

**The influence of Red deer population control on the regeneration of Scots pine
within a Scottish Highland estate**



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~ Nothing in the world is single;

All things, by a law divine

In one another's being mingle ~

(Percy Bysshe Shelley (1792-1822), 'Love's Philosophy')

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List of acronyms

NTS: National Trust for Scotland
 SNH: Scottish Natural Heritage
 NDVI: Normalised Difference Vegetation Index
 NAO: North Atlantic Oscillation

Abstract

The Caledonian pinewood once covered much of the Scottish highlands. Roughly 1% of the original expanse of pinewood remains today (Steven and Carlisle, 1996). In more recent decades, Red deer (*Cervus elaphus*) overabundance within the Scottish highlands has become a barrier to regeneration of native pinewood (Steven and Carlisle, 1996; Gill et al, 2000). Management within some Scottish highland estates is now tailored towards reducing deer abundance to achieve regeneration of native pinewoods. Mar Lodge is one such estate, wherein the principal management objective is the reduction of deer density to achieve extensive regeneration of Scots pine (*Pinus sylvestris*). However, deer numbers are still too high within the estate to allow regeneration of Scots pine to proceed at an acceptable level (Rao, 2008, unpublished data).

This study explored the interaction between Red deer hind demographic rates and Scots pine regeneration rates based on time series data collected within Mar Lodge Estate. Linear modelling of these parameters showed that hind density is a significant constraint on both Scots pine sapling density and growth. Scots pine sapling density shows a high degree of sensitivity to changes in hind density whereas Scots pine sapling growth shows a much lower degree of sensitivity to changes in hind density. The analysis also reveals that a continued culling effort is required to achieve sustained Scots pine regeneration.

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1: Introduction

1.1: Landscape dynamics

Originally, the Caledonian forest covered around 1.5 million hectares of the Scottish highlands. Roughly 1% of this vast expanse of woodland remains today (Steven and Carlisle, 1996). Initial reduction in the prevalence of pine woodland within Scotland is attributable to increased timber demands since the 17th century and particularly during both World Wars (Bains et al, 1994). The Scots pine (*Pinus sylvestris*) is the largest and longest lived species within the Caledonian forest and plays a key role in ecosystem functioning (Steven and Carlisle, 1996). Scots pine-dominated woodlands support populations of several distinctive Scottish species, such as the pine martin (*Martes martes*), Scottish crossbill (*Loxia scottica*), red squirrel (*Sciurus vulgaris*) and capercaillie (*Tetrao urogallus*) (Holl et al, 2002; NTS, 2009). Further loss of Scots pine-dominated woodlands could have profound repercussions on these and other species native to Scotland (Anderson, 1994), diminishing the conservation and economic value of the Scottish landscape.

1.2: Deer pressure

In more recent times, deer overabundance has become a barrier to natural regeneration of these depleted Caledonian woodlands (Steven and Carlisle, 1996). The increase in popularity of hill stalking in the 19th century led to an elevation in Red deer (*Cervus elaphus*) numbers in the Scottish highlands (Clutton Brock and Albon, 1989). Deer numbers are deemed to have been higher than the carrying capacity of their winter-constrained habitat for some duration (Cameron, 1923). Consistent under-culling of hinds and low winter mortality has exacerbated the situation in recent decades (Clutton Brock and Albon, 1989). Red deer are known to browse upland vegetation communities, which include Scots pine (Miller et al, 1998). Scots pine saplings are particularly sensitive to browsing, with senescence in growth and fecundity resulting from even low levels of browse (Scottish National Heritage, 1994; Miller et al, 1998). Therefore, a significant reduction in current Scottish Red deer densities is likely to be necessary to achieve extensive natural regeneration of native pinewood (Andren and Angelstam, 1993; Miller et al, 1998; Palmer and Truscott,

2003). This is widely acknowledged within many Scottish highland estates, and management within these estates is now partially tailored towards reducing deer numbers. Management tailored towards achieving pinewood regeneration is justified in conservation terms, as it constitutes the release of a suppressed species that, under more natural deer densities, would be an integral component of the Scottish landscape (Miller et al, 1998).

1.3: Management and Mar Lodge Estate

Mar Lodge Estate is situated in Aberdeenshire (figure 1) and encompasses almost 800 hectares of Caledonian pine forest. The National Trust for Scotland (NTS) took over ownership of the estate in 1995 and has been carrying out a program of deer reduction within its Regeneration zone (figure 2) since then, with the principal objective of achieving natural regeneration of native pinewoods towards landscape restoration (Luxmoore, 2002, unpublished data). Red deer numbers and Scots pine regeneration rates have been monitored independently since 1995 and 2002 respectively, with a steady decline in deer numbers corresponding with a steady increase in Scots pine regeneration (Rao, 2008, unpublished data). However, it is acknowledged that deer numbers within the Regeneration zone are still too high to allow regeneration of Scots pine to proceed at an acceptable level (Rao, 2008, unpublished data).

The degree and nature of interaction between suppression of deer numbers and the increase in regeneration rates has yet to be quantified. The nature of this interaction is likely to be complex (Myserud et al, 2001; Putman et al, 2008) and will probably implicate multiple deer and Scots pine demographic rates (Crawley, 1989). Despite these complexities, rough estimation of this interaction would provide the NTS with a greater appreciation of the effectiveness of reducing Red deer numbers in achieving Scots pine regeneration.

1.4: Project aims

The principal aim of this study is to elucidate, through logical progression, the cumulative effect that hind density has on the regeneration of Scots pine within Mar Lodge estate. This will be achieved through a series of models exploring the multiple

interactions between and within hind demographic rates and Scots pine demographic rates using linear modelling. The main causal pathways of interest are the direct interaction between hind density and Scots pine regeneration and the indirect interaction between hind density and Scots pine regeneration, via shifts in hind demographic rates (figure 3, pathway D and pathway A, F). Once these interaction rates have been elucidated, they will be combined into a model to illustrate the cumulative interaction between hind density and Scots pine regeneration. The final aim of this study is to make a tentative projection of these interaction rates, to visualise how the interaction may change under different management approaches. Other studies exploring plant-herbivore interaction typically restrict their use of herbivore parameters to herbivore density. The use of multiple herbivore demographic rates in this study may yield new insight into the complexities of plant-herbivore interaction that will implicate on further research avenues. For this study, additional hind population parameters utilised in modelling interactions include: mean hind weight, mean hind age, proportion of lactating hinds that are also pregnant, calving rate and transience rate. These rates are explained further in subsequent sections.

The principle objective of this study is to determine the bearing and relative influence that reducing hind density has on Scots pine regeneration to inform on management within Mar Lodge estate; in their commitment to deer reduction, in setting realistic deer reduction targets and in anticipation of the required duration of this commitment.



Figure 1: Location of Mar Lodge Estate (© Google Earth, 2009)

Mar Lodge Estate (area within the yellow square) is situated within Aberdeenshire and encompasses 29,340 hectares of wild Scottish land

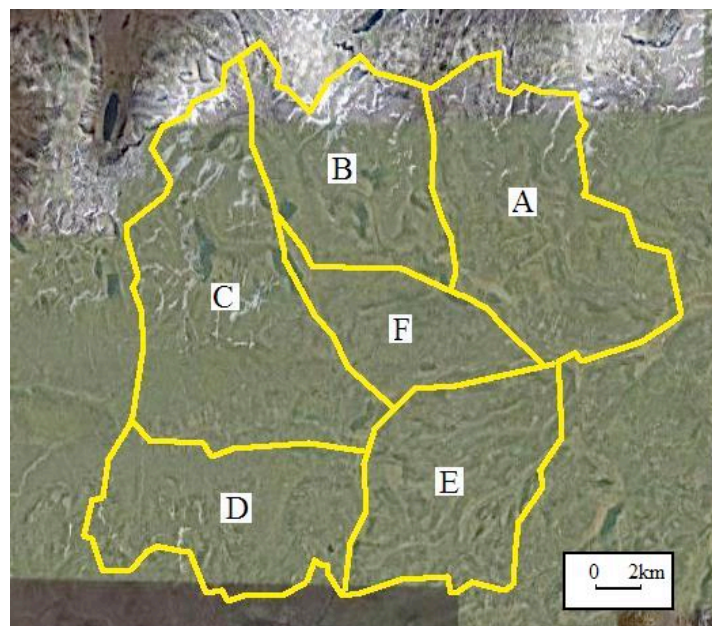


Figure 2: Management zones within Mar Lodge Estate (© Google Earth, 2009)

