biomass eaten throughout most of the study period. While it is not possible to be certain of a causal relationship, the strength of boar availability as a predictor of boar use suggests that wolf diet was tracking the fluctuations in boar densities. Roe deer, while an important prey item, usually made up a smaller portion of wolf diet. The percentage biomass of roe deer in wolf diet appeared to peak when boar densities were low, not when roe deer densities were highest. In Catenaia, the relatively stable roe deer population may represent an alternative prey source which suffers higher predation when wild boar densities decline. That the extent of wolf predation on roe deer can fluctuate widely, even when roe deer are relatively stable, underlines the importance of taking a community perspective to investigate and predict predation impacts on any given species (Abrams and Ginzburg 2000, Garrott et al. 2007). Integrating other species into simulations of population dynamics, such as those presented in Ch. 5, could lead to modifications of the impacts of predators, and therefore the trajectory of population density over time.

The strength of selection for boar in Catenaia raises the question of why similar selectivity is not seen throughout Europe. There could be two reasons for this. Firstly, many European ungulate communities include red deer, which appear to be a favoured prey of wolves in many sites (reviewed by Okarma 1995). The scarcity of red deer (completely absent until 2007) in Catenaia could lead to stronger selection for wild boar and could drive the dietary response of wolves to changes in boar availability observed in this study. Secondly, wild boar in Mediterranean areas are relatively small; for example, adult boar in Catenaia, weighed 66.5 ± 0.48 kg (based on mass data for 1,286 adult boar carcasses collated by the Province of Arezzo). In more northern areas of Europe, where adult male boar can exceed 300 kg in size (Smietana and Klimek 1993), their active defence behaviour can, reportedly, make them dangerous prey for wolves (Jedrzejewski et al. 1992). This makes it especially difficult to infer patterns of wolf selection in the northern sites where wild boar have newly colonized (such as the Swedish sites that are examined earlier in this thesis; see Ch. 5). This small size of adults in Catenaia may make boar less threatening as prey and, in combination with their large litter sizes (often exceeding 5 piglets per litter; Bywater et al. 2010) and grouping behaviour, may encourage wolves to select boar over roe deer (Mattioli et al. 1995, Meriggi et al. 1996, Mattioli et al. 2011).

The importance of intra-annual uncertainty when considering variation in prey selection

Variation in wolf predation patterns (e.g. disparate prey selection among sites with similar prey communities) may reflect underlying differences in the ecology of distinct sites or a failure to assess accurately the uncertainty inherent in estimates of wolf feeding habits. The estimates of prey selection indices presented here had very wide confidence intervals, suggesting high levels of uncertainty in the data on prey use (from wolf scats) and, in particular, the data on prey availability (from drive censuses). Sampling error is difficult to avoid and is present in all datasets. Uncertainty in this study arose particularly from the estimation of annual prey densities, because of the low number of “density samples” (drive censuses from different areas of the study site) in each year. This is a common situation in European ungulate research and many datasets will incorporate similar levels of uncertainty in their density estimates.

Without considering uncertainty, these results would suggest substantial variation among years in the strength of selection for boar by the wolves in Catenaia. However, when the observed variation is considered in the context of within-year uncertainty it is not possible to say with any confidence that prey selection in the site differed from one year to the next. This finding also compels caution when comparing selectivity estimates between different sites. For example, comparing the point estimates of Manly's α from this study to those observed in other areas could suggest geographic variation in selection (especially if the studies being compared were of short duration or if results had been pooled across years). While such variation may very well exist, in some cases, reported differences in wolf predatory habits among sites (or time periods within sites) might disappear when uncertainty in estimated metrics (such as selection indices) is accounted for.

Caveats and considerations for future research

The findings presented here should be considered in light of several important caveats. The first two relate to the fact that only one census of prey was possible each year. While the prey selection observed in this study could arise for the reasons described above (relating to community composition and boar body size), it could also be partially driven by variation in prey vulnerability due to temporal fluctuations in population age structure. In particular, because wild boar can produce two litters within a single year and boar piglets are likely to be more vulnerable as prey, there is a high potential for both inter- and intra-annual variation in the overall vulnerability of wild boar (Bieber and Ruf 2005). Estimating the age structure of prey populations multiple times each year would help isolate the influence of changing prey vulnerability on selection by wolves. Additionally, seasonal movement of prey species could affect their relative availability, and such intra-annual variation will not be reflected by annual drive censuses. However, telemetry studies at the site suggest that the mean home range areas (Minimum Convex Polygons) of the prey species (roe deer: 4.0 ± 4.43 km^2, n = 162 home ranges, 69 individuals; wild boar: 7.5 ± 9.50 km^2, n = 58 home ranges, 49 individuals; unpublished data, Apollonio 2012) were substantially smaller than the study site (120 km^2), suggesting that such intra-annual migration was unlikely to be a major factor.

Three further caveats suggest general lessons for studies of dietary selectivity. Firstly, it is not known how much of the prey consumption that was observed could be due to scavenging upon carcasses rather than direct predation. In the future, closer observation of individual wolves, using radio-telemetry, may provide estimates of scavenging frequency and allow researchers to adjust estimates of predation accordingly. Secondly, all density estimation methods incorporate some degree of error due to unobserved individuals and the drive censuses used in this study are no exception. McCullough (1979) estimated that errors in drive census estimates can be as large as 20-30% of the true population size. Estimates of wild boar densities are particularly challenging due to their wide-ranging behaviour and aggregated distributions (Barret 1982). Capture-mark-recapture estimates might provide more accuracy but can be more resource intensive (in terms of time, equipment and labour). When capture-mark-recapture estimates are not possible, researchers can form more robust conclusions from studies requiring density estimates by acknowledging the uncertainties associated with chosen methods and, when possible, by comparing estimates based on a variety of methods (e.g. pellet counts, camera surveys etc.) simultaneously. Finally, on a related note, the spring density estimates took place before the birth of new roe deer fawns but after the initial pulse of boar births. This means that the relative availability of boar within this two-prey system might be overestimated, resulting in an underestimation of the strength of selection for boar as prey. The conservative estimates of boar selection presented here would most likely be strengthened if it was possible to use post-reproductive roe deer densities. In the future, this bias could be avoided by either using estimates of roe deer reproduction to estimate post-reproductive densities or by surveying ungulate densities later in the spring.

Conclusion

Wild boar are the primary prey of wolves in Catenaia, Italy. For the wolves in this area, roe deer represent an alternative prey source which increases in dietary importance when boar densities decline. While accounting for sampling uncertainty in the data used, these analyses show that boar were significantly selected for during the majority of the years studied. Boar use throughout the study period was strongly related to the relative availability of wild boar within this predominantly two-prey community, a finding which suggests a dietary response by wolves to the availability of wild boar. The high natural variability of wild boar populations (Bieber and Ruf 2005, Sabrina et al. 2009) thus could have important ramifications for predator impacts on roe deer in sites where these two species co-exist.

These findings demonstrate that failing to account for uncertainty when interpreting inter-annual variation in studies of predator diet might lead to conclusions that are not fully supported by the data. In addition to presenting multi-year datasets without pooling data across years, when possible, future studies of prey selection should strive to account for possible sources of uncertainty due to sampling procedures. While the comparison of a predator’s dietary composition and prey selection across years and sites can yield important information about large-scale patterns of predation, such analyses often incorporate uncertainty from multiple sources. Caution must be taken to describe such uncertainty before drawing ecological conclusions, so that the nature of complex predator-prey relationships is properly represented.

Chapter 7 – General discussion

Introduction

In this thesis, I examine the potential impacts of climate change on the population dynamics of a temperate ungulate, the roe deer (*Capreolus capreolus*). The ecological position of roe deer as an herbivore and a prey species meant that explorations of the effects of vegetation (a food resource) and predation (a source of mortality) on roe deer were instrumental to an understanding of its population dynamics. To date, many studies of climatic effects on wildlife have overlooked trophic interactions in favour of treating climate-related metrics (e.g. temperature and precipitation) as direct predictors of variation in species range extent, phenology, vital rates or other measures of biological performance such as body mass (Post and Stenseth 1999, Pearson and Dawson 2003, Van der Putten et al. 2010, Walther 2010). Additionally, many projections of species' responses to climate change have omitted population dynamics altogether (but see Huntley et al. 2010, Conlisk et al. 2013 and Ch. 1 for a growing list of exceptions).

In contrast to the vast majority of prior work on species' responses to climate change, the work presented in this thesis explicitly includes trophic interactions and mechanistically models population growth in response to both climatic and non-climatic drivers. These analyses suggest that this approach can yield substantial insight into the complex manner in which climate impacts wildlife populations. Consideration of population size instead of just whether a species is present or absent allows me to identify effects of climate that are unlikely to have been indicated by a more traditional "species distribution modelling" approach. By considering drivers beyond those that are strictly climatic, I shed light on the pathways by which climate impacts population dynamics (e.g. by modifying vegetation productivity), and suggest management options to ameliorate these impacts. However, my analyses also identified some weaknesses in this approach and gaps in the data used. These factors resulted in a large amount of uncertainty that propagated across the projections of vegetation and vital rates to affect projections of overall population growth substantially. Given the effort spent collecting data on the study populations (> 20 years of monitoring in the two Swedish sites), it is disheartening to realise that deficiencies in the understanding of roe deer ecology still limit the confidence with which changes in these population can be projected. Long-term datasets on many other wildlife populations seem likely to present similar challenges. It seems important, therefore, to explore the advances and limitations associated with analysing such datasets. In the following text I first synthesise the ecological implications of the findings of this thesis. I then discuss the values of a mechanistic approach that includes population dynamics and trophic interactions for describing a species' potential response to climate change and discuss the constraints for such approaches contributing to long-term management policies.

Synthesis of findings and implications

Collectively, the findings of this thesis have implications for: 1) the impacts of climate change on the ecological communities studied; 2) future wildlife management in these communities; and 3) more broadly, understanding the role of climate in population ecology. Each of these topics is discussed below.

Climate change driven modifications of primary productivity, explored in Chapter 2, are likely to affect roe deer population dynamics at the study sites (Bogesund, Grimsö and Catenaia; Ch. 3-5). Describing such impacts on roe deer dynamics were the primary focus of this thesis; however, it is worth noting that the implications of changes in vegetation production are potentially very far-reaching. Altered primary productivity will probably influence all herbivores, with knock-on implications for species they interact with (e.g. predators). Roe deer provide a good example of this: as prey, roe deer provide a food resource for several predators (Ch. 6, Aanes et al. 1998, Basille et al. 2009) and as a consumer of vegetation, they affect plant populations (Cederlund et al. 1998) and interact with other herbivores (Focardi et al. 2006, Ferretti et al. 2008). Therefore, the projected increases in roe deer population growth at Bogesund (Ch. 5), could affect the entire community. The simulated increases were due to climate-driven increases in productivity (Ch. 2) which, in turn, caused increases in roe deer survival (Ch. 3 and 5). This pathway is biologically realistic and supports previous predictions of increases in net primary productivity in northern Europe (Slayback et al. 2003, Fronzek and Carter 2007), which could be accompanied by increases in roe deer abundance and range extent (Melis et al. 2009, Apollonio et al. 2010). Climate change could realistically have similar effects on roe deer, not only in Grimsö (where vegetation productivity also increased survival; Ch. 2), but potentially across northern European sites where vegetation production may increase. Inferences for Catenaia are more tentative not only because of the poor performance of the vegetation models at that site, but also because, contrary to the model predictions in Chapter 2, previous studies have suggested that areas of southern Europe may experience decreases in net primary productivity (Boisvenue and Running 2006, Parmiggiani et al. 2006, Penuelas et al. 2007). Furthermore, the data needed to model roe deer population dynamics at this site were not available.

If climate change does increase roe deer population growth, this will have implications for how sites are managed. An over-abundance of roe deer could cause crop damage, reduced tree recruitment in forests and increased traffic accidents (McShea et al. 1997, Cederlund et al. 1998). Harvest and natural predation could offer two potential approaches to counteracting climate-driven increases in roe deer population growth (Ch. 3-5). The predictive models presented here can be used to set management goals, estimate the harvest (and predation pressure) necessary to achieve a desired population density (Ch. 5), and thus guide adaptive management actions at Bogesund (Walters 1986, Mills 2007). However, the analyses of predation effects at the Swedish sites were relatively simplistic. The examination of prey selection by wolves in Catenaia (Ch. 6) highlights the complexity of interactions between prey and their predators. In Catenaia, the use of roe deer by wolves was related to the availability of an alternative prey species, wild boar. Therefore, predation on one species, like roe deer, can be dependent on the wider prey community. This has implications for roe deer mortality at sites like Grimsö where a variety of predators and prey species co-exist. The arrival of wolves (2003) and wild boar (2006) adds to the complexity of the mammal community at Grimsö, which is now inhabited by three predators of roe deer and three ungulate prey species (not to mention non-ungulate prey such as hares, *Lepus* spp. another common prey of lynx; Jedrzejewski et al. 1999, Sunde et al. 2000, Sidorovich 2006). Prey use by predators is affected by multiple factors (see Ch. 6 for a discussion), which were not considered in the simulations presented in Chapter 5. Therefore, while predation might aid managers by counteracting the effects of climate change on roe deer population growth, a greater understanding of predator-prey interactions is necessary before predation can be considered a management tool in this system.