Mar Lodge Estate is divided into six compartments. Five of these constitute beats and are managed by individual stalkers. They are named the Quoich (A), the Derry (B), North Geldie (C), South Geldie (D) and Dalvorar (E). The Quoich and the Derry comprise the Regeneration zone and the other three beats comprise the Moorland zone. The Regeneration zone is

managed with the dual objective of reducing deer numbers to achieve Scots pine regeneration. The Moorland zone is managed more for the estate's sporting interest and higher deer densities are tolerated. Area F, named Feith na Sgor, is typically assigned to the Derry. However, it is not managed as part of the Regeneration zone. It was decided to exclude data pertaining to this area from the analysis, to avoid confusion in the conclusions drawn

This project utilises data on deer counts, deer cull and Scots pine regeneration, collected within the Mar Lodge estate since 2001. Models are built using data on hinds only. Winter-limited area of occupancy is used as the context for hind densities. These delineations are justified in later sections. All modelled parameters are adjusted to the resolution of beat and year, to correspond with the level at which cull quotas are set and deer density is measured. This way, the quantified management output (regeneration of Scots pine) is equivalent to the resolution of management input (deer counts and cull quotas).

2: Background

2.1: Overview of background literature

The focus of much recent ecological research has been on the influence of density dependence on population dynamics (Coulson et al, 2001; Coulson et al, 2004; Putman et al, 2008). This literature generally concludes that population density is an omnipresent character of the dynamics of most populations (Coulson et al, 2004). The literature also explores the effect of density independence on population dynamics and proposes that both density dependence and density independence may influence the population dynamics of the same population, albeit to different extents and on different demographic rates (Albon et al, 1983; Albon et al, 1987; Leirs et al, 1997). The data used in these studies is sourced by two principal means; through observations of individuals within a population (for example: Clutton Brock et al, 2002; Coulson et al, 2004) and through examination of culled individuals (for example: Mysterud et al, 2001; Yoccoz et al, 2002; Carranza et al, 2004). This review additionally appraises the branch of literature centring on plant-herbivore dynamics; another heavily researched branch of ecology. Herbivory is widely recognised as having numerous and highly complex effects on plant community dynamics

(Crawley, 1983; Alverson et al, 1988; McInnes et al, 1992) which ultimately alters the balance of mortality and recruitment within these populations. Plant-herbivore interactions are modelled in a number of ways with varying complexity within the literature. This review primarily focuses on the wide use of linear models and generalized linear models in elucidating the relative strength and direction of parameter interaction.

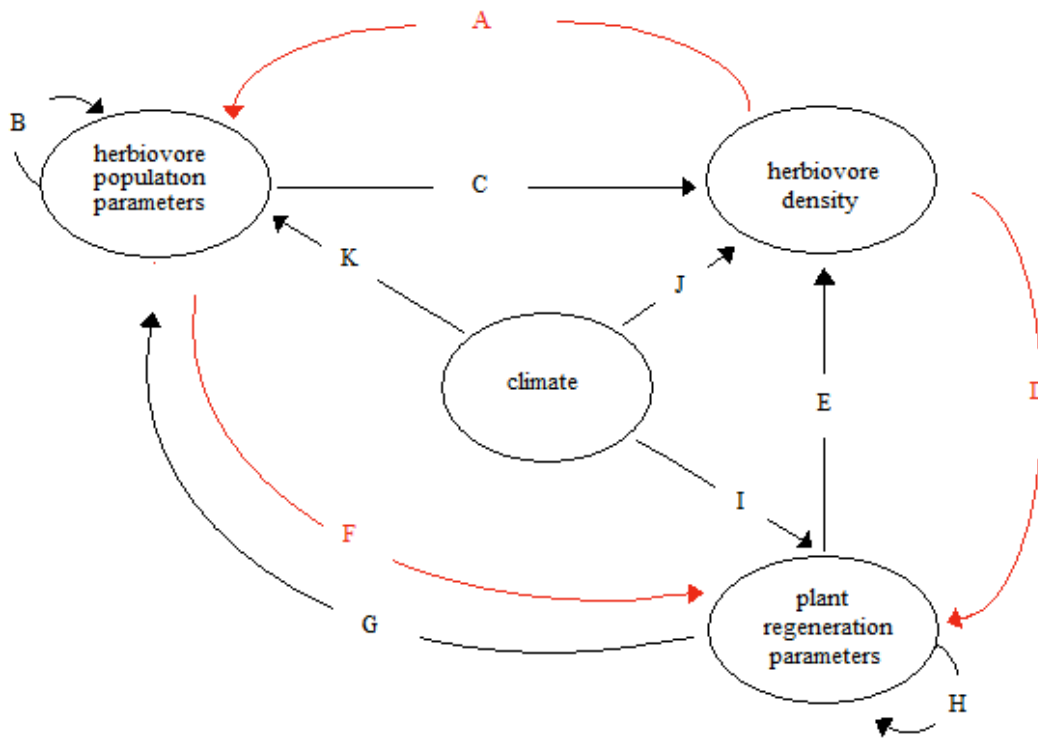


Figure 3: Principal interactions explored in the literature

These interactions are documented to varying degrees within the relevant literature. Pathways A (e.g. Coulson et al, 2001), B (e.g. Clutton Brock et al, 1983), C (e.g. Clutton Brock et al, 1983), D (e.g. Gill and Beardill, 2001) and I, J and K (e.g. Hallett et al, 2004) are most widely documented within literature relating to this study. The red pathways indicate the interactions that this study focuses on

2.2 Herbivore demographics

2.2.1: Long term studies

This study utilises cull data collected over the last 8 years to elucidate any strong covariance in demographic rates with counted measures of population density. Other

long term studies have permitted a more comprehensive understanding of the complexities of density dependence and the relative role of different demographic rates within this mechanism, revealing the utility of extended time series data. In particular, the extensive individual-based studies on the Red deer of Rum have yielded considerable insight into the effects of density and climate on deer demographic rates such as fecundity, survival, immigration and sex ratios (Clutton Brock et al, 1982, 1985, 1987, 1997; Albon and Clutton Brock, 1988; Coulson et al, 1997).

Demographic rates can also be qualified and quantified through examination of culled individuals, though if this is the exclusive mode of research, it does preclude elucidation of immigration and survival rates. Several extended time series analyses have been conducted using cull data (Forchhammer et al, 1998; Mysterud et al, 2001) with substantial ecological insight gained. There is some uncertainty over how representative cull data are; owing to the selective nature of most culling regimes (Martinez et al 2005). However, when the deer are culled for conservation management purposes, culling effort should be less discriminate and these concerns should be largely assuaged.

2.2.2: Definition of population parameters

Some of the parameters used in this study are exclusively based on data observations, such as weight and age. Others, such as calving rate and transience rate (immigration/emigration rate - assumed to be temporary) are inferred from available data and constitute rough estimates.

Density is one such parameter estimate that requires discretion when defining an appropriate area of occupancy and will depend, in part, on the response variables of interest. Coulson et al (1997) propose that determination of intrinsic population parameters could depend very much on the scale at which density is measured. Kruuk et al (1999) add to this by stating that the proportion of low ground is an important determinant of deer demographic rates such as fecundity and mortality, a view shared by Hallett et al (2004). The significance of low ground-area is also acknowledged in studies of plant- herbivore interaction, where winter-limited herbivore density is

viewed as the closest predictor of vegetation growth rate (Augustine and Jordan, 1998). The general conclusion being that winter-limited herbivore density is the best spatial descriptor of herbivore population parameters and vegetation regeneration.

Immigration rate is not an estimate generally inferred from cull data, but is used widely in observation-based studies (e.g. Clutton Brock et al, 1997; Milner-Gulland et al, 2001; Clutton Brock et al, 2002). In these studies it is viewed as a temporary or permanent movement exclusive to males, with females typically assumed to be philopatric (Milner-Gulland et al, 2004). However, disruptions caused to matrilineal groups by sustained heavy culls and general landscape management heterogeneity may result in temporary or permanent shifts in these groups that could be considered as immigration in the context of explicit estate boundaries.

Similarly, calving rate is not a parameter typically inferred from cull data, with other proxies for fecundity, such as proportion of hinds lactating and/or pregnant being used instead (e.g. Yoccoz et al, 2002). Observation-based studies, such as Clutton-Brock et al (2002) are able to estimate fecundity at specific spatial, temporal and demographic scales, further evidencing the profound ecological utility of such studies.

2.2.3: Parameter interaction

Once clearly defined and estimated, these parameters provide the component parts for quantifying parameter interaction and inferring pathways of cause and effect within population dynamics. Each parameter, as Mysterud et al (2001) explain, will have multiple dynamic interactions (Figure 3), varying widely in the degree of determination they comprise within these connections. Putman et al (2008) acknowledge the difficulty in determining the significance of each factor in influencing population structure.

Much of the literature explores the effect of population density on determination of demographic rates. Density is generally found to be a significant constraint on fecundity, survival and dispersal rates (Albon et al, 1987). These effects are most significant when populations are at high density, near to carrying capacity (Fowler, 1981, Albon et al, 2000), which large ungulate populations often are (McCullough,

1999). Mysterud et al (2001) use cull data to explore the finer-scale intricacies of density dependence, assessing sex and age-specific response to changes in population density. Their study reveals a greater rate of senescence in fecundity and weight for stags (but not hinds) when populations are at high densities. Clearly density dependence operates at multiple demographic scales.

Some studies have added further complexity to assessing parameter interaction, by investigating the significance of these interactions within different spatial and temporal scales. Coulson et al (1997) explore the significance of a range of spatial scales in determining calf winter survival in Red deer, concluding that higher resolution scales are the best predictor of this demographic rate. Subsequent to this, Coulson et al (2004) explore the significance of population density at different temporal scales in influencing population structure. Their study incorporates extensive time series data on Red deer population parameters with a view to elucidating the degree of persistence that deer density exerts on future population demographics. Their analyses reveal that a major shift in population density can have repercussions on recruitment and sex-specific survival rates for up to 30 years. In combination, these studies demonstrate the importance of considering different temporal and spatial components in population dynamics. However, in this study, it is the more direct repercussions of a shift in density that are of particular interest, to determine the significance of annual changes in management.

2.2.4: Modelling these interactions

Parameter interaction rates in this study were elucidated through linear modelling. Numerous other ecological studies have used linear or generalized linear modelling to examine multivariate interactions (Crawley, 2007). The wide use of this approach to model interactions makes for greater ease in comparisons between studies.

The premise of such models is to start with a maximal model, which incorporates all possible explanatory variables. Non-significant explanatory variables are then sequentially taken out of the model, unless this significantly reduces the variance explained by the model. The resulting construct is the minimal model, which only

includes variables that contribute towards description of the response variable (Guisan et al, 2002; Crawley, 2007).

Studies have often focused exclusively on modelling intrinsic population interactions (Albon et al, 1987), although more recently, environmental variation has been explored within these models as a widely acknowledged additional driver of demographic rates. Martinez-Jauregui et al (2009) incorporate measures of vegetation productivity (Normalised Difference Vegetation Index; NDVI) and broad-scale climatic variation (North Atlantic Oscillation; NAO) in modelling determination of density, weight, lactation and pregnancy rates within Red deer populations. This study does not incorporate such measures, with the intention being to model changes in demographic rates attributable exclusively to hind density.

2.3: Plant-herbivore interaction

Within this area of literature, the focus is typically on describing the demographic response of plant populations to herbivore density. As such, it is helpful to place the following literature in the context of the more detailed studies on herbivore demographics (as detailed above), to have a greater appreciation of the complexities in both plant and herbivore population dynamics and their interaction.

2.3.1: Long term studies

This project component utilises data on regeneration rates (annual measurements of density and growth) of Scots pine saplings collected over the last 7 years. Other similar studies have utilised extended time series data to elucidate the long term effects of herbivory on plant regeneration rates and plant community structure. Virtanen et al (2002) use data collected over 20 years to compare plant community structure when subjected to herbivory with community structure in the absence of herbivory; the duration of study being integral to the observations made. Similarly, Gill and Beardill (2001) use data from 13 studies of varying duration to appraise the effects of herbivory on woodland communities.

2.3.2: Parameters utilised

The parameters used to quantify the pressure exerted by herbivores on plant regeneration are typically observed levels of browse (Frelich and Lorimer, 1985; Welch et al, 1991; Beaumont et al, 1995; Gonzalez-Martinez and Bravo, 2001), observed herbivore density (Anderson, 1994; Augustine and Jordan, 1998; Forchhammer et al, 1998; Virtanen et al, 2002) or herbivore density inferred from pellet counts (Welch et al, 1991, Rao, 2008 (unpublished data)). Browse severity is the most widely used measure of stress exerted by herbivores, but should be quantified in relation to herbivore density to bear greater relevance to management intervention. Pellet counts provide a good estimate of locally explicit transient activity within vegetation stands, but may fail to capture the perennial pressure exerted by herbivores that count data (especially of philopatic demographic groups) may better capture. However, estimation of herbivore density presents the same quandaries as outlined in section 2.2.2, primarily in defining the appropriate spatial and temporal context for density estimation. As in this study, Augustine and Jordan (1998) use winter herbivore density to capture both spatial and temporal dimensions over a period of heightened herbivore pressure on plant communities (Brandner et al, 1990; Augustine and McNaughton, 1998). Table 7 and 8 (Appendix 1, p54) illustrate that, for the data resolution used in this study, hind density interacts more closely with Scots pine regeneration rate than either browse intensity or pellet count.

The parameters used to quantify the response of plants to herbivore presence are less subjective and include measures of stand density (Miller and Cummins, 1982; Welch et al, 1991; Gonzalez-Martinez and Bravo, 2001), sapling growth rate (Gonzalez-Martinez and Bravo, 2001), sapling recruitment (Vila et al, 2003), community diversity (Virtanen et al, 2002) and sapling mortality (Canham et al, 1994). This study uses growth rate and sapling density to assess regeneration rates.

A number of studies addressing plant-herbivore interactions used additional constraint parameters when modelling regeneration rate and community structure. These include soil type (Palmer and Truscott 2003), distance from seed source (Scott et al, 2000), availability of germination niches (Low 1988) and ground vegetation type and cover

(French et al, 1997). Inclusion of additional constraint parameters was beyond the scope of this study.

2.3.3: Plant-herbivore parameter interaction

It is generally accepted that herbivores limit that regeneration capacity of plants through browsing (Miller and Cummins, 1982; Forchhammer et al, 1998; Gonzalez-Martinez and Bravo, 2001). Some plant species, such as Scots pine, are more sensitive to browsing than others (Palmer and Truscott, 2003). The growth of browse-sensitive plant species is therefore likely to be more strongly determined by herbivore density. These species share characteristics such as a low growth rate and a low capacity to compensate for losses in biomass (Gonzalez-Martinez and Bravo, 2001).

The interaction between plant regeneration and herbivore browsing is complex and can vary widely depending on extrinsic factors such as season and intrinsic factors such as the stage-class of saplings (Crawley, 1989; Welch et al, 1991). With regard to the latter, as plants mature, the effects of herbivory typically transition from outright mortality to reductions in fecundity and growth rate (Crawley, 1983, 1989). Other intrinsic determinants include stand density, where stands of higher density have a greater resistance to herbivory and sapling height, where saplings of intermediate height are most vulnerable and sensitive to browsing (Welch et al, 1991).