More broadly, the results of this thesis highlight that climatic effects on wildlife populations do not take place inside a vacuum. They are inextricable from the context of the biotic systems in which they operate. Trophic interactions (both bottom-up and top-down), which may traditionally have been considered non-climatic drivers of population dynamics, accounted for more than half of the effects in the vital rate models developed in this study (considering the selected best models only; Ch. 3 and Ch. 4). It is interesting to note that the relative importance of trophic interactions documented in Chapters 3-5 is broadly consistent with previous assertions that bottom-up factors are likely to have a primary role in determining population growth while top-down factors modify these bottom-up influences on populations (Power 1992, Sinclair and Krebs 2002). Many of the effects of climate on wildlife populations appear likely to take place via bottom-up trophic interactions. This is evidenced by the relationship between climate and vegetation productivity (Ch. 2, also see Nemani et al. 2003, Slayback et al. 2003, Fronzek and Carter 2007) and by the prevalence of vegetation effects in the survival models (Ch. 3). Climate is also likely to have effects via top-down interactions (Cederlund and Lindström 1983, Okarma 1995, Post et al. 1999, Nilsen et al. 2009b). Although I did not have the opportunity to thoroughly explore the potential for top-down impacts of climate in this study, I did document top-down effects of predation and harvest which could influence the net response of populations to climate (Ch. 5; see also Wilmers et al. 2007a). While climate will drive ecological change over the next century, many of its impacts will be mediated by tropic interactions. Therefore, climatic impacts and trophic interactions are best understood through simultaneous examination.

Advantages of modelling population dynamics in response to climate change

Exploiting long-term datasets on roe deer and species they interact with allowed temporal changes in roe deer populations to be modelled mechanistically in response to a variety of climatic and non-climatic factors, including trophic interactions. This led to at least four unique insights regarding the ecology and future management of the study sites that would have been difficult to gain through a more traditional “species distribution modelling” approach. Firstly, the projections presented in Chapter 5 indicated that changes in roe deer population growth and abundance are likely. Generally species distribution models have been used to project whether or not areas will have “suitable” climate to support a species’ presence in the future; relative abundance, given presence, is not considered further. Because changes in abundance are likely to happen more quickly than changes in geographic range, such “presence-absence” approaches are likely to underestimate climate change impacts (Shoo et al. 2005). As discussed in Chapter 1, some species distribution models now incorporate population dynamics (e.g. Keith et al. 2008). Knowledge gained through the analyses presented in this thesis could support the development of such models for roe deer and potentially other species.

Secondly, the mechanistic approach used to model population dynamics in this thesis links the population response of roe deer to the effects of drivers of roe deer vital rates (Ch. 3 and 4). This suggests possible avenues for the development of management plans targeted to counteract climate-related changes; using increased harvest to counterbalance increased survival rates due to climate change (Ch. 5) would be an example of this. It is worth noting that if I had omitted non-climatic factors, such as harvest, from the modelling process, the preliminary assessment of management possibilities in Ch. 5 would not have been supported.

Thirdly, by evaluating the uncertainty in simulations and linking it to specific vital rates, I was able to highlight priorities for future research (Ch. 5). Further data on the survival of roe deer (of all ages) could improve the precision, and perhaps the accuracy of simulations of roe deer population growth in response to climate change. There are more than 25 years before the largest changes in roe deer population growth are projected to occur (after 2040; Ch. 5, Fig. 5.4). This provides time for targeted data collection to fill the gaps identified and inform future population models.

Finally, by considering non-climatic variables and explicitly incorporating the indirect pathways by which climatic effects can occur, the mechanistic approach used here is likely to provide more realistic projections and assessments of uncertainty than approaches which consider only the direct effects of climate. For example, the exclusion of vegetation or lynx predation from the survival models would have meant a decrease in model performance (i.e. higher AIC and potentially lower predictive ability; Ch. 2). The inclusion of non-climatic variables also allowed for their statistical control when estimating the effects of climate. Furthermore, treating indirect pathways as direct relationships may underestimate projection uncertainty. This is especially true when extrapolating to novel conditions (as expected with climate change) because correlations between the ultimate (e.g. climate) and proximate (e.g. vegetation) drivers of population dynamics may not remain the same. In this thesis, I estimated both the relationship between climate and vegetation (Ch. 2) and between vegetation and survival (Ch. 3). I then considered the uncertainty associated with both relationships in projections (Ch. 5). Had I omitted vegetation and estimated this relationship between climate and survival in one step, the resulting projections might have misrepresented the total uncertainty. For these reasons, several authors have stressed the importance of a more mechanistic approach that incorporates climatic and non-climatic drivers in projections of climate change impacts (Berteaux et al. 2006, Conlisk et al. 2012, Evans 2012).

Limitations of research contributions to future management

The insights into roe deer dynamics gained in this thesis provide some general guidance regarding the future management of roe deer under climate change (see discussion above). However, the simulations presented in Chapter 5 are still a long way from providing the robust understanding of roe deer population growth necessary to support firm plans for the management of this species. The limitations of the analyses presented here and of their use for management fall into three general categories: 1) the inability to achieve the statistical complexity that is representative of roe deer ecology, 2) the uncertainty regarding future conditions and the estimated response of roe deer populations, and 3) the site-specificity of these analyses and their results. Each of these subjects is discussed below.

Ecology, defined as “the scientific study of the interactions that determine the distribution and abundance of organisms” (Krebs 1972), is complex. Therefore, despite an emphasis on the desirability of parsimonious models, a realistic description of a species’ ecology is likely to involve substantial complexity and many predictors (Evans 2012). This is the case with roe deer population dynamics. Despite the apparent complexity of the simulations presented in Chapter 5 (involving at least 9 environmental predictors), these simulations represent a simplified description of roe deer ecology. The complexity of the models of roe deer vital rates, developed in Ch. 3 and Chapter 4, was limited by data availability. In order to avoid over-fitting, no more than two environmental predictors were allowed in the models. This meant that interactions among predictors (such as density and vegetation, which might have indicated food availability) were not always considered (c.f. ovulation models in Ch. 4).

Moreover, ecological processes with potential to impact roe deer population dynamics (such as implantation rates, Ch. 4, and predator preferences, Ch. 6) could not be modelled at all due to a lack of data. If more data were available and these omissions could be addressed, then the ability of the simulations to reproduce observed patterns of population change might be improved and the projections of roe deer population growth given climate change could be considered more reliable.

The projections of increased vegetation and roe deer population growth presented in this thesis are surrounded by considerable uncertainty (see Ch. 2 and Ch. 5), which makes it difficult for managers to rely on these projections and develop definite strategies for the future. Uncertainty is a pervasive component of ecological research and some uncertainty is unavoidable when the goal is to project into the future (Dovers et al. 1996, Giorgi 2005). Assuming it is the job of ecologists to enable future management efforts, management plans must be made in the face of ecological uncertainty (Dovers et al. 1996). Uncertainty surrounding the impacts of climate change generally comes from either a) statistical uncertainty surrounding the parameterisation of the models used in projections or b) ignorance of the future conditions used as inputs in those models. In the projections of roe deer dynamics presented in Chapter 5, I considered uncertainty in the estimation of parameters in the component models. I also considered uncertainty in greenhouse gas emissions. Nevertheless, other sources of uncertainty were not quantified. Projections were based on one model of each process, when other models suggesting alternative mechanisms might lead to very different results. Model averaging techniques (including the multi-model ensembles often used in research on climate change; Araujo and New 2007, Thuiller et al. 2009), could be used to quantify this uncertainty (Burnham and Anderson 2002, Whittingham et al. 2006). Additionally, the future trajectories of variables (e.g. climate, predator abundance, land use) used as drivers in models are uncertain. The consideration of numerous scenarios incorporating realistic variation in all these drivers (i.e. only alternative emission scenarios were considered in Ch. 5) would be a useful route for future research. Finally, variation in processes such as embryo implantation and prey selection could not be incorporated here, but could magnify the overall uncertainty regarding future roe deer dynamics. Addressing these gaps and exposing associated uncertainties will enable the development of policies that are robust to a wider range of contingencies.

The models and projections of roe deer dynamics that are presented in this thesis are site-specific. For the managers at Bogesund, Grimsö and Catenaia, this site-specificity could be considered an advantage; these analyses are customised to their ecological systems and the results are, therefore, directly applicable (Evans 2012). However, in the context of projecting the impacts of global climate change on roe deer as a species, this could be considered a substantial constraint on the value of this research as a management tool. There are a couple of mitigating factors that should be considered before making this judgment. Firstly, small-scale management plans seem more likely to be implemented than many large-scale initiatives. Wildlife managers generally operate on a site-specific level (Mills 2007) and the challenges involved in coordinating management across multinational areas are considerable (Apollonio et al. 2010). Indeed, animal populations from the same habitat "patch" are often managed very differently on two sides of a border (e.g. the Bialowieza Primeval Forest has been managed differently in Poland and Belarus; Okarma 1995, Jedrzejewska et al. 1997, Jedrzejewska et al. 2005). Therefore, despite grand schemes for conserving biodiversity at large geographic scales (e.g. regional, continental or global; Carroll et al. 2010, Fuller et al. 2010, Dawson et al. 2011, Bagchi et al. 2013), much of the management of ecological systems seems likely to be completed at the small-scale where site-specific analyses are useful. Secondly, the existence of models of species responses to climate change at a large geographic scale provides little guarantee that results will apply to the sites managers are interested in (Evans 2012). In fact, the differences in model selection among Bogesund, Grimsö and Catenaia (Ch. 2-4), suggest that the drivers of vegetation productivity and animal vital rates can vary a great deal from one site to the next (see also Grotan et al. 2008). Future species distribution models might incorporate such spatial variation in the drivers of population dynamics. In the meantime, the modelling framework used here could be applied in other sites with long-term datasets.

Conclusion

With these analyses, I have established the importance of considering trophic interactions when projecting the response of a widespread herbivore to climate change. I used long-term data on managed roe deer populations to model roe deer population dynamics mechanistically as a response to changes in climate, vegetation resources, predation and human management actions. This mechanistic approach provided unique insights regarding the management of roe deer under climate change and, more broadly, concerning the role of climate as just one of many interacting factors driving wildlife population dynamics. In particular, I provided evidence that climate change could indirectly cause increases in roe deer population growth by driving increases in vegetation production. I also identified combinations of predation pressure and human harvest that might prevent that growth. Moreover, I have demonstrated how an analysis of the uncertainty surrounding projected population growth can highlight gaps in the understanding of a population's ecology and provide guidance for future research priorities. While there are limitations to these results, which constrain their current utility for management planning, many of these limitations are common to all ecological and climate change research. The approach used here would not have been possible without the long-term datasets collected on managed ungulate populations. Collectively these analyses demonstrate the value of these datasets and of explicitly considering a species' population dynamics when modelling the ecological impacts of climate change.

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Appendix 1 – Chapter 1 supplementary material

Text A1.1: Literature reviewed on European roe deer vital rates (see Table A1.1)

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Table A1.1: Vital rates of roe deer in European populations as reported[a] in published literature (a non-exhaustive list).

Source	Study location	Years of study	Deer in study	Age group[b]	Female survival (SE) [c]	Male survival (SE) [c]	Per female repro. rate [d]	% females breeding
Kjellander & Nordström (2003)	Grimsö, Sweden	28	55 ± 26.8 per year (mean ± SD)				0.81_{Fa}	
Jarnemo & Liberg (2005)	Ekenäs, Sweden		216	Fawn (<2 months)	0.47 (0.083)			
Panzacchi et al. (2008) (also in Nilsen et al. 2009)	Oster-dalen, Norway	3	62	Fawn				
				Sub.	0.5			
				Adult	0.68			
Panzacchi et al. (2008) & Ratikainen et al. 2007 (2007) (also in Nilsen et al. 2009)	Akershus / Ostfold, Norway	4	116	Fawn				
				Yearling	0.49			
				Adult	0.7			
Focardi et al. (2002)	Collinaccia, Tredozio, Italy	4	104	Fawn	0.45			
				Adult (> 1 year)	0.90		1.25_{Em}	
	Monti, Tredozio, Italy			Fawn	0.33			
				Adult (> 1 year)	0.94		1.61_{Em}	
Borg (1970)	Through-out Sweden	21	34	Adult (2 years)			2.38_{Ov}/ 2.24_{Em}	
			82	Adult (3-5 years)			2.54_{Ov}/ 2.39_{Em}	
			35	Adult (6-7 years)			2.54_{Ov}/ 2.26_{Em}	
			28	Sen. (> 8 years)			2.54_{Ov}/ 2_{Em}	
Strand-gaard (1972)	Kalø, Denmark	1	10	Adult (> 2 years, incl. two 2 year olds)			2.2_{Ov} / 2.1_{Em}	
	Løven-holm, Denmark	1	10	Adult (> 1 year)			1.8_{Ov} / 1.7_{Em}	
	Borris, Denmark	1	4	Adult (> 1 year)			2_{Ov}/ 2_{Em}	
Cobben et al. (2009)	Storfosna Norway	3	352	Fawn (0 - 2 months)	0.81	0.83		
				Fawn (3 – 12 months)	0.99	0.99		
				Adult (> 1 year)	0.99	0.99		
Andersen & Linnell (1998)		4	321	Fawns (< 2 months)	0.82[c]			