The majority of studies consider these additional intrinsic and extrinsic factors, but the principal focus is typically on the effect of herbivore density on growth and the balance of recruitment and survival of targeted plant species. This has been documented for a wide range of both plant and herbivore species. Frelich and Lorimer (1985) studied the impacts of White-tailed deer (*Odocoileus virginianus*) on hemlock (*Tsuga sp.*) within the forests of Michigan, concluding that higher deer densities correlate with a reduction in fecundity and consequent recruitment in hemlock. Brandner et al (1990) assessed the impacts of moose (*Alces alces*) herbivory on Balsam fir (*Abies balsamea*), also within Michigan. They conclude that with increasing moose density, Balsam fir growth was suppressed and recruitment of saplings fell. Gill and Beardill (2001) express the particularly severe impacts of deer browsing on sapling growth rate. They refer to a study carried out by Shaw et al

(1974), which reported that high levels of browsing could keep oak (*Quercus sp.*) saplings at <50cm in height for up to 25 years. Presumably similar growth suppression is possible for Scots pine saplings if Red deer numbers are not controlled.

2.3.4: Modelling these interactions

Linear modelling or generalised linear modelling lends itself well to analysing plant-herbivore interactions, assuming there is spatial and temporal correspondence between parameters. Rooney et al (2000) use generalised linear modelling to disentangle the multivariate determination of hemlock recruitment, one of the explanatory variables being White-tailed deer density. They initially model each explanatory variable against hemlock recruitment separately, with several incidences of significance in interaction. However, in their multivariate generalised linear model, they fail to detect any significant interactions. Their analysis reveals the utility of using multivariate linear modelling to elucidate true significance in interaction terms, with the model's capacity to disentangle autocorrelation (which is often hidden when using univariate modelling). They also describe the shortcomings of such models, which include the assumption of interaction linearity and the ambiguity of causal order.

The concepts of predator-prey interaction have more recently been applied to modelling the interaction between plants and herbivores (Caughley and Lawton, 1981; Brandner et al, 1990), where the numbers of both predator and prey fluctuate in accordance with one another in a lagged time frame. The degree of intimacy between herbivore and plant densities (and generally predator-prey interaction) will depend largely on the feeding behaviour of the herbivore/ predator, particularly whether it is a specialist or a generalist feeder (Gill et al, 2000). Red deer are generalist feeders (Forsyth et al, 2000) and consequently, deer density is likely to have a greater bearing on Scots pine regeneration than Scots pine density will on Red deer density. As such, for the purpose of this study, the causal order of plant-herbivore interaction is considered to be principally unidirectional.

2.4: Model Projection

In this study, the interactions elucidated are built into a deterministic model to project Scots pine regeneration rates based on projected Red deer hind densities. Such a forecast model will inevitably fail to accurately project these demographic rates, but can still be of interest. None of the aforementioned studies used temporal extrapolation of parameter interaction. Rooney et al (2000) discuss spatial extrapolation of parameter interaction, deciding, however, that habitat heterogeneity precludes such extrapolation.

3: Methods

3.1: Data collection

This study has utilised data from three separate datasets, two pertain to Red deer demographic rates, the other pertains to Scots pine regeneration rates. Data for each of these was collected within Mar Lodge estate over the last 15 years. All values for deer demographics are based exclusively on hind data. Hinds are philopatric (e.g. Milner-Gulland et al, 2004), therefore there will be a greater degree of intercorrelation between their demographic rates and spatially explicit extrinsic factors, such as vegetation regeneration rate. The demographic rates utilised in this study pertain to measurements taken at different times and over different durations. The mode of grouping these demographic rates by year is illustrated in figure 6 (Appendix 1, p59).

3.1.1: Count data

Annual Red deer counts have been carried out in late winter since the National Trust for Scotland took over ownership of Mar Lodge estate in 1995. However, due to discontinuity in counting method, count data for this study pertains to the period 2001-2008. With raw count data additionally delineated by beat, the total sample size for count data is 40. With these data being annual and beat-specific rates, it was consequently necessary to transform cull and regeneration data into annual and beat-specific rates.

3.1.2: Cull data

Cull data has also been collected since 1995. Cull data used for this study correspond with the temporal span of data used from deer count records: 2001-2008. Within the raw data, this period pertains to a sample size of 3340. However, to model these data against annual count and regeneration data, annual and beat-specific means are calculated for continuous cull data and proportions are calculated for binomial cull data, resulting in a sample size of 40.

3.1.3: Regeneration data

Regeneration data have been collected since 2002 within 17 regeneration quadrats within the Regeneration zone. These quadrats were established to determine annual sapling regeneration rates in subjection to browsing by Red deer. Within these quadrats, 259 Scots pine saplings were initially marked for annual quantification of regeneration rate. This total sample size diminished over successive years due to sapling mortality up until 2007, when an additional 235 Scots pine saplings were marked. For this study, mean annual values for these data were calculated for the period 2002-2008 and further delineated by beat, with a resultant sample size of 14 (the Regeneration zone, where these data were collected, comprises 2 out of the estate's 5 beats (figure 2)). This conversion was necessary for modelling Scots pine regeneration rate against count and cull data.

3.2: Parameters used in analysis

All parameters used in this study were extracted from the aforementioned datasets. Parameters are delineated and modelled as beat and year-specific rates. The spatial delineation of 'beat' was used to maximise the sample size. However, it is the spatial delineation of 'zone' that is used as the spatial explanatory variable in model series 1, to explore the disparities in hind population parameters attributable to management disparities (principal management disparities are zone specific as opposed to beat specific).

3.2.1: Description of deer population parameters utilised

Hind density is a division of the number of counted hinds by the winter-limited area of occupancy (winter density also used by Kruuk et al, 1999; Catchpole et al, 2000; Coulson et al, 2001; Hallett et al, 2004). Values for winter-limited area of occupancy are taken from Luxmoore (2002, unpublished data) and constitute the beat-specific area under 600 meters. Hind density is the principal explanatory variable used in the analyses. Weight and age constitute continuous variables in the raw cull data and are therefore converted into mean values within the summary dataset.

Fecundity is calculated as the number of lactating hinds that are pregnant. There are a number of ways in which fecundity could be calculated. However, the condition of being in milk and pregnant is a suitable response variable, being that the condition is particularly sensitive to changes in population density (Clutton-Brock et al 1982, Albon et al, 1983). ‘Hinds lactating’ and ‘hinds pregnant’ both constitute binomial variables within the raw cull data. Their correspondence is also binomial (hinds lactating and pregnant/ hinds not lactating and pregnant). The incidence of this correspondence is calculated as a proportion of all hinds culled (a division of the number of hinds lactating and pregnant by the total number of hinds) for entry into the summary dataset. This measure of fecundity will now be denoted ‘MP’, for hinds in milk (lactating) and pregnant.

Transience rate and calving rate are variables inferred from the count and cull data. These values are rough estimates intended as comparative measures (between beats and over successive years) and should not be taken out of this comparative context.

Calving rate is calculated retrospectively: calves parturated in year $x-1$ is calculated as the number of calves counted (year x) added to the number of lactating hinds culled (year x). The corresponding hind spring-population for year $x-1$ is calculated as the number of hinds counted (year x) added to the number of hinds culled (year x). Calving rate is inferred to be the division of calves’ parturated by the corresponding hind spring-population-estimate (for more detailed description of this calculation, refer to section 7.2, Appendix 1, p55).

Transience rate is calculated as: observed population (year x) minus estimated population (year x) divided by beat area (km^2). A similar methodology is used by Armstrong et al (2001). The estimated population principally comprises addition of recruited hinds and subtraction of culled hinds to the observed population of year $x-1$. The premise of this comparison is to infer a rate of hind movement based on the degree of disparity between the observed and estimated population values (for more detailed description of this calculation, refer to section 7.3, Appendix 1, p55). It is generally accepted that there is some degree of hind movement over the Mar Lodge estate boundary and between beats (Luxmoore, 2002, unpublished data). A positive transience rate equates to assumed hind immigration, a negative transience rate equates to assumed hind emigration.