Andersen & Linnell (2000)		3	34	Adult (2 years)			2.13_{Fa}	0.81
			79	Adult (>2 years)			2.32_{Fa}	0.88
Heurich et al. (2012)	Bavarian Forest National Park, Germany	9	187	All ages	0.8 (0.041)			
Gaillard et al. (1997)	Chizé	7	7-22 per year	Fawns (<8 months)	0.60 (0.065)			
	Trois Fontaines	7	20-50 per year	Fawns (<8 months)	0.68 (0.064)			
Gaillard et al. (1992)	Chizé, France	4	47 yearlings / 315 adults	Sub. (20 months)				0.872
				Adult (> 20 months)				0.981
Gaillard et al. (1993)		11	125 males / 132 females	Fawn and Sub. (8 – 20 months)	0.88 (0.038)	0.83 (0.059)		
				Adult (20 months to 7 years)	0.93 (0.017)	0.82 (0.030)		
				Sen. (> 7 years)	0.71 (0.078)	0.42 (0.164)		
	Trois Fontaines	13	155 males / 157 females	Fawn and Sub. (8 - 20 months)	0.77 (0.043)	0.74 (0.053)		
				Adult (20 months to 7 years)	0.97 (0.014)	0.86 (0.026)		
				Sen. (> 7 years)	0.73 (0.080)	0.83 (0.011)		
Hewison (1996) (also in Andersen et al. 1998)	UK (across 15 populations)	6 to 21 years at each site	> 5000 deer across all sites	Fawn				0.006
				Sub.				0.659
				Adult			1.7_{Em},	0.808
Fruzinkski and Labudzki (1982)	Poland	5	71	Fawn	0.63			
				Sub.	0.7		1.40_{Em}	0.714
				Adult (survival only ages 2 to 7)	0.72		1.9_{Em}	0.876
Kurt (1968) (in Andersen et al. 1998)	Switzerland	Unknown, original sources non-English		Adult			1.69_{Em}	

Stubbe and Passarge (1979) (in Andersen et al. 1998)	Germany		Adult			1.7_{Em}	
Szederjei (1967) (in Andersen et al. 1998)	Hungary		Adult			1.55_{Em}	

[a] To condense the results of multi-year studies when summarised values were not presented in the published text, rates were averaged across sampling periods.

[b] Unless otherwise stated the fawns are < 1 year old, subadults (abbreviated Sub.) are 1 year olds and adults are individuals 2 years old or greater. Senescents are abbreviated “Sen.”.

[c] Note that survival estimation methods varies among studies. In the case of Andersen and Linnell (1998), fawn survival rates include the deaths of stillborn fawns.

[d] Subscript denotes method of estimation for litter size. A subscript of “Fa” indicates counts of fawns per female (typically over early summer), “Em” indicates counts of embryos in utero, and “Ov” indicates counts of corpora lutea in ovaries (a measure of ovulation). Counts of embryos and corpora lutea were typically completed per reproductive female (i.e. zeros from non-reproductive females appear to have been excluded).

Appendix 2 – Chapter 2 supplementary material

Table A2.1: Focal site climate conditions: observed (1982-2006) and projected (2001-2100) under three IPCC climate change scenarios

		Obs. mean	A1FI scenario mean		A2 scenario mean		B1 scenario mean	
Focal site	Climate metric	1982-2006	2001-2050	2051-2100	2001-2050	2051-2100	2001-2050	2051-2100
Global (all sites)	CO_2 (ppm)	359.6	442.2	752.0	434.9	663.0	422.9	521.0
Catenaia	Tmp (°C)	9.7	11.2	15.3	11.0	13.9	11.0	12.6
	Pre (mm)	700.9	749.2	666.2	750.1	680.0	733.8	680.4
	Gdd (°C)	2048.6	2541.5	3933.6	2463.4	3461.9	2465.8	2999.8
	Dry (mm)	-4.4	-5.0	-24.4	-4.2	-19.5	-6.3	-16.7
Grimsö	Tmp	4.7	5.8	9.0	5.7	8.3	5.6	7.0
	Pre	688.1	701.0	761.9	698.9	746.1	706.0	738.6
	Gdd	1149.9	1378.6	2071.5	1361.2	1891.5	1337.1	1585.8
	Dry	14.4	13.4	11.6	13.4	11.9	13.9	13.7
Bogesund	Tmp	6.7	7.9	11.5	7.8	10.7	7.9	9.6
	Pre	450.3	469.5	503.7	467.0	491.4	478.4	503.0
	Gdd	1468.8	1777.8	2771.8	1758.3	2544.5	1800.5	2254.6
	Dry	-9.6	-10.0	-15.0	-10.0	-14.2	-9.8	-11.8

[a] See Ch. 2 text and Table 2.1 for variable definitions, data sources, and calculation methods. All data involved were originally acquired on a monthly time-scale. Monthly measures of temperature and dryness were averaged across months and then years to create values shown. Monthly measures of precipitation and growing degree days were summed across months (within years) and then annual sums were averaged to create displayed period means.

Table A2.2: AIC comparison of multi-site yearly models of annual INDVI

Multi-site yearly model of INDVI [a]	Predictors	*K*	Δ AIC	ω_i
Reduced seasonal Tmp and Pre	Spring Tmp, Spring Pre, Summer Tmp * Summer Pre, CO_2, Sea distance, Site ID	11	0	1
Miami (Leith 1974)	Miami Index, CO_2, Sea distance, Site ID	7	34.4	0
Annual Tmp and Pre	Tmp * Pre, CO_2, Sea distance, Site ID	9	37.7	0
Annual bioclimatic	Gdd * Dry, CO_2, Sea distance, Site ID	9	47.9	0
Reduced seasonal bioclimatic	Spring Gdd, Spring Dry, Summer Gdd * Summer Dry, CO_2, Sea Distance, Site ID	11	55.1	0
Full seasonal Tmp and Pre	Spring Tmp * Spring Pre, Summer Tmp * Summer Pre, Autumn Tmp * Autumn Pre, CO_2, Sea distance, Site ID	15	65.2	0
CO_2 control	CO_2, Sea distance, Site ID	6	68.8	0
Full seasonal bioclimatic	Spring Gdd * Spring Dry, Summer Gdd * Summer Dry, Autumn Gdd * Autumn Dry, CO_2, Sea distance, Site ID	15	122.2	0
Null	Site ID (intercept only)	4	268.3	0
Spatial control	Sea distance, Site ID	5	270.6	0

[a] Model fit and predictive ability is addressed in the Results section of the text and also in Figures 2.2 and 2.3. Annual INDVI data from 103 sites (3 focal sites plus 100 random sites) over 25 years (from 1982-2006) was modelled as response to temporal and geographic predictors. See Ch.2 text and Table 2.1 for variable definitions and calculation methods. Sea distance was included in models in order to control for the distance of sites to the large bodies of water. Site ID was included as random effect in all models including the null model. In addition to the predictors listed, all models included one parameter for the intercept, one for the residual deviance (variance) and one representing temporal auto-regression (Phi).

Table A2.3: Comparison of observed INDVI (1982-2006) and INDVI projections (2001-2100) across focal sites, IPCC climate change scenarios and models

		Observed mean INDVI	Mean INDVI projected with climate change [a]					
			A1FI scenario		A2 scenario		B1 scenario	
Focal site	Model [b]	1982-2006	2001-2050	2051-2100	2001-2050	2051-2100	2001-2050	2051-2100
Catenaia	Yearly with CO_2	14.23	15.26	18.44	15.18	17.66	15.02	16.13
	Yearly excl. CO_2		14.32	14.42	14.32	14.42	14.30	14.32
	Monthly		15.87	20.43	15.75	19.46	15.51	17.32
Bogesund	Yearly with CO_2	10.00	11.06	15.07	10.96	13.99	10.81	12.15
	Yearly excl. CO_2		10.05	10.33	10.05	10.29	10.07	10.22
	Monthly		10.20	10.91	10.18	10.77	10.20	10.54
Grimsö	Yearly with CO_2	12.60	13.70	17.46	13.61	16.52	13.45	14.80
	Yearly excl. CO_2		12.68	13.04	12.67	12.98	12.67	12.83
	Monthly		12.90	13.68	12.88	13.52	12.87	13.20

[a] Annual INDVI was projected under three of the IPCC climate change scenarios (A1FI, A2, and B1, see text for more detail) for each of the focal sites using three different models. The 21st Century was broken into two different sub-periods: 2001-2050 and 2051-2100.

[b] The best AIC multi-site yearly model included global CO_2 concentrations, and seasonal temperature and precipitation conditions (from the spring and summer) as predictors of INDVI (see Ch. 2 text and Table A2.2 for details). Using this yearly model, projections were created with (the “Yearly with CO_2” model) and without the effect of CO_2 (the “Yearly excl. CO_2” model). The model used to create the projections excluding CO_2 was generated by refitting the best yearly model without using CO_2 as a predictor (but including the other selected predictors). Finally projections were created using the best AIC single-site “Monthly” model selected for each focal site (see Ch. 2 text and Table A2.4 for details).

Table A2.4: AIC comparison of single-site monthly models of INDVI$_m$ with Δ AIC ≤ 6

Focal Site	Model [a]	K	Δ AIC	ω_i
Catenaia	Dry$_{m}$, CO$_{2\,m}$, Pre$_{m}$ * Gdd$_{m}$, Month	19	0.00	0.40
	Pre$_{m}$, CO$_{2\,m}$, Gdd$_{m}$ * Dry$_{m}$, Month	19	1.74	0.17
	Dry$_{m}$, Dry$_{m\text{-}1}$, Pre$_{m}$ * Gdd$_{m}$, Month	19	2.85	0.10
	Gdd$_{m}$, CO$_{2\,m}$, Pre$_{m}$ * Dry$_{m}$, Month	19	3.25	0.08
	Dry$_{m}$, Pre$_{m\text{-}1}$, Pre$_{m}$ * Gdd$_{m}$, Month	19	4.14	0.05
	Pre$_{m}$, Dry$_{m\text{-}1}$, Gdd$_{m}$ * Dry$_{m}$, Month	19	4.65	0.04
	Pre$_{m}$ *Dry$_{m}$, Gdd$_{m}$ * Pre$_{m}$, Month	19	4.89	0.03
	Dry$_{m}$, Gdd$_{m}$ * Pre$_{m}$, Gdd$_{m\text{-}1}$, Month	19	5.04	0.03
	Dry$_{m}$, Gdd$_{m}$ * Pre$_{m}$, Month	18	5.07	0.03
	Dry$_{m}$, Gdd$_{m}$, Tmp$_{m}$ * Pre$_{m}$, Month	19	5.87	0.02
	Pre$_{m}$, Gdd$_{m}$ * Dry$_{m}$, Pre$_{m\text{-}1}$, Month	19	5.93	0.02
	Pre$_{m}$ * Dry$_{m}$, Gdd$_{m}$ * Dry$_{m}$, Month	19	5.99	0.02
	Null (intercept-only)	3	474.72	
Bogesund	Tmp$_{m}$, Dry$_{m}$, Tmp$_{m\text{-}1}$, Tmp$_{m\text{-}2}$, Gdd$_{m\text{-}2}$, Month	19	0.00	0.36
	Dry$_{m}$, Tmp$_{m\text{-}1}$, Tmp$_{m\text{-}2}$ * Gdd$_{m\text{-}2}$, Month	19	1.38	0.18
	Tmp$_{m}$, Pre$_{m}$, Tmp$_{m\text{-}1}$, Tmp$_{m\text{-}2}$, Gdd$_{m\text{-}2}$, Month	19	2.02	0.13
	Tmp$_{m}$, Tmp$_{m\text{-}1}$, Tmp$_{m\text{-}2}$ * Gdd$_{m\text{-}2}$, Month	19	2.40	0.11
	Tmp$_{m}$, Dry$_{m}$, Tmp$_{m\text{-}1}$, Gdd$_{m\text{-}1}$, Tmp$_{m\text{-}2}$, Month	19	2.52	0.10
	Tmp$_{m}$, Dry$_{m}$, Tmp$_{m\text{-}1}$, Gdd$_{m\text{-}1}$, Month	18	2.98	0.08
	Tmp$_{m}$, Dry$_{m}$, Tmp$_{m\text{-}1}$, Tmp$_{m\text{-}2}$, Dry$_{m\text{-}2}$, Month	19	5.38	0.02
	Null	3	506.79	
Grimsö	Tmp$_{m}$, Dry$_{m}$, Tmp$_{m\text{-}1}$ * Dry$_{m\text{-}1}$, Month	19	0.00	0.93
	Tmp$_{m}$, Pre$_{m}$, Tmp$_{m\text{-}1}$ * Dry$_{m\text{-}1}$, Month	19	5.33	0.07
	Null	3	481.13	

[a] Monthly INDVI$_m$ was modelled as a response to current and lagged monthly climatic conditions over a 25 year period (1982-2006) at each of the three focal sites. Model selection and fitting conducted separately for each site. Predictors listed with a subscript of "*m*" are from the same month as the INDVI$_m$ response being modelled. Subscripts of "*m*-1" and "*m*-2" denote a one, and two month time-lag respectively. Month was included in all models as a categorical variable. In addition to the predictors listed, all models included one parameter for the intercept, one for the residual deviance (variance) and one representing the degree of temporal auto-correlation (Phi$_m$). See Ch. 2 text and Table 2.1 for variable definitions and calculation methods. Model fit and predictive ability is addressed in the Results section of the text and also in Figures 2.5 and 2.6.