Weight, age, MP, calving rate and transience rate are herein referred to as 'hind population parameters', distinct from hind density.

3.2.2: Description of Scots pine regeneration parameters utilised

Regeneration parameters pertain to 7 years of data collected within 2 of the estate's 5 beats, with a resultant sample size of 14 for each modelled parameter. Consequently, analyses that incorporate these data have low statistical power and should be viewed with caution.

Sapling density is measured as saplings per hectare. This measure gives a quantitative estimate of the dynamic between sapling recruitment and sapling mortality, both of which can be influenced by herbivore browsing (Canham et al, 1994; Gill and Beardill, 2001). When mortality exceeds recruitment, sapling density will decrease, with the reverse dynamic, sapling density will increase. Density estimates per hectare are extrapolated from sapling density within the regeneration quadrats.

Sapling growth rate is measured in centimetres per year and is a widely used measure of herbivore impact (Cermak, 1998; Gill and Beardill, 2001). Caution was proposed by the National Trust for Scotland (R. Luxmoore, pers comm) in interpreting these data in relation to deer density, based on the notion that adjacent vegetation height is the greater constraint on Scots pine sapling growth. This issue is addressed further

within the discussion, but for the following analyses it is assumed that deer density is the principal hierarchical determinant of sapling and adjacent vegetation growth, and therefore is an adequate explanatory parameter.

3.2.3: Additional parameters utilised

A temporal component, denoted 'year' and a spatial component, denoted 'zone' provide the two final parameters used in the analysis (for further exploration of these parameters, refer to Coulson et al (1997) and Coulson et al (2004)). These extrinsic parameters are included to enable assignment of additional residual variation to an approximate context, to inform any further investigations. The temporal scale is self-explanatory. The spatial scale pertains to the two overarching management zones; the Moorland zone (which comprises three beats) and the Regeneration zone (which comprises two beats). These zones have disparate management objectives that may determine variation in response variables that cannot be attributed to variation in intrinsic parameters. It could also be that significance at this spatial scale relates to distinctions in zone-specific topography/ climate/ habitat type (Clutton Brock et al, 1982). The parameter 'zone' is only implicated in model series 1, which includes data on the Moorland and Regeneration zone. Model 2-4 are based on data pertaining to the Regeneration zone only.

3.3: Data analyses

3.3.1: Functions used in R

All analyses were carried out using the statistical program R, a recently developed environment for data analysis and graphics (Crawley, 2007).

Linear modelling (denoted `lm` in R) was used to quantify parameter interactions for all the models within the analysis. It assumes a Gaussian (i.e. normal) distribution (Crawley, 2007) for all variables and a predefined link function (such as logarithm) for each parameter interaction (Crawley, 2007). Models comprise a single response variable (fitted on the y axis) and one or more explanatory variables (fitted along the x axis). Explanatory variables are chosen to explain as much residual variation in the

response variable as possible. The total variation in the response variable is denoted SSY (sum of squares along y axis). The unexplained variation in the response variable is denoted SSE (sum of squares error). As such, the variation explained by the explanatory variables can be written as $SSY - SSE$ (Crawley, 2007) and is stated as an R^2 value. An R^2 of 1 accompanies a model that explains all of the variation in the response variable. An R^2 of 0 accompanies a model that explains none of the variation in the response variable.

Linear modelling or generalised linear modelling has been used in similar studies to elucidate the degree of interaction between (and within) herbivore population parameters and plant regeneration parameters (e.g. Welch et al, 1991; Clutton Brock et al, 1997; Rooney et al, 2000; Martinez-Jauregui et al, 2009).

3.3.2: Model description

Model series 1 explores the variation in hind population parameters that is attributable to changes in hind density. Model series 2 explores the interaction between these hind population parameters, hind density and Scots pine regeneration parameters. Model series 3 attempts to determine the degree of variation in Scots pine regeneration parameters that is directly attributable to changes in hind density and indirectly attributable to changes in hind density (by way of its interaction with hind population parameters and their interaction with Scots pine regeneration). Model series 4 attempts a temporal extrapolation of the cumulative interaction between hind density and Scots pine regeneration under different culling regimes.

Model series 1: Hind population parameters ‘weight’, ‘age’, ‘MP’, ‘calving rate’ and ‘transience rate’ are first modelled individually against hind density, to examine the univariate interactions. Additional exploration is made into whether parameter interactions with hind density are stronger for year x or year $x-1$. Minimal multivariate models were then constructed for each hind population parameter to determine the degree of interaction exclusively attributable to hind density. The maximal models incorporate each of the other hind population parameters, hind density, zone and year as explanatory variables.

Model series 2: Scots pine regeneration parameters ‘density’ and ‘growth’ are first modelled individually against hind density, to explore the degree of univariate interaction. Additional exploration is made into whether parameter interactions with hind density were stronger for year x or year $x-1$. Minimal multivariate models are then constructed for each regeneration parameter to determine the degree of interaction exclusively attributable to hind density, as in Model series 1. The maximal models incorporate all hind population parameters, hind density and year as explanatory variables.

Model series 3: This model aims to elucidate the cumulative effect of hind density on each of the Scots pine regeneration parameters. The model is constructed from the interaction terms elucidated in the minimal Models of series 1 and 2. The cumulative effect of hind density is calculated by multiplying the degree of interaction between hind population parameters and hind density (within the minimal multivariate models of series 1) with the degree of interaction between hind population parameters and Scots pine regeneration (elucidated from the minimal models of series 2). Added to this is the direct interaction estimate between hind density and Scots pine regeneration (also a component of Model series 2).

Model series 4: The parameters from Model series 3 are then used to construct a deterministic matrix model to project the interaction between hind density and Scots pine regeneration. The model initially utilises the parameter intercept values elucidated in Model series 1 and 2 (adjusted for the Regeneration zone), which are then projected based on the parameter interaction values and year of interaction, also elucidated in Model series 1 and 2. Four such matrices are built in all. The first two matrices project the interaction between hind density and Scots pine growth under two disparate culling regimes, a zero cull and a high cull (2.5 hinds/ km²). The second two matrices make the same projection for interaction between hind density and Scots pine density.

4: Results

4.1: Model series 1

These interactions pertain to pathway A (figure 3) for univariate interactions and pathways A and B (figure 3) for multivariate interactions

| Response variable | | | Explanatory variable | | | | | |
|-------------------|-----------------|----------------|----------------------|------|-----------|-----------------------|--------------------|----------|
| Model | Variable name | Transformation | <i>F</i> | d.f. | std error | <i>R</i> ² | Variable name | Estimate |
| 1a | weight (kg) | None | 3.9 | 1,38 | 1.92 | 0.07 | hind density (x) | -0.049 |
| 1b | age | None | 0.57 | 1,33 | 1.24 | -0.13 | hind density (x-1) | -0.013 |
| 1c | MP (%) | None | 2.54 | 1,38 | 0.09 | 0.04 | hind density (x) | -0.002 |
| 1d | calving rate | log10 | 1.26 | 1,28 | 0.34 | 0.01 | hind density (x-1) | -0.006 |
| 1e | transience rate | None | 8.36* | 1,33 | 8.65 | 0.18 | hind density (x-1) | -0.34 |

Table 1: Univariate interaction with hind population parameters

F values marked with a star (*) denote models that show significance in trend for $p = > 0.05$. The degree of interaction between explanatory variables and the response variable is given by the Estimate. For this model, the Estimate states the change in the response variable (based on the corresponding units of measurement) resulting from an increase in hind density of 1 hind /km². Response variable units: weight in kg, age in years, proportion of hinds MP, calving rate/ hind, transience rate/ km².