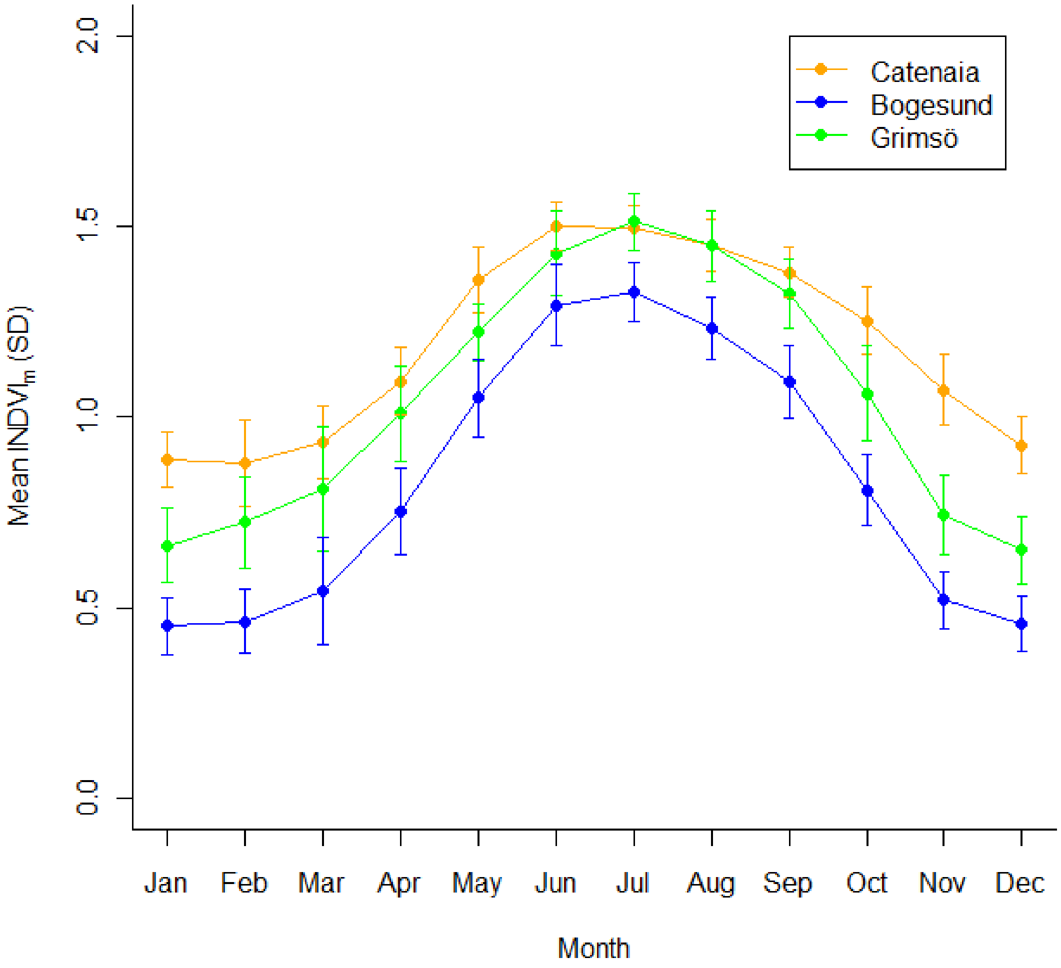

Figure A2.1: Values of NDVI, a proxy of vegetation production, typically show an intra-annual cycle with a peak in mid-summer. This seasonal cycle is evident in the observed NDVI time-series for the three focal sites (Catenaia, Bogesund, and Grimsö). Observed values of NDVI were available in bimonthly increments for 25 years (1982-2006). Monthly INDVI (INDVI$_m$) values were calculated as the sum of bimonthly values (see Ch. 2 text and Table A2.1 for more detail) and were averaged across years. Error bars represent the standard deviations of INDVI$_m$ values across years.

Appendix 3 – Chapter 3 supplementary material

Table A3.1: Pearson’s correlations between candidate predictors of roe deer survival in Bogesund (white cells, n = 18 years) and Grimsö (grey cells, n = 22 years). [a]

Candidate variable [b]	Den$_{t-1}$	Harvest$_t$	INDVI$_t$	INDVI$_{t-1}$	Pre$_{t-1}$	Gdd$_{t-1}$	WinTmp$_{t-1}$	Snow$_{t-1}$	LynxDen$_t$	LynxPres$_t$
Den$_{t-1}$	■	**0.75**		-0.2	0.06	-0.02				
Harvest$_t$	**0.43**	■		0.02	0.09	-0.28				
INDVI$_t$	0.18	-0.15	■							
INDVI$_{t-1}$	0.02	-0.11	0.15	■	0.14	-0.17				
Pre$_{t-1}$	-0.12	0.08	**-0.43**	**-0.59**	■	-0.37				
Gdd$_{t-1}$						■				
WinTmp$_{t-1}$	-0.37	0.06	**0.44**	0.27	-0.29		■			
Snow$_{t-1}$	-0.02	-0.18	**-0.57**	-0.29	0.31		**-0.7**	■		
LynxDen$_t$	**-0.6**	**-0.47**	-0.05	0.12	0.08		0.09	-0.18	■	
LynxPres$_t$	**-0.59**	**-0.56**	-0.03	0.18	-0.01		0.06	-0.19	**0.92**	■

[a] Empty cells denote variable combinations not tested in final model sets (i.e. variables not selected in preliminary models of climate-related mortality; see Ch. 3 text for detail). In the case of correlations with lynx presence (a categorical variable) a bi-serial correlation was used. Values in bold denote variable combinations with Pearson’s *r* > 0.4 which were not allowed in final model sets.

[b] See Ch. 3, Table 3.1, for definitions of variables and abbreviations.

Table A3.2: AIC comparision of preliminary models of survival rates based only on climate-related mortalities. These models allowed the identification of predictors of potential importance in each site.[a]

Survival (*S*) ~	*K*	Model type [b]	Δ AIC
Bogesund			
Age, Sex, Den $_{t\text{-}1}$, Pre $_{t\text{-}1}$	7	Beta-binomial	0
Age, Sex, Den $_{t\text{-}1}$, INDVI $_{t\text{-}1}$	7	Beta-binomial	3.41
Age, Sex, INDVI $_{t\text{-}1}$, Pre $_{t\text{-}1}$	7	Beta-binomial	4.43
Age, Sex, Gdd $_{t\text{-}1}$, Pre $_{t\text{-}1}$	7	Beta-binomial	5.83
Age, Sex	5	Beta-binomial	14.67
Age, Sex	4	Binomial	35.20
Null model (intercept-only)	2	Beta-binomial	38.23
Null model	1	Binomial	86.52
Grimsö			
Age, Sex, Den $_{t\text{-}1}$, INDVI $_{t}$	6	Binomial	0
Age, Sex, Pre $_{t\text{-}1}$, INDVI $_{t}$	6	Binomial	0.45
Age, Sex, Den $_{t\text{-}1}$, Pre $_{t\text{-}1}$	6	Binomial	1.92
Age, Sex, INDVI $_{t\text{-}1}$, INDVI $_{t}$	6	Binomial	2.07
Age, Sex, INDVI $_{t}$	5	Binomial	2.11
Age, Sex, Den $_{t\text{-}1}$, WinTmp $_{t\text{-}1}$	6	Binomial	2.20
Age, Sex, Snow $_{t\text{-}1}$, Pre $_{t\text{-}1}$	6	Binomial	4.85
Age, Sex, Pre $_{t\text{-}1}$	5	Binomial	4.90
Age, Sex, Den $_{t\text{-}1}$	5	Binomial	5.45
Age, Sex	4	Binomial	12.62
Age, Sex	5	Beta-binomial	12.65
Null model	2	Beta-binomial	46.13
Null model	1	Binomial	52.60

[a] See Ch. 3, Table 3.1, for definitions of temporal variables (i.e. not Age or Sex). Variables appearing in the site-specific models shown (with Δ AIC ≤ 6) were identified as potentially important predictors of climate mortalities (within that site) and considered in later models of survival for each site. Age and Sex were categorical variables. Deer were divided into three age groups: fawns (< 1 year old), subadults and adults (1-7 years old), and senescents (> 7 years old).

[b] Beta-binomial models contain an extra parameter which accounts for over-dispersion in the data.

Table A3.3: Comparison of observed and model estimated survival rates of roe deer among age groups, sexes, and sites.

		Fawn survival (SE) [b]		Adults and subadult survival (SE)		Senescent survival (SE)	
Site	Estimate source [a]	Female	Male	Female	Male	Female	Male
Bogesund	Observed	0.80 (0.050)	0.80 (0.053)	0.82 (0.036)	0.82 (0.041)	0.72 (0.039)	0.52 (0.098)
	BB model	0.81 (0.029)	0.79 (0.031)	0.83 (0.027)	0.81 (0.029)	0.65 (0.037)	0.62 (0.038)
	CMR model	0.61 (0.028)	0.56 (0.028)	0.81 (0.019)	0.78 (0.021)	0.59 (0.028)	0.54 (0.029)
Grimsö	Observed	0.95 (0.017)	0.92 (0.028)	0.80 (0.012)	0.67 (0.032)	0.54 (0.051)	0.46 (0.111)
	BB model	0.95 (0.004)	0.91 (0.006)	0.79 (0.012)	0.67 (0.016)	0.62 (0.017)	0.46 (0.018)
	CMR model	0.67 (0.008)	0.54 (0.009)	0.75 (0.007)	0.63 (0.008)	0.57 (0.009)	NA [c]

[a] "Observed" denotes the observed survival rates calculated based on the records of roe deer and their deaths (see Ch. 3 text). "BB model" denotes estimates from the selected best binomial and beta-binomial models. "CMR model" denotes estimates from the selected best capture-mark-recapture models (see Ch. 3 text for detail on model fit and selection).

[b] The values shown represent the mean and standard error of the estimated survival rates across the years modelled in each site (in Bogesund, n = 18 years, and in Grimsö, n = 22 years).

[c] In Grimsö, data on senescent males were insufficient to estimate survival using the CMR models.

Table A3.4: AIC comparison of models of roe deer survival in Bogesund.[a]

Binomial and beta-binomial models

Survival (S) ~	Model type[b]	K	Δ AIC	ω_i
Age, Sex, Harvest $_t$, INDVI $_{t-1}$	Beta-binomial	7	0	0.88
Age, Sex, Harvest $_t$, Pre $_{t-1}$	Beta-binomial	7	4.00	0.12
Age, Sex	Beta-binomial	5	49.31	
Null model (intercept-only)	Beta-binomial	2	57.76	
Age, Sex	Binomial	4	112.39	
Null model	Binomial	1	128.08	

Capture-mark-recapture models[c]

Survival (S) ~	K	Δ AIC	ω_i
Age, Sex, Harvest $_t$, INDVI $_{t-1}$	13	0	1
Age, Sex	11	45.35	
Control model[c]	8	89.28	
Null model	5	158.52	

[a] See Ch. 3, Table 3.1, for definitions of temporal variables (i.e. not Age or Sex). Age and Sex were categorical variables. Deer were divided into three age groups: fawns (< 1 year old), subadults and adults (1-7 years old), and senescents (> 7 years old). Model fit and predictive ability is addressed in the Results section of Ch. 3 and also in Figures 3.5 and A3.1.

[b] Beta-binomial models contain an extra parameter which accounts for over-dispersion in the data. The null models include only an intercept for *S* and, in the case of beta-binomial models, the over-dispersion parameter.

[c] The type of CMR model used was a Barker model (see Ch. 3 methods). This model type includes six parameters (*p*, *F*, *F'*, *r*, *R*, *R'*), other than *S* (survival). Covariates for some of these "control" parameters were included to control for different sources of heterogeneity in the data. Capture effort (CapDates) was included as a covariate of *p*, and radio-collared status as a covariate of *r* and *R*. These covariates were consistent across models for Bogesund (see Ch. 3 methods for more detail). The "control model" (listed for comparison; CMR only) included these covariates, but included no predictors of survival (*S*). The null CMR model included only intercepts for all parameters.

Table A3.5: AIC comparison of models of roe deer survival in Grimsö.[a]

Binomial and beta-binomial models

Survival (*S*) ~	Model type[b]	*K*	Δ AIC	ω_i
Age, Sex, LynxPres $_t$, INDVI $_t$	Binomial	6	0	0.34
Age, Sex, LynxPres $_t$, INDVI $_{t-1}$	Beta-binomial	7	2.05	0.12
Age, Sex, Den $_{t-1}$, WinTmp $_{t-1}$	Beta-binomial	7	3.01	0.07
Age, Sex, LynxPres $_t$, INDVI $_{t-1}$	Binomial	6	3.02	0.07
Age, Sex, LynxPres $_t$, Pre $_{t-1}$	Beta-binomial	7	3.14	0.07
Age, Sex, LynxPres $_t$, Snow $_{t-1}$	Beta-binomial	7	3.34	0.06
Age, Sex, LynxPres $_t$	Beta-binomial	6	3.44	0.06
Age, Sex, Den $_{t-1}$, WinTmp $_{t-1}$	Binomial	6	3.46	0.06
Age, Sex, LynxPres $_t$, Snow $_{t-1}$	Binomial	6	3.80	0.05
Age, Sex, LynxPres $_t$, Pre $_{t-1}$	Binomial	6	3.90	0.05
Age, Sex, LynxPres $_t$	Binomial	5	4.33	0.04
Age, Sex	Beta-binomial	5	19.34	
Age, Sex	Binomial	4	23.13	
Null model (intercept-only)	Beta-binomial	2	95.77	
Null model	Binomial	1	128.01	

Capture-mark-recapture models[c]

Survival (*S*) ~	*K*	Δ AIC	ω_i
Age, Sex, LynxPres $_t$, WinTmp $_{t-1}$	16	0	0.29
Age, Sex, LynxPres $_t$	15	0.44	0.23
Age, Sex, LynxDen $_t$, WinTmp $_{t-1}$	16	1.12	0.17
Age, Sex, LynxDen $_t$	15	1.66	0.13
Age, Sex, WinTmp $_{t-1}$	15	1.88	0.11
Age, Sex	14	2.87	0.07
Control model[c]	11	30.90	
Null model	7	126.05	

[a] See Ch. 3, Table 3.1, for definitions of temporal variables (i.e. not Age or Sex). Age and Sex were categorical variables. Deer were divided into three age groups: fawns (< 1 year old), subadults and adults (2-7 years old), and senescents (> 7 years old). Model fit and predictive ability is addressed in the Results section of Ch. 3 and also in Figures 3.7 and A3.1.

[b] Beta-binomial models contain an extra parameter which accounts for over-dispersion in the data. The null models include only an intercept for *S* and, in the case of beta-binomial models, the over-dispersion parameter.

[c] The CMR model used, a Barker model, includes six parameters (*p*, *F*, *F'*, *r*, *R*, *R'*), other than *S* (survival). Covariates for these "control" parameters were included to control for heterogeneity in the data. Capture effort (CapDates) was included as a covariate of *p*, radio-collared status as a covariate of *r* and *R*., and age (only 2 groups considered: fawns vs. >1 year olds) as a covariate of *F*. These covariates were consistent across models for Grimsö (see Ch. 3 methods for detail). The "control model" (listed for comparison; CMR only) included these covariates, but included no predictors of survival (*S*). The null CMR model included only intercepts for all parameters.

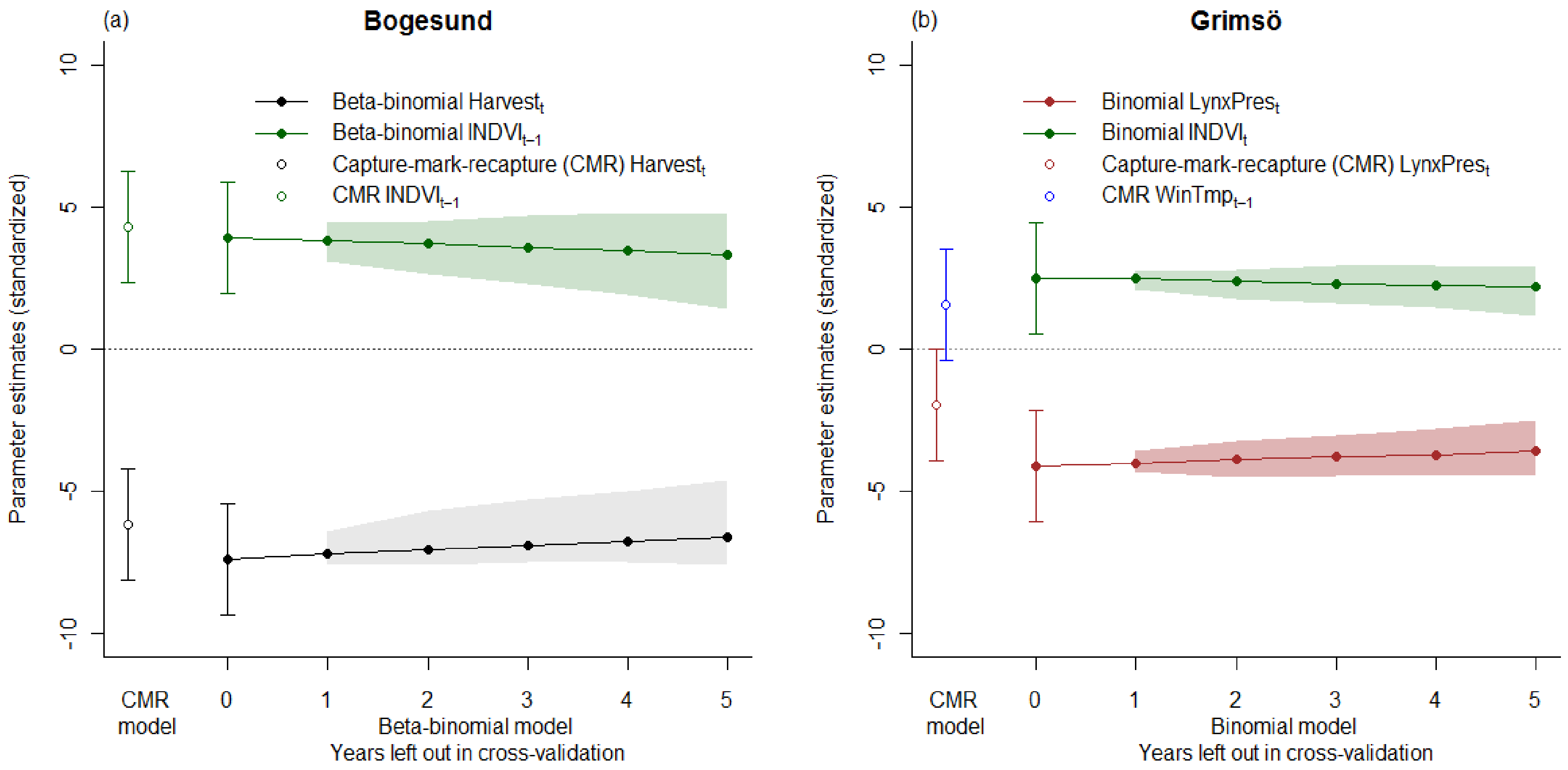

Figure A3.1: The effect size of predictors included in the best AIC model of roe deer survival in each site and modelling method are compared (see Ch. 3 for details). Error bars represent 95% confidence intervals surrounding parameter estimates from beta-binomial, binomial, and capture-mark-recapture (CMR) models. In Bogesund (panel a) top models included the annual harvest (Harvest$_t$), the previous year's INDVI (INDVI$_{t-1}$). In Grimsö (panel b), top models included the current years INDVI (INDVI$_t$), the previous winter's mean temperature (WinTmp$_{t-1}$), and lynx presence (LynxPres$_t$). A cross-validation procedure was used to investigate the robustness of binomial and beta-binomial model parameters to changes in sample size. The uncertainty in parameter estimates was evaluated by examining the 95% quantiles (shaded regions) of parameter estimates over 1000 iterations for each simulation in which 1-5 years were excluded from the dataset used to fit models.

Appendix 4 – Chapter 4 supplementary material

Table A4.1: Correlations amongst candidate predictors of ovulation for the modelled years for Bogesund (white cells, n = 13 years) and Grimsö (grey cells, n = 23 years).[a]

Candidate variable[b]	Den_t	Den_{t-1}	$INDVI_t$	$INDVI_{t-1}$	$WinTmp_{t-1}$	$WinPre_{t-1}$	$Snow_{t-1}$
Den_t		**0.51**	-0.02	-0.14	0.35	-0.02	-0.22
Den_{t-1}	**0.68**		0.14	-0.16	**0.50**	-0.31	-0.18
$INDVI_t$	0.10	-0.04		0.14	0.38	0.09	**-0.45**
$INDVI_{t-1}$	0.02	0.23	0.16		-0.09	0.03	-0.21
$WinTmp_{t-1}$	-0.11	-0.32	**0.64**	0.24		**0.53**	-0.07
$WinPre_{t-1}$	-0.24	-0.31	-0.31	-0.11	0.19		0.23
$Snow_{t-1}$	0.11	0.14	**-0.71**	-0.20	**-0.76**	0.20	

[a] Values in bold denote variable combinations with Pearson's $r > 0.4$, which were not allowed in final model sets.

[b] See Ch. 4, Table 4.1 for definitions of variables and abbreviations.

Table A4.2: AIC comparison of models of ovulation in Bogesund.

Corpora lutea ~ [a]	K	Δ AIC	ω_i
age, Den_t	6	0	0.76
age * $WinTmp_{t-1}$	8	3.75	0.12
age, Den_{t-1}	6	4.86	0.07
Age	4	5.37	0.05
Null	2	40.35	

[a] See Table 4.1 for definitions of temporal variables (i.e. not Age). Deer were divided into two age groups: subadult reproducers (1 year old when first ovulating) and mature reproducers (> 1 year old when first ovulating). In these multinomial models, there are two intercepts and two parameters estimated for each additional predictor listed. There is one parameter set describing the relative probability that a female produces 1 corpora lutea and one set describing the relative probability that she produces > 1 (the probability of producing zero corpora lutea is implicit). Model fit and predictive ability is addressed in the Results section of Ch. 4 and also in Figures 4.3 and A4.1.

Table A4.3: Correlations amongst candidate predictors of fawn survival for the modelled years for Bogesund (white cells, n = 12 years) and Grimsö (grey cells, n = 6 years). [a]

Candidate variable [b]	Den$_t$	BirthINDVI$_t$	BirthTmp$_t$	BirthPre$_t$	FoxHar$_t$/ FoxLit$_{t-1}$ [c]	Oak$_{t-1}$
Den$_t$		0.31	**0.52**	-0.02	-0.37	-0.26
BirthINDVI$_t$	-0.01		0.30	-0.23	-0.37	-0.14
BirthTmp$_t$	-0.10	**0.96**		-0.33	0.11	**-0.61**
BirthPre$_t$	0.33	**-0.85**	**-0.78**		-0.04	0.20
FoxHar$_t$/FoxLit$_{t-1}$ [c]	-0.36	**-0.75**	**-0.67**	**0.64**		-0.02
Oak$_{t-1}$						

[a] Values in bold denote variable combinations with Pearson's $r > 0.4$.

[b] See Ch. 4, Table 4.1, for definitions of variables and abbreviations.

[c] The variable FoxHar$_t$ was used in the Bogesund analysis, while FoxLit$_{t-1}$ was used in the Grimsö analysis (see Ch. 4 methods for detail).

Table A4.4: AIC comparison of models of early fawn survival in Bogesund

Fawns per female ~ [a]	*K*	Δ AIC	ω_i
FoxHar$_t$	3	0	0.76
BirthINDVI$_t$	3	3.23	0.15
Null	2	4.45	0.08

[a] See Table 4.1 for variable definitions. All lognormal models shown include one parameter for the intercept and one parameter for the residual deviance (variance). All models included an offset term equal to the estimated pregnancy rate the spring preceding observations of fawns per female in autumn (so that residual variation in number of fawns per female represents variation in fawn survival over the summer period; see text for more detail). Model fit and predictive ability is addressed in the Results section of Ch. 4 and also in Figures 4.4 and A4.1.

Table A4.5: AIC comparison of models of ovulation in Grimsö

Corpora lutea ~ [a]	K	Δ AIC	ω_i
Age, WinPre $_{t\text{-}1}$, WinTmp $_{t\text{-}1}$	8	0	0.56
Age, WinPre $_{t\text{-}1}$, Snow $_{t\text{-}1}$	8	1.24	0.30
Age, WinPre $_{t\text{-}1}$, INDVI$_t$	8	3.48	0.098
Age, WinPre $_{t\text{-}1}$	6	4.88	0.05
Age	4	17.32	
Null	2	27.41	

[a] See Table 4.1 for definitions of temporal variables (i.e. not Age). Deer were divided into two age groups: subadult reproducers (1 year old when first ovulating) and mature reproducers (> 1 year old when first ovulating). In these multinomial models, there are two intercepts and two parameters estimated for each additional predictor listed. There is one parameter set describing the relative probability that a female produces 1 corpora lutea and one set describing the relative probability that she produces > 1 (the probability of producing zero corpora lutea is implicit). Model fit and predictive ability is addressed in the Results section of Ch. 4 and also in Figures 4.6 and A4.2.

Table A4.6: AIC comparison of models of early fawn survival in Grimsö

Fawns per female ~ [a]	*K*	Δ AIC	ω_i
BirthPre$_t$	3	0	0.86
BirthNDVI$_t$	3	4.56	0.087
FoxLit$_t$	3	5.60	0.05
Null	2	9.49	

[a] See Ch. 4, Table 4.1, for variable definitions. All lognormal models shown include one parameter for the intercept and one parameter for the residual deviance (variance). All models included an offset term equal to the estimated pregnancy rate the spring preceding observations of fawns per female in autumn (so that residual variation in number of fawns per female represents variation in fawn survival over the summer period; see text for more detail). Model fit and predictive ability is addressed in the Results section of Ch. 4 and also in Figures 4.7 and A4.2.