In all univariate interactions, variables are negatively correlated, indicating that hind density acts as a constraint on each of the modelled hind population parameters. Based on these interaction estimates, a reduction in hind density would result in an increase in the rate of each modelled response variable. Weight and MP interact directly with hind density. Age, calving rate and transience rate interact more closely with hind density in the year ^{x-1}. Hind density describes very little of the residual variation in the modelled response variables, with the exception of transience rate (*R*² 0.18). Transience rate is also the only parameter to show significance in trend with hind density.

| Response variable | | | Explanatory variables | | | | | |
|-------------------|-----------------|----------------|-----------------------|-------|-----------|-----------------------|--------------------|----------|
| Model | Variable name | Transformation | <i>F</i> | d.f. | std error | <i>R</i> ² | Variable name | Estimate |
| 1f | weight (kg) | None | 4.08* | 10,29 | 1.48 | 0.44 | age | 0.457 |
| | | | | | | | MP | 5.11 |
| | | | | | | | zone | 1.3 |
| | | | | | | | year | NA |
| 1g | age | None | 3.84* | 8,26 | 0.95 | 0.4 | hind density (x-1) | -0.006 |
| | | | | | | | weight | 0.211 |
| | | | | | | | year | NA |
| | | | | | | | hind density (x) | 0.01 |
| 1h | MP (%) | None | 1.96 | 10,24 | 0.08 | 0.22 | age | 0.02 |
| | | | | | | | transience rate | -0.0002 |
| | | | | | | | zone | 0.05 |
| | | | | | | | year | NA |
| | | | | | | | hind density (x) | 0.005 |
| 1i | calving rate | log10 | 4.99* | 9,25 | 0.1 | 0.51 | age | 0.02 |
| | | | | | | | zone | 0.2 |
| | | | | | | | year | NA |
| | | | | | | | hind density (x) | 0.005 |
| 1j | transience rate | None | 8.92* | 2,32 | 7.88 | 0.32 | hind density (x-1) | -0.59 |
| | | | | | | | zone | -9.8 |

Table 2: Multivariate interaction with hind population parameters

Listed explanatory variables are those that contribute to description of the corresponding response variable and hence constitute the most parsimonious model. There is no single interaction estimate for year, hence exclusion of these rates from this summary table.

In these models, a multivariate approach is applied to disentangle the multiple causal factors influencing hind population parameters. This series of models additionally incorporates intra-parameter (pathway B, figure 2) and spatio-temporal (zone and year) determination of hind population parameters. Consequently, these models permit greater accuracy in estimating the degree of parameter variation exclusively attributable to hind density. Hind density retains descriptive power within models 1g to 1j (hind age, MP, calving rate and transience rate). In contrast to the corresponding univariate models, model 1h and 1i show that hind density is a positive correlate of MP and calving rate. However, the switch in interaction is insubstantial, with interaction estimates for all four of these models being very low. Calving rate is directly determined by hind density in model 1i, whereas in model 1d (univariate interaction) it interacts more closely with hind density in the year x-1. Year acts as a partial determinant of parameter variation in weight, age, MP and calving rate but not transience rate. Zone acts as a partial determinant of weight, MP, calving rate and

transience rate, where hinds in the Regeneration zone have a higher estimate of weight, MP and calving rate but a significantly lower estimate of transience rate (tending towards considerable emigration). All the multivariate models describe the response variable with reasonable success, the lowest R^2 being 0.22 for model 1h (description of MP). Equally, only model 1h lacks significance in trend between explanatory and response variables.

4.2: Model series 2

These interactions pertain to pathway D (figure 3) for univariate interactions and pathways D and F (figure 3) for multivariate interactions.

| Response variable | | | Explanatory variable | | | | | |
|-------------------|---------------|----------------|----------------------|------|-----------|-------|--------------------|----------|
| Model | Variable name | Transformation | <i>F</i> | d.f. | std error | R^2 | Variable name | Estimate |
| 2a | density/ ha | None | 8.42* | 1,12 | 4619 | 0.36 | hind density (x-1) | -2520.2 |
| 2b | growth (cm) | None | 23.99* | 1,12 | 1.39 | 0.64 | hind density (x) | -1.32 |

Table 3: Univariate interaction with Scots pine regeneration parameters

Response variable units: sapling density/ hectare, sapling growth in cm

In the univariate interactions, hind density is a negative correlate of both Scots pine sapling density and sapling growth, indicating that hind density acts as a constraint on both these rates. Model 2a predicts that Scots pine sapling density is particularly sensitive to changes in hind density, where a reduction in 1 hind/ km² results in an estimated gain of 2520.2 saplings/ ha. Scots pine sapling growth is much less responsive to changes in hind density, where a reduction in 1 hind/km² results in a gain in height of just 1.32cm. The interaction between hind density and sapling growth is direct, whereas sapling density interacts more strongly with hind density in the year ^{x-1}. Despite being univariate analyses, both models have high R^2 values and both show a high degree of significance in trend.

| Response variable | | | Explanatory variable | | | | | |
|-------------------|---------------|----------------|----------------------|------|-----------|-----------------------|--------------------|----------|
| Model | Variable name | Transformation | <i>F</i> | d.f. | Std error | <i>R</i> ² | Variable name | Estimate |
| 2c | density/ ha | None | 2.49 | 7,4 | 4040 | 0.49 | hind density (x-1) | -5230 |
| | | | | | | | calving rate | 26691 |
| | | | | | | | year | NA |
| 2d | growth (cm) | None | 88.32* | 7,6 | 0.33 | 0.99 | hind density (x) | -0.85 |
| | | | | | | | year | NA |

Table 4: Multivariate interaction with Scots pine regeneration parameters

Listed explanatory variables are those that contribute towards description of the corresponding response variable and hence constitute the most parsimonious model. As with models 1f to 1j, there is no single interaction estimate for year, hence exclusion of these rates from this summary table.

Hind density retains its interaction with Scots pine density and growth in the multivariate models. The direction and year of interaction between hind density and Scots pine regeneration parameters is the same in model 2c and 2d as in the corresponding univariate models. The magnitude of interaction is altered in both cases, with the sensitivity of sapling density to changes in hind density doubling and the sensitivity of sapling growth to changes in hind density being approximately halved (model 2c response of -5230, model 2a response of -2520; model 2d response of -0.85, model 2b response of -1.32). There is a degree of temporal determination in the response variable of both Scots pine sapling density and growth. For sapling growth, year constitutes the only additional explanatory variable and adds considerably to the description of sapling growth (*R*² of 0.99 compared to 0.64 in the univariate model; 2b). Model 2d shows a high significance in trend at the $p = > 0.05$ level.

For sapling density, calving rate is an additional interaction term. The model estimates that an increase in calving rate of 1 (i.e. a change in calving rate from 0% to 100%), corresponds with an increase in sapling density of 26691 saplings/ ha. The direction and magnitude of this interaction is implausible. The magnitude of interaction cannot be adjusted without disregarding the entire model. However, a switch in causal pathway between the two parameters, making sapling density the explanatory variable, results in a more plausible interaction (figure 3; switch from pathway *F* to

pathway G). Model 2c shows no significance in trend but performs relatively well in describing sapling density (R^2 0.49).