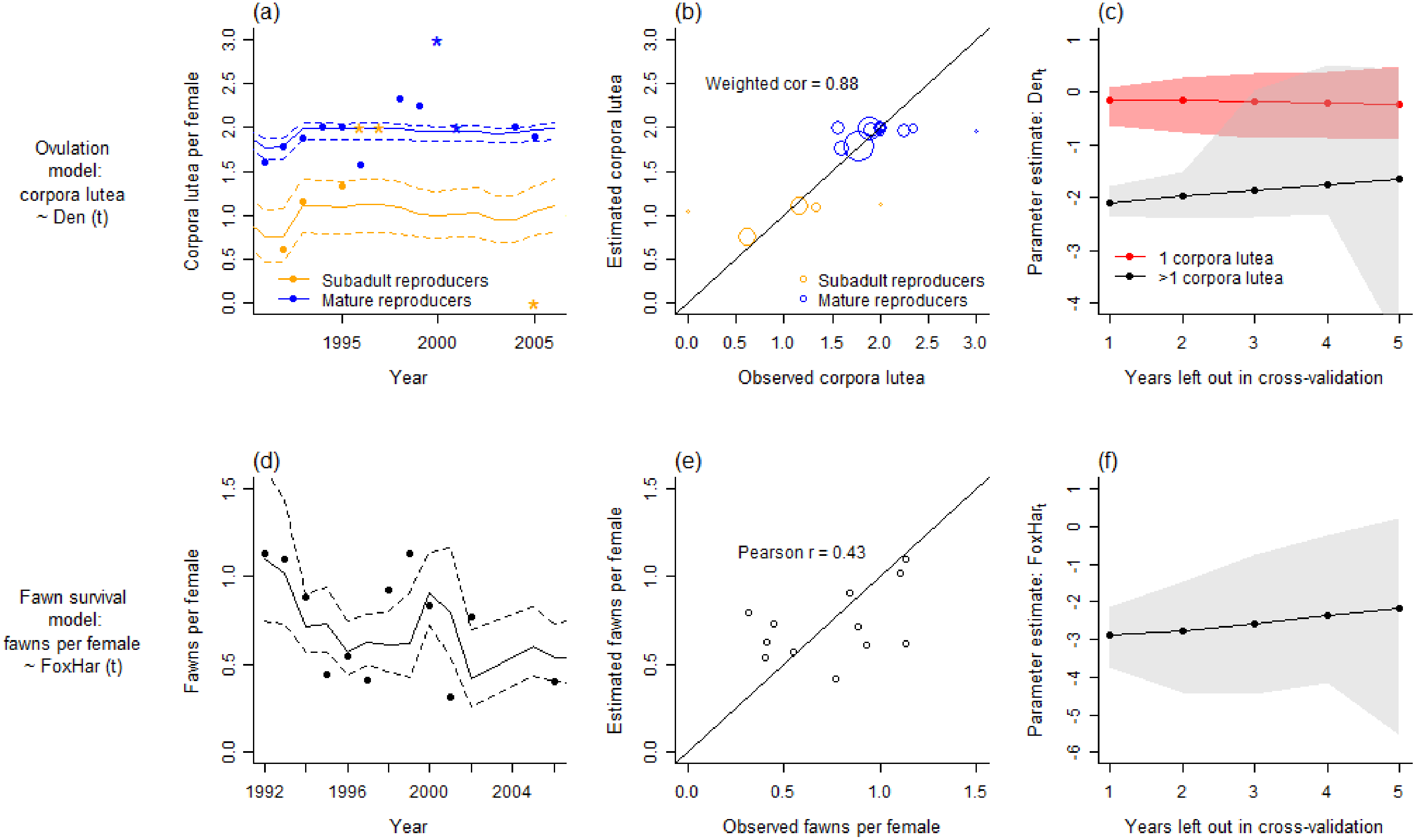

Figure A4.1: Legend see over.

Figure A4.1: The performance of the AIC best models of ovulation (multinomial model including roe deer density, Den_t, as a predictor; panels a, b, & c) and fawn survival (lognormal model including fox harvest, $FoxHar_t$; panels d, e, & f) in Bogesund. Ovulation rates were measured through the number of corpora lutea per female and fawn survival through the mean number of fawns per female observed in autumn. Models were first evaluated by comparing model estimates against observed values. In panels (a) and (d) solid lines represent model estimates (with 95% CI, dashed lines) and points represent observed values across years; asterisks denote years in which only one female was examined for corpora lutea. The correlation between estimated and observed values of ovulation and fawns per female is illustrated in panels (b) and (e) respectively. In panel (b) point size is proportional to the sample size for ovulation in a given year and a sample-size weighted correlation coefficient is given. Pearson's correlation coefficient is given for the points in panel (e). Finally, a cross-validation procedure was used to investigate the robustness of model parameters (standardised median values shown) to changes in sample size (c & f). The uncertainty in parameter estimates was evaluated by examining the 95% quantiles (shaded regions) of parameter estimates over 1000 iterations for each simulation, in which 1-5 years were excluded from the dataset used to fit models.

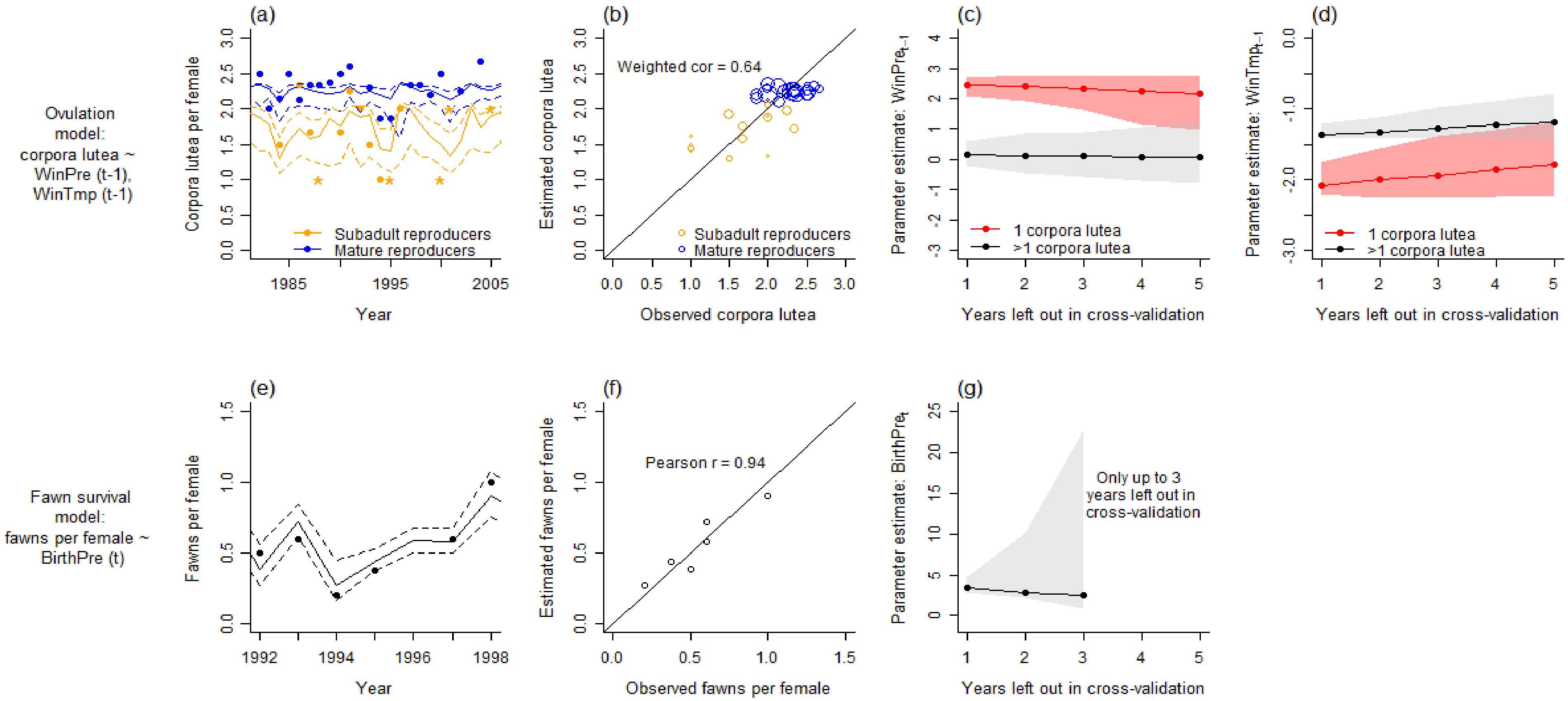

Figure A4.2: Legend, see over.

Figure A4.2: The performance of the AIC best models of ovulation (multinomial model including the previous winter’s temperature and precipitation, WinPre$_{t-1}$ and WinTmp$_{t-1}$, as predictors; panels a, b, c & d) and fawn survival (lognormal model including precipitation surrounding the fawn birth period, BirthPre$_{t}$; panels e, f, & g) in Grimsö. Ovulation rates were measured through the number of corpora lutea per female and fawn survival through the mean number of fawns per female observed in autumn. Models were first evaluated by comparing model estimates against observed values. In panels a and d, solid lines represent model estimates (with 95% CI, dashed lines) and points represent observed values across years; asterisks denote years in which only one female was examined for corpora lutea. The correlation between estimated and observed values of ovulation and fawns per female is illustrated in panels (b) and (f) respectively. In panel (b) point size is proportional to the sample size for ovulation in a given year and a sample-size weighted correlation coefficient is given. Pearson’s correlation coefficient is given for the points in panel (f). Finally, a cross-validation procedure was used to investigate the robustness of model parameters (standardised median values shown) to changes in sample size (c, d, & g). The uncertainty in parameter estimates was evaluated by examining the 95% quantiles (shaded regions) of parameter estimates over 1000 iterations for each simulation in which 1-5 years were excluded from the dataset used to fit models.

Appendix 5 – Chapter 5 supplementary material

Table A5.1: Conditions used to estimate starting age distribution for roe deer density simulations.

Study site	Driving environmental condition [a]	Associated component model	Value used to calculate starting age distribution for simulations of observed period [b]	Value used to calculate starting age distribution for simulations of projected period [c]
Bogesund	Starting density (deer per km^2)	NA	10.3	12.96
	INDVI$_{t-1}$	Survival	10.22	10.17
	Harvest$_t$ (deer killed per capita)	Survival	0	0.10
	Den$_t$	Ovulation	6.89	12.96
	FoxHar$_t$ (foxes killed per km^2)	Early fawn survival	0.10	0.345
Grimsö	Starting density	NA	5.4	NA
	INDVI$_t$	Survival	12.60	
	LynxPres$_t$	Survival	Absent	
	WinTmp$_{t-1}$(°C)	Ovulation	-8.00	
	WinPre$_{t-1}$ (mm)	Ovulation	97.7	
	NbPre$_t$ (mm)	Early fawn survival	258.3	

[a] A starting age distribution was estimated for each site. This distribution was multiplied by the starting density estimate and used at the beginning of simulations. The age distribution for each site was calculated by running the simulation (see text for more detail) for 500 "years" assuming constant driving conditions.

[b] When simulating densities for the observed period in each site, conditions from the years just before the simulated period were used. The conditions used to estimate ovulation were drawn from the year prior to the conditions used for other component models. This meant that the values used to estimate ovulation were associated with 1988 in Bogesund and 1980 in Grimsö, while other values shown were associated with 1989 in Bogesund and 1981 in Grimsö. Estimates from these years were not available for all cases. Density in Bogesund was not estimated prior to 1989, thus the density used to estimate ovulation rates in Bogesund had to be inferred from the density observed in 1989 (10.3 deer per km^2). This was done assuming the same growth rate to that observed from 1989 to 1990 (lambda = 1.49), when the population was not harvested (as in 1988). The value of INDVI used to estimate survival rates in Grimsö was unavailable prior to 1982, thus, mean INDVI from the years 1982-2006 was used.

[c] The age distribution used to start the simulations of projected roe deer density in Bogesund was calculated using the mean of all observed values from the simulated period, 1989-2006. Projections of roe deer dynamics were not conducted for the Grimsö site.

Table A5.2: Within-year distribution of natural, non-harvest related, roe deer deaths

Sub-annual period	Proportion of natural, non-harvest, deaths[a]	
	Bogesund	Grimsö
April-May	0.297	0.259
June-August	0.165	0.179
September-February	0.257	0.313
February- April	0.280	0.248

[a] Any deaths of roe deer not due to harvest were considered “natural”. The proportions shown were calculated using 229 deaths of roe deer observed in Bogesund from 1989-2011 and 383 deaths in Grimsö from 1972 until 2012. In the simulations of density in each site, non-harvest related mortality, was distributed throughout the year according to the proportions shown.