4.3: Model series 3

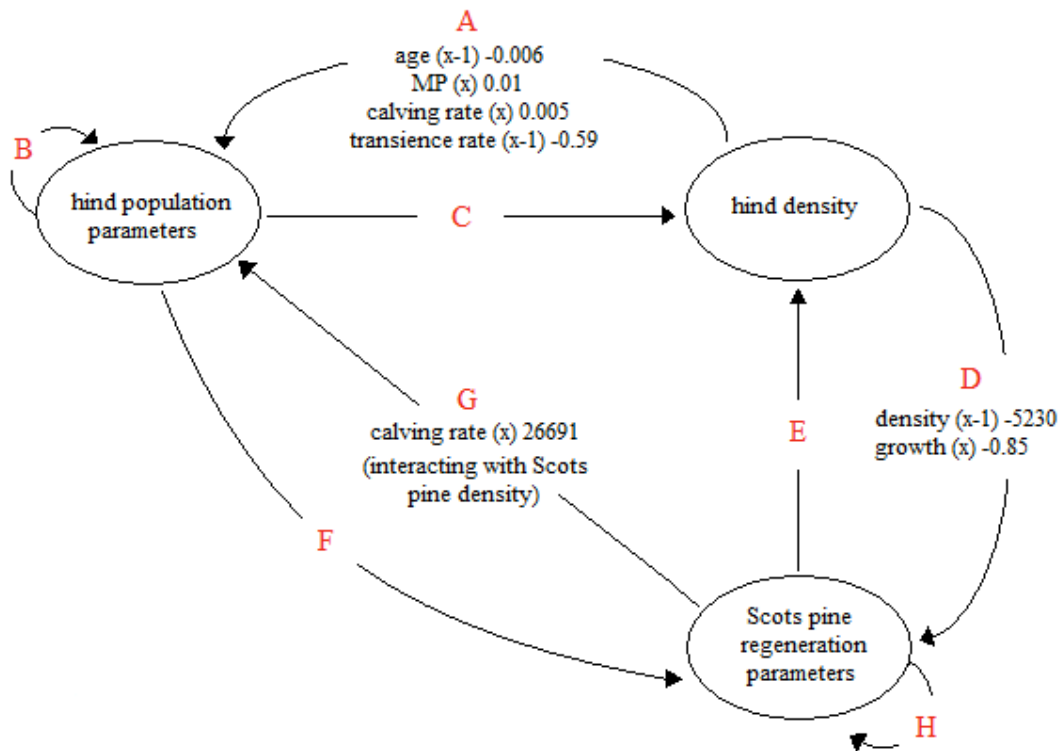


Figure 4: Causal flow diagram of interactions elucidated in Model series 1 and 2

The year of interaction for each pathway is given in brackets. Interaction rates are those elucidated in model series 1 and 2

The principal aim of this model is to calculate the cumulative interaction rate between hind density and Scots pine regeneration. Supposing synchrony in interaction terms between pathways A and F, the annual rate of increase in sapling height, as determined by changes in hind density, can be written as follows:

$$SG = ((H^x - H^{x-1}) * Di) + [(H^x - H^{x-1}) * (Ai * Fi)]$$

Based on the same assumption, the annual rate of increase in sapling height, as determined by changes in hind density, can be written as follows:

$$SD = ((H^{x-1} - H^{x-2}) * Di) + [(H^{x-1} - H^{x-2}) * (Ai * Fi)]$$

Where SD is the sapling density, SG is sapling growth, H is the hind density, D is the interaction rate between hind density and sapling regeneration, A is the interaction rate between hind density and any given hind population parameter and F is the interaction rate between said hind population parameter and sapling regeneration. A change in hind density influences each of these other interaction rates and ultimately the rate of Scots pine regeneration. The square brackets enclose the equation component for indirect interaction. This component is repeated (as a further addition to either SD or SG) for any additional parameters implicated in pathways A and F. Supposing $(H^x - H^{x-1}) = 1$, the interaction values will be those stated in figure 4. However, given that there is no synchrony in parameters implicated in pathways A and F (figure 4), the equation is simplified to:

For Scots-pine growth rate: $SG = ((H^x - H^{x-1}) * Di)$

For Scots-pine density: $SD = ((H^{x-1} - H^{x-2}) * Di)$

Hind density acts as a direct constraint on Scots pine regeneration, but does not affect regeneration by any indirect pathways, excluding those that involve feedback loops, e.g. causal pathway A-C-D (figure 4).

4.4: Model series 4

In this model series, the interaction between hind density and Scots pine regeneration rate is projected to gain greater insight into how this dynamic may change under disparate culling regimes. In summary, the model predicts Scots pine regeneration via the causal pathway A-C-D (figure 4), where the loop A-C predicts hind density over successive years, which then determines the annual rate of Scots pine regeneration (pathway D). The hind parameters utilised in this model are those that equate to a direct increase or decrease in hind density. Values for year and rate of interaction between hind density (explanatory variable) and calving rate and transience rate

(response variables) are taken from the previous models (pathway A, figure 4). For the purpose of this model, these rates are assumed to be constant for both response to and explanation of hind density (causal feedback pathway A-C, figure 4). Section 6.4 (appendix 1, p56) provides a more detailed description of the calculations involved in building these models.

4.4.1: Model 4a

| Year | Cull | Transience rate/ ha | Calving rate/ hind | Hind density/ km ² | Scots pine density/ ha | Scots pine height (cm) |
|------|------|---------------------|--------------------|-------------------------------|------------------------|------------------------|
| 2009 | 2.5 | 1.83 | 0.26 | 0.70 | 1885.71 | 0.29 |
| 2010 | 2.5 | 2.04 | 0.26 | 0.48 | 3690.38 | 0.48 |
| 2011 | 2.5 | 2.17 | 0.26 | 0.30 | 4868.24 | 0.63 |
| 2012 | 2.5 | 2.27 | 0.26 | 0.18 | 5773.75 | 0.74 |
| 2013 | 2.5 | 2.34 | 0.26 | 0.09 | 6415.19 | 0.81 |
| 2014 | 2.5 | 2.39 | 0.26 | 0.02 | 6885.10 | 0.87 |

Table 5: Coupled projection based on a high cull

Table 5 shows a coupled projection of hind density and consequent Scots pine regeneration in relation to an annual cull of 2.5 hinds/ km². This model required preliminary input of two sequential estimates for transience rate, calving rate and hind density (based on intercept and estimate values elucidated in model series 1 and 2) to then operate independently. The first line of tabulated values in model 4a differ from those of model 4b based on the disparate culling regimes and their effect on the aforementioned preliminary parameter estimates (these preliminary estimates are not tabulated). This difference does not affect the principal aim of the model, which is to appraise the interaction between parameters as opposed to their precise numeric correspondence

A cull of 2.5 hinds/ km² results in a steady decrease in hind density, a rapid increase in Scots pine sapling density and a steady increase in Scots pine sapling height. The projection of Scots pine regeneration shows exponential decay, whereas the projection of hind density shows reverse exponential decay (figure 5, plot A and B). This can be attributed to transience rate, which increasingly compensates for reductions in hind density (through hind immigration - tabulated as positive transience). This progressive compensation slows the rate of decrease in hind density, which in turn slows the rate of increase in Scots pine sapling density and height.

4.4.2: Model 4b

| Year | Cull | Transience rate/ha | Calving rate/hind | Hind density/km ² | Scots pine density/ha | Scots pine height (cm) |
|------|------|--------------------|-------------------|------------------------------|-----------------------|------------------------|
| 2009 | 0 | -0.21 | 0.28 | 5.22 | -3246.23 | -0.59 |
| 2010 | 0 | -0.62 | 0.29 | 5.67 | -6891.85 | -0.97 |
| 2011 | 0 | -0.88 | 0.29 | 6.04 | -9224.72 | -1.29 |
| 2012 | 0 | -1.10 | 0.29 | 6.32 | -11176.49 | -1.52 |
| 2013 | 0 | -1.27 | 0.29 | 6.54 | -12618.45 | -1.71 |
| 2014 | 0 | -1.39 | 0.29 | 6.70 | -13757.61 | -1.85 |

Table 6: Coupled projection based on a zero cull

A coupled projection of hind density and consequent cumulative Scots pine regeneration in relation to a zero annual cull

A zero cull results in a steady increase in hind density, a rapid decrease in Scots pine sapling density and a steady decrease in Scots pine sapling height. The premise of this model is the same as for model 4a. The projections are the reverse of those estimated in model 4a. An increase in hind density has little effect on calving rate, owing to the low interaction estimate between these parameters. Increase in hind density results in a steady increase in hind emigration rate (negative transience rate) which results in exponential decay in hind density increase (figure 5, plots C and D). This trend results in reductions in Scots pine sapling density and height, following a reverse exponential decay curve.