A: Apr 15th – May 31st, survival (natural mortality)

	Fawn	Subadult	Adult 1	. . .	Adult 6	Senescent
Fawn	S_N	0	0	. . .	0	0
Subadult	0	S_N	0	. . .	0	0
Adult 1	0	0	S_N	. . .	0	0
. . .	. . .	. . .	. . .	. . .	. . .	. . .
Adult 6	0	0	0	. . .	S_N	0
Senescent	0	0	0	. . .	0	S_N

B: Jun 1st, all deer age one year

	Fawn	Subadult	Adult 1	. . .	Adult 6	Senescent
Fawn	0	0	0	. . .	0	0
Subadult	**1**	0	0	. . .	0	0
Adult 1	0	**1**	0	. . .	0	0
. . .	. . .	. . .	. . .	. . .	. . .	. . .
Adult 6	0	0	0	. . .	0	0
Senescent	0	0	0	. . .	**1**	**1**

C: Jun 1st – Aug 31st, survival (natural mortality)

	Fawn	Subadult	Adult 1	. . .	Adult 6	Senescent
Fawn	0	0	0	. . .	0	0
Subadult	0	S_N	0	. . .	0	0
Adult 1	0	0	S_N	. . .	0	0
. . .	. . .	. . .	. . .	. . .	. . .	. . .
Adult 6	0	0	0	. . .	S_N	0
Senescent	0	0	0	. . .	0	S_N

D: Sep 1st, fawns added per female

	Fawn	Subadult	Adult 1	. . .	Adult 6	Senescent
Fawn	0	0	**F**	. . .	**F**	**F**
Subadult	0	**1**	0	. . .	0	0
Adult 1	0	0	**1**	. . .	0	0
. . .	. . .	. . .	. . .	. . .	. . .	. . .
Adult 6	0	0	0	. . .	**1**	0
Senescent	0	0	0	. . .	0	**1**

E: Sep 1st – Feb 14th, survival (natural & harvest mortality)

	Fawn	Subadult	Adult 1	. . .	Adult 6	Senescent
Fawn	$S_{N \& H}$	0	0	. . .	0	0
Subadult	0	$S_{N \& H}$	0	. . .	0	0
Adult 1	0	0	$S_{N \& H}$	. . .	0	0
. . .	. . .	. . .	. . .	. . .	. . .	. . .
Adult 6	0	0	0	. . .	$S_{N \& H}$	0
Senescent	0	0	0	. . .	0	$S_{N \& H}$

F: Feb 15th – Apr 14th, survival (natural mortality)

	Fawn	Subadult	Adult 1	. . .	Adult 6	Senescent
Fawn	S_N	0	0	. . .	0	0
Subadult	0	S_N	0	. . .	0	0
Adult 1	0	0	S_N	. . .	0	0
. . .	. . .	. . .	. . .	. . .	. . .	. . .
Adult 6	0	0	0	. . .	S_N	0
Senescent	0	0	0	. . .	0	S_N

Figure A5.1: Legend see over.

Figure A5.1: The structure of the transition matrices (blue text, A-F) used to simulate changes in roe deer density. Each of these matrices corresponds to the sub-annual periods which were combined to simulate roe deer population dynamics from one April to the next (see Ch. 5 text and corresponding blue text in Fig. 5.1). The roe deer population was progressed through the sub-annual periods by multiplying the relevant 9 x 9 age-structured transition matrix by the current age-structured population vector (9 x 1). All transition matrices included nine age classes: fawns (< 1 year old), subadults (1 year old), six annual adult classes (2-7 years old), and a senescent age class (all deer > 7 years old). Age-group specific survival rates (S) were estimated given the site-specific survival models (see text) and differed amongst three age groups: fawns (≥ 4 months < 1 year; the survival of younger fawns was modelled separately, see below), subadults and adults (1 – 7 years old), and senescents (see Ch. 3 for detail on model specification). The survival associated with natural mortality (S_N) during each period was calculated as that predicted by the survival model when harvest was set to 0, multiplied by the proportion of the total natural mortality which was observed during the relevant sub-annual period (see Table A5.2). The age-specific harvest-related mortality (Bogesund only) was estimated using the survival model for each site and the observed harvest at the site. This was incorporated (along with natural mortality) into survival during the harvest season ($S_{N\&H}$, matrix E). Recruitment into the population (F, matrix D) was estimated as the number of fawns per female surviving until September using the site-specific models of ovulation and early fawn survival (fawns 0-3 months old) (see Ch. 4 for detail on model specification). Ovulation rates and, thus, recruitment differed between subadult reproducers (which are 2 years old when giving birth) and mature reproducers (> 2 years old when giving birth). Females less than 2 years old did not produce fawns (because there is a time lag between ovulation and birth).

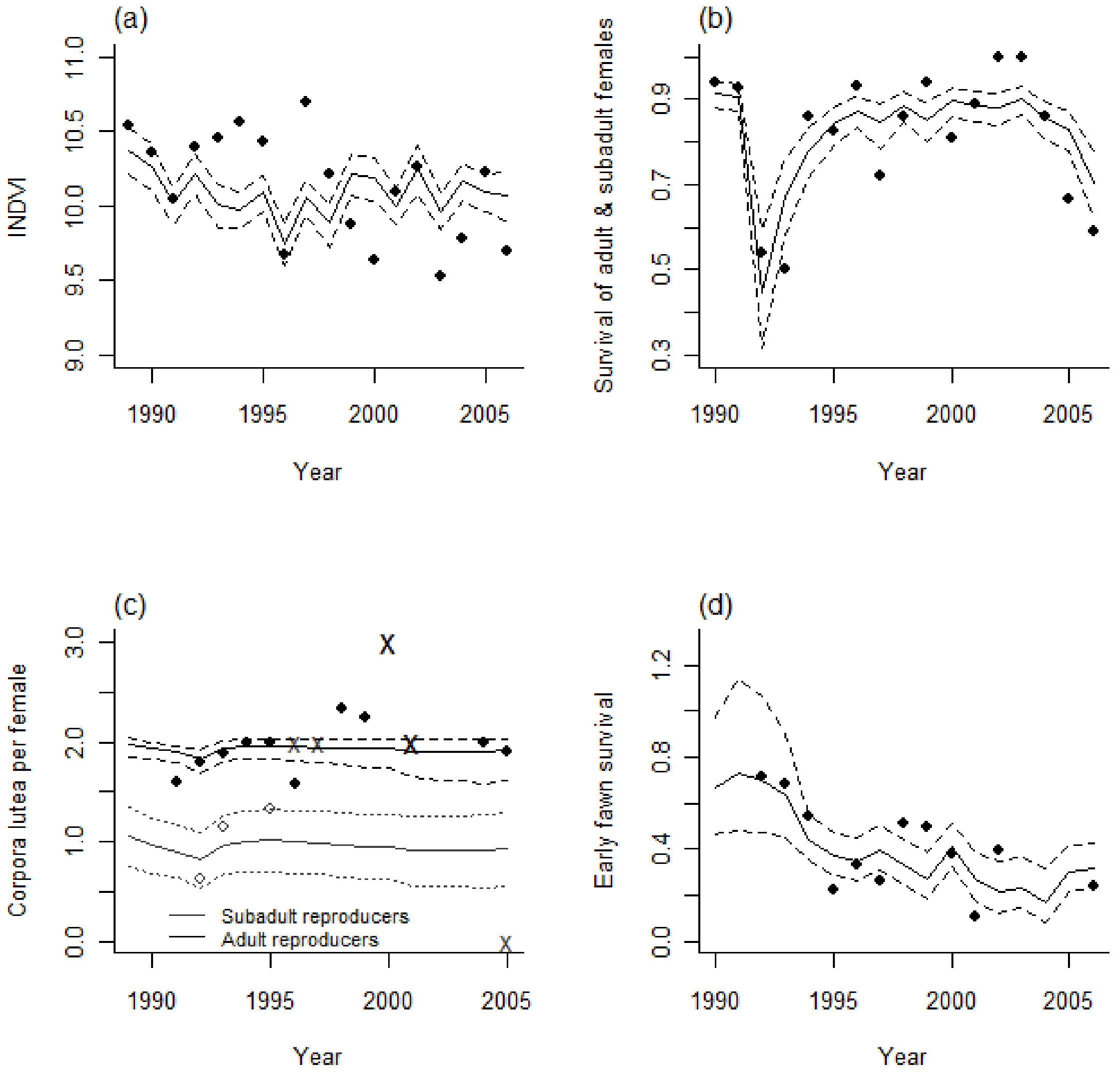

Figure A5.2: The vegetation productivity (indicated by INDVI) and vital rates of roe deer in Bogesund were estimated in response to observed environmental conditions and were used to simulate roe deer density from 1991 to 2007. In all panels, solid lines represent simulated values, dashed lines represent 95% quantile intervals of those values (across 1000 iterations), and points represent observed values. INDVI, an indicator of vegetation productivity, was modelled in response to observed climate conditions (panel a). Survival was modelled as a response to the preceding year's INDVI (positive effect), current year's harvest (negative effect), and age group; the survival rates shown are those of adult and subadult females (panel b). Ovulation was modelled as a response to density (negative effect) and maternal age group (panel c). In panel (c), x's are used to denote years in which the observed value represents an observation of only one individual (i.e. n = 1). Grey symbols (solid, small dashed lines, open circles, and small x's) are associated with subadult reproducers. Black symbols (solid lines, long dashed lines, solid circles, and large x's) are associated with mature reproducers. Early fawn survival (panel d) was modelled as a response to the abundance of red fox (as indicated by annual fox harvests, negative effect). For more detail on models, simulations, and predictors involved see Ch. 5 text.

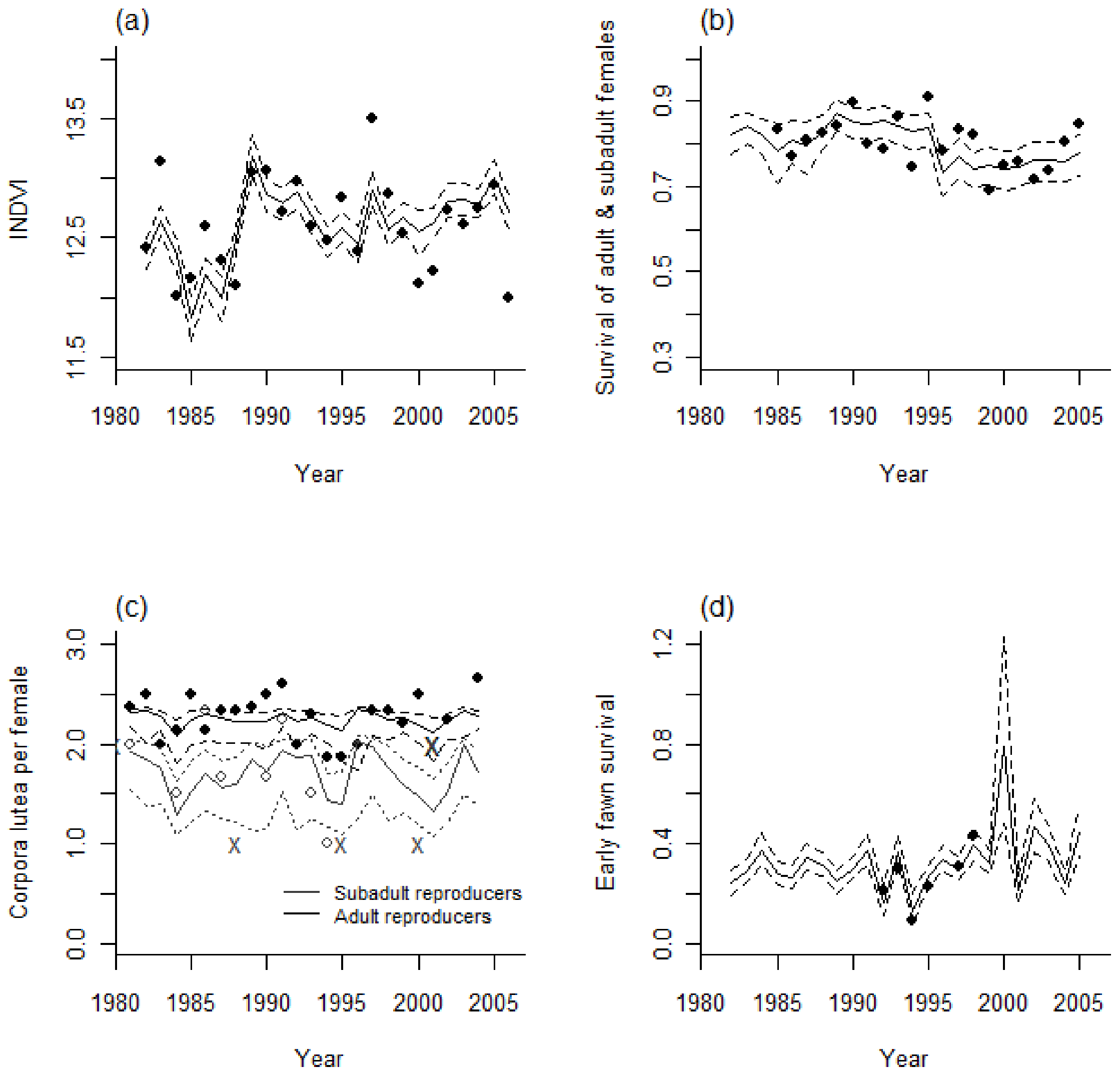

Figure A5.3: The vegetation productivity (indicated by INDVI) and vital rates of roe deer in Grimsö were estimated in response to observed environmental conditions and were used to simulate roe deer density from 1983 to 2006. In all panels, solid lines represent simulated values, dashed lines represent 95% quantile intervals of those values (across 1000 iterations), and points represent observed values. INDVI, an indicator of vegetation productivity, was modelled in response to observed climate conditions (panel a). Survival was modelled as a response to the current year's INDVI (positive effect), lynx presence (negative effect), and age group; the survival rates shown are those of adult and subadult females (panel b). Ovulation was modelled as a response to the preceding winter's (December, January, and February) temperature (positive effect) and precipitation (negative effect), and to maternal age group (panel c). In panel (c), x's are used to denote years in which the observed value represents an observation of only one individual (i.e. n = 1). Grey symbols (solid, small dashed lines, open circles, and small x's) are associated with subadult reproducers. Black symbols (solid lines, long dashed lines, solid circles, and large x) are associated with mature reproducers. Early fawn survival (panel d) was modelled as a response to precipitation from the months surrounding fawn births (May, June, and July; positive effect). For more detail on models, simulations, and predictors involved see Ch. 5 text.

Appendix 6 – Chapter 6 supplementary material

Text A6.1: Literature reviewed on European wolf diet (see Table A6.1).

Ansorge, H., G. Kluth, and S. Hahne. 2006. Feeding ecology of wolves *Canis lupus* returning to Germany. Acta Theriologica **51**:99-106.

Barja, I. 2009. Prey and prey-age preference by the Iberian wolf *Canis lupus* signatus in a multiple-prey ecosystem. Wildlife Biology **15**:147-154.

Capitani, C., I. Bertelli, P. Varuzza, M. Scandura, and M. Apollonio. 2004. A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. Mammalian Biology **69**:1-10.

Ciucci, P., L. Boitanti, E. R. Pelliccioni, M. Rocco, and I. Guy. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. Wildlife Biology **2**:37-48.

Cuesta, L., F. Barcena, F. Palacios, and S. Reig. 1991. The trophic ecology of the Iberian wolf (*Canis-lupus*-signatus, Cabrera, 1907) - a new analysis of stomachs data. Mammalia **55**:239-254.

Gazzola, A., I. Bertelli, E. Avanzinelli, A. Tolosano, P. Bertotto, and M. Apollonio. 2005. Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. Journal of Zoology **266**:205-213.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, and A. L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieza-Natural-Park, Poland. Oecologia **90**:27-36.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, K. Schmidt, K. Zub, and M. Musiani. 2000. Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. Journal of Mammalogy **81**:197-212.

Lesniewicz, K. and K. Perzanowski. 1989. The winter diet of wolves in Bieszczady Mountains. Acta Theriologica **34**:373-380.

Macdonald, D. W., L. Boitani, and P. Barrasso. 1980. Foxes *Vulpes-vulpes* wolves *Canis-Lupus* and conservationin the Abruzzo Mountains Italy. Pages P223-236 Zimen, E.

Marucco, F., D. H. Pletscher, and L. Boitani. 2008. Accuracy of scat sampling for carnivore diet analysis: Wolves in the Alps as a case study. Journal of Mammalogy **89**:665-673.

Mattioli, L., M. Apollonio, V. Mazzarone, and E. Centofanti. 1995. Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. Acta Theriologica **40**:387-402.

Mattioli, L., C. Capitani, A. Gazzola, M. Scandura, and M. Apollonio. 2011. Prey selection and dietary response by wolves in a high-density multi-species ungulate community. European Journal of Wildlife Research **57**:909-922.

Meriggi, A., A. Brangi, C. Matteucci, and O. Sacchi. 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. Ecography **19**:287-295.

Meriggi, A., P. Rosa, A. Brangi, and C. Matteucci. 1991. Habitat use and diet of the wolf in Northern Italy. Acta Theriologica **36**:141-151.

Nores, C., L. Llaneza, and M. A. Alvarez. 2008. Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain. Wildlife Biology **14**:44-51.

Olsson, O., J. Wirtberg, M. Andersson, and I. Wirtberg. 1997. Wolf *Canis lupus* predation on moose Alces alces and roe deer Capreolus capreolus in south-central Scandinavia. Wildlife Biology **3**:13-25.

Patalano, M. and S. Lovari. 1993. Food-habits and trophic niche overlap of the wolf *Canis-lupus*, L 1758 and the red fox *Vulpes-vulpes* (L 1758) in a Mediterranean mountain area. Revue D Ecologie-La Terre Et La Vie **48**:279-294.

Pezzo, F., L. Parigi, and R. Fico. 2003. Food habits of wolves in central Italy based on stomach and intestine analyses. Acta Theriologica **48**:265-270.

Reig, S., L. de la Cuesta, and F. Palacios. 1985. The impact of human activities on the food habits of red fox and wolf in Old Castille, Spain. Terre Et La Vie **40**:151-155.

Salvador, A. and P. L. Abad. 1987. Food-habits of a wolf population (*Canis-lupus*) in Leon Province, Spain. Mammalia **51**:45-52.

Smietana, W. and A. Klimek. 1993. Diet of wolves in the Bieszczady Mountains, Poland. Acta Theriologica **38**:245-251.

Valdmann, H., Z. Andersone-Lilley, O. Koppa, J. Ozolins, and G. Bagrade. 2005. Winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Estonia and Latvia. Acta Theriologica **50**:521-527.

Zunna, A., J. Ozolins, and A. Pupila. 2009. Food habits of the wolf *Canis lupus* in Latvia based on stomach analyses. Estonian Journal of Ecology **58**:141-152.

Table A6.1: Published studies of wolf diet in Europe surveyed for analysis of uncertainty and inter-annual variability in estimates of dietary composition and prey selection.

	Study details			Dietary composition		Prey selection		
Source	Country	Method[a]	Yrs	Calculated intra-annual uncertainty	Examined inter-annual variability	Evaluated in study	Calculated intra-annual uncertainty	Examined inter-annual variability
Ansorge et al. (2006)	Germany	S	3	No	No	Yes	No	No
Barja (2009)	Spain	S	5	No	Yes	Yes	No	No
Capitani et al. (2004)	Italy	S	1	No	NA	Yes	No	NA
Ciucci et al. (1996)	Italy	S	2	No	No	No	NA	NA
Cuesta et al. (1991)	Spain	OS	15	No	No	No	NA	NA
Gazzola et al. (2005)	Italy	S	3	No	No	Yes	No	No
Jedrzejewski et al. (1992, 2000)	Poland	KS	11	No	Yes	Yes	No	No
Lesniewicz & Perzanowski (1989)	Poland	O	2	No	No	No	NA	NA
Macdonald (1980)	Italy	S	3	No	No	No	NA	NA
Marucco et al. (2008)	Italy	KS	3	Yes	Yes	Yes	Yes	Yes
Mattioli et al. (1995, 2011)	Italy	S	11	No	Yes	Yes	Yes	Yes
Meriggi et al. (1991)	Italy	S	1	No	No	No	NA	NA
Meriggi et al. (1996)	Italy	S	5	No	Yes	Yes	No	No
Nores et al. (2008)	Spain	S	1	No	NA	No	NA	NA
Olsson et al. (1997)	Sweden & Norway	S	4	No	No	No	NA	NA
Patalano & Lovari (1993)	Italy	S	2	No	Yes	No	NA	NA

Pezzo et al. (2003)	Italy	O	5	No	No	No	NA	NA
Reig et al. (1985)	Spain	O	4	No	No	No	NA	NA
Salvador & Abad (1987)	Spain	S	2	No	Yes	No	NA	NA
Smietana & Klimek (1993)	Poland	S	3	No	No	No	NA	NA
Valdmann et al. (2005)	Latvia & Estonia	OS	4	No	No	No	NA	NA
Zunna (2009)	Latvia	O	6	No	No	No	NA	NA

[a] The methods of dietary analysis used in each study were broadly categorized. Studies generally relied on samples of scats (S), internal organs (O) (i.e. stomachs and intestines from killed wolves), or carcasses found of prey killed by wolves (K). Some studies combined more than one method.

Text A6.2: The analysis of boar use in response to season (methods and results)

When collecting scats the “season” of collection was recorded. While collected year-round (see Ch. 6 methods), scats were classified into two seasons: “summer” lasting from May to October and “winter” from November to April. Over the nine-year study period, 802 “summer” scats and 1172 “winter” scats were collected. When near the limits of these seasonal periods special care was taken to assess the age of the scat sample and likely date of deposition. The decision to divide the year into these two periods was made *a priori* because of the biology of both predator and prey species. During the “summer” season wolves have new pups and pack activities are therefore localized around den areas (contrasting the winter when wolves are more nomadic). Also during the summer period, both wild boar and roe deer are more likely to have young which make vulnerable prey. All these factors could contribute to distinct patterns of selection between these two seasons.

I estimated the seasonal biomass consumed of boar and roe deer based on the scats from each season throughout the nine-year study period. I then calculated the relative use of boar (within the two-prey community including boar and roe deer), U_B, separately for each summer and winter. All calculations followed the procedure described in the main text for assessment of wolf diet and prey use (see Ch. 6 methods). I modelled seasonal values of boar use (16 estimates of use across eight years, based on summer and winter scat samples) as a response to season, annual availability ($U_{A,}$ see Ch. 6 for methods) and their interaction. I tested the significance of these parameters using a repeated measure ANOVA with year as the error term; this provided control for only having one measure of availability per year. I found the effects of season on relative boar use to be non-significant (Table A6.2). I did not consider seasonal variation further in my analyses, therefore, but modelled the annual estimates of boar use (based on all scats collected each year) as a response to the relative availability of this species (see Ch. 6 text).

Table A6.2: Repeated measure ANOVA [a] of the effects of boar availability, season and their interaction on seasonal use of boar by wolves (relative to the wild ungulate community including boar and roe deer) [b]. Data were collected from 2000-2009 in the Catenaia study site.

Model parameters [ab]	Num. Df	Denom. Df	Sum of Sq.	MS	Res. MS	F	*P* (> F)
Boar availability	1	6	0.145	0.145	0.007	20.595	0.004
Season	1	6	0.006	0.006	0.006	1.020	0.352
Boar availability * Season	1	6	0.006	0.006	0.006	1.095	0.336

[a] Year was included as the error term when testing for effect of boar availability as there was only one measure of availability per year.

[b] Wild boar availability and use in wolf diet are calculated based on biomass (kg per km^2) relative to the availability and use of the main ungulate community in Alpe di Catenaia consisting of wild boar and roe deer only. Boar use was calculated seasonally based on collected wolf scats. Seasons were defined as either summer (May to October) or winter (November to April). Boar availability was calculated using annual estimates of ungulate density based on drive censuses. See text A6.2 and Ch. 6 methods for more detail.

Table A6.3: Composition of wolf diet was assessed based on scat samples collected in Catenaia.

		Wolf diet composition from 2000 through 2009[b]: percentage of biomass consumed per prey item									
		2000	2001	2002	2003	2004	2005	2006	2007	2008	
Prey item	Scat samples[a]	178	242	262	293	232	143	144	208	272	Mean (SE) n = 9
Wild boar	1284	55.9	48.2	68.5	71.2	48.8	46.1	68.7	76.5	69.6	61.5 (3.90)
Roe deer	804	42.1	47.6	26.3	26.1	48.2	39.9	29.8	20.1	22.9	33.7 (3.61)
Red deer	12	0	0	0	0	0	0	0	0.4	6.1	0.7 (0.67)
Hare	26	0	0	0.6	1.8	1.1	4.5	0.6	1.0	0	1.1 (0.47)
Small rodents	18	0.4	0.2	0.3	0.4	1.2	0	0	0	0.3	0.3 (0.12)
Sheep	29	1.6	3.7	4.3	0.5	0.8	8.5	0	0	0.3	2.2 (0.95)
Goat	3	0	0.4	0	0	0	1.0	1.0	0	0	0.3 (0.14)
Cattle	3	0	0	0	0	0	0	0	2.0	0.8	0.3 (0.22)

[a] Scat samples per year sum to the total number of samples used in all analysis over 9 years (1,974). Scat samples per prey item are defined as the total number of scats found containing that prey item in any proportion and may, therefore, sum to more than the total number of scat samples collected.

[b] For analysis purposes data years began in May and ended in April; the 2000 year represents all scats collected between 1 May 2000 and 30 April 2001.

Table A6.4: Selection of wild boar as a prey species based on estimates of boar use by wolves and relative availability within Catenaia.

Year [a]	Scat samples	Relative wild boar availability [b]	Relative wild boar use	Manly's standardised selection ratio, calculated for wild boar use in wolf diet [c]	Bootstrapped 95% confidence intervals on Manly's standardised selection ratio	
					Lower limit	Upper limit
2000	178	0.47	0.57	0.60	0.41	0.84
2001	242	0.30	0.50	0.71	0.45	0.97
2002	262	0.39	0.72	0.81	0.66	0.94
2003	293	0.53	0.73	0.71	0.56	0.87
2004	232	0.18	0.50	0.82	0.68	0.95
2005	143	0.32	0.54	0.71	0.50	0.93
2006	144	NA	0.70	NA	NA	NA
2007	208	0.54	0.79	0.77	0.49	0.99
2008	272	0.50	0.75	0.75	0.58	0.95
Mean (SE)		0.40 (0.043)	0.65 (0.039)	0.73 (0.023)		

[a] Data years began in May and ended in April; the 2000 year represents all scats collected between 1 May 2000 and 30 April 2001.

[b] Wild boar availability and use in wolf diet are calculated based on biomass (kg per km^2) relative to the availability and use of the main ungulate community in Catenaia consisting of wild boar and roe deer only. See Ch. 6 methods for more detail.

[c] For Manly's standardised selection ratio, values approximately equal to 0.5 indicate prey use in proportion to availability in a two-prey system while selection for and against the prey type of focus would be indicated by higher and lower values respectively.