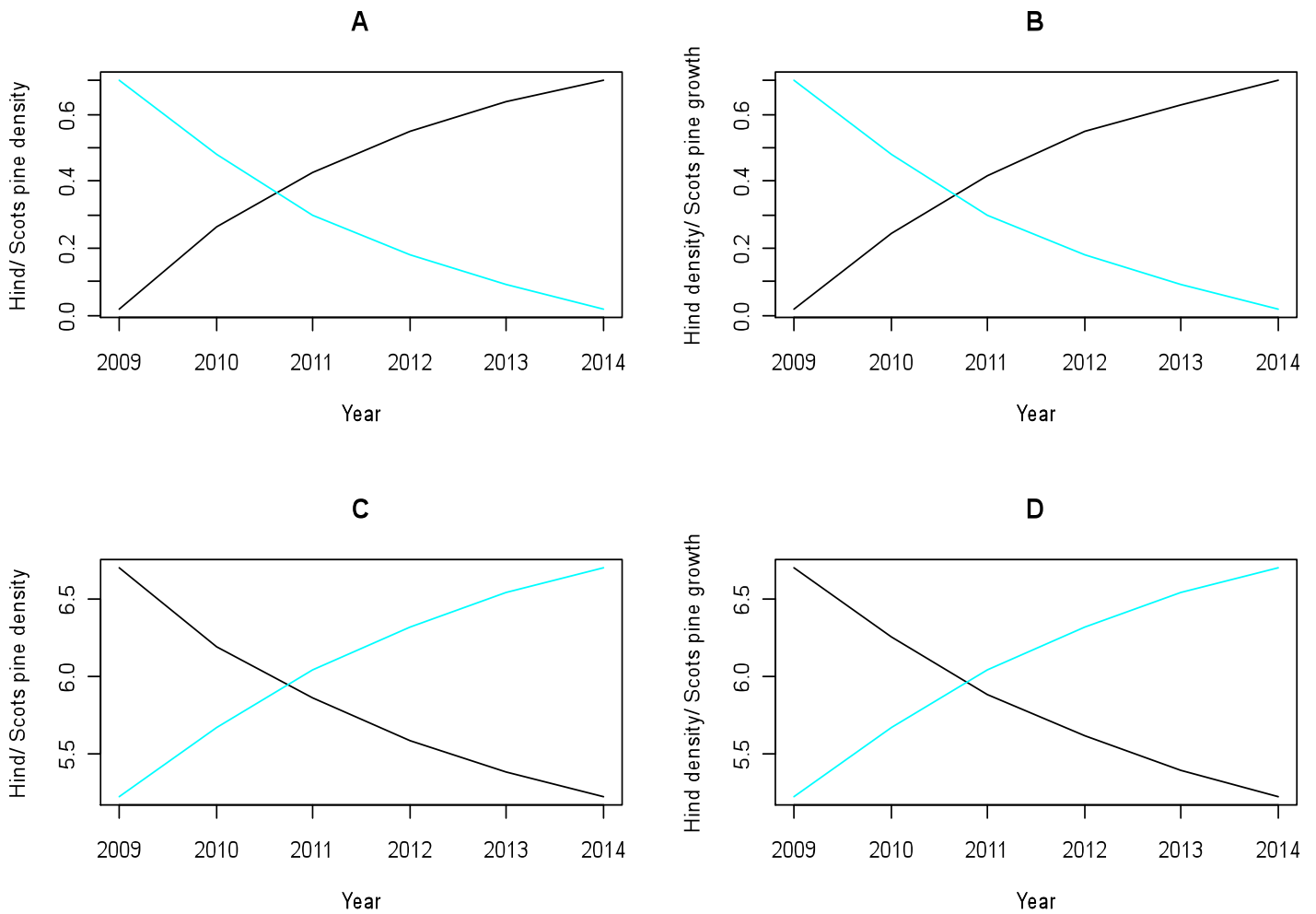


Figure 5: Graphical representation of projections

Plots A and B pertain to model 4a, plots C and D pertain to model 4b. Black lines represent the change in rate of Scots pine regeneration. Blue lines represent the change in rate of hind density. Plots C and D show exact inversions of the projected interactions estimated in plots A and B. The scale on the y axis pertains to hind density.

5: Discussion

5.1: Results in context

5.1.1: Model series 1

This series was primarily concerned with elucidating the effect of hind density on hind demographic rates (pathway A, figure 2). In the univariate models, hind density is found to interact negatively with all demographic rates, as would typically be

expected (Albon et al, 1987, Clutton Brock et al, 2002). The closest and most negative interaction is with transience rate, where higher hind densities predict higher hind emigration rates. Some of these interactions changed when modelling multivariate parameter interaction. Calving rate and MP both became positive correlates of hind density, although the degree of correlation in both univariate and multivariate models was low for these parameters. MP and calving rate can be roughly interpreted as fecundity; a more widely used term in the literature. Fecundity is generally observed to be a strong negative correlate of hind density (Albon et al, 1983; Clutton-Brock et al, 1987; Albon et al, 1987; Mysterud et al, 2001). The opposing correlation between fecundity and hind density observed in this study is possibly erroneous, but may also be attributable to the low deer densities within the estate, resulting in density exerting less of an influence on demographic rates (Fowler, 1981; Albon et al, 2001, Smart et al, 2008). Hind weight shows no interaction at all with hind density in the multivariate model. Again, this can possibly be explained by the reduced effect of density dependence when populations are already small (Fowler, 1981). Only hind age and transience rate retain both their explanatory power and direction of interaction with hind density. The interaction between hind density and transience is of particular interest, as hinds are typically believed to be philopatric (Milner-Gulland et al, 2004). However, if there was no boundary interchange of hinds within the southern Cairngorms, Mar Lodge estate would have extirpated their hind population long ago through intensive culling. Model 1j confirms that reductions in hind density within the estate correspond with an increase in hind transience rate; which here denotes immigration (a reduction in 1 hind/km² corresponds with an increase in immigration rate of 0.59 hinds/ km²).

Model series 1 also incorporated spatial and temporal parameters. The spatial parameter delineated data by management zone; either 'Moorland' or 'Regeneration'. The Moorland zone is managed for the estate's sporting interest and the Regeneration zone is managed with the objective of achieving Scots pine regeneration. As such, cull severity is greater within the Regeneration zone. Hinds in the Regeneration zone were found to have higher rates of weight, age and calving, which likely pertains to the lower hind densities within this area. Conversely, the Regeneration zone accounted for lower transience rates (tending towards emigration), which could be attributed to the high severity of annual culls disrupting site fidelity of matrilineal

groups. Martin and Baltzinger (2002) explored the effect of hunting on White-tailed deer density and found that increased hunting pressure was a major disruption to deer movements and their degree of transience. Based on the interaction rates of model series 1, it is likely that the interaction between zone and transience rate counteracts the effect of reducing deer densities on transience rate. Coulson et al (2001) explore the significance of different spatial scales in determination of deer demographic rates, however, their analysis relates to spatial scales irrespective of management. The spatial differences in demographic rates observed in this study are more likely to pertain to management disparities. Coulson et al (2004) also explore the significance of multiple temporal scales in determination of deer demographic rates. Variation in both age and transience rate were found to interact more closely with hind density in the previous year. Based on the observations of Coulson et al (2004), these demographic rates could show a degree of interaction with hind density many years previous. All parameters except transience rate showed further temporal determination in their interaction with ‘year’.

5.1.2: Model series 2

The aim of this model series was to determine the degree of interaction between hind density and hind population parameters and Scots pine density and growth rate. In the univariate analyses, hind density is a significant negative correlate of both regeneration parameters; sapling growth and sapling density. This correlation is widely reported within the literature (e.g. Welch et al, 1999; Gill and Beardill, 2001; Gonzalez-Martinez and Bravo, 2001). The multivariate models elucidate few other hind parameter interactions with Scots pine regeneration, but affirm the strong interaction between hind density and regeneration rates.

Sapling density shows particular sensitivity to hind density, with a reduction in hind density of $1/\text{km}^2$ corresponding with an increase in sapling density of 5230/ha. Sapling density combines both mortality and recruitment rate, both of which are reported to be highly sensitive to herbivore densities (Putman et al, 1989; Healey, 1997; Gill and Beardill, 2001). Mortality is clearly a direct response to herbivory, whereas recruitment is an indirect consequence of browsing pertaining to reduced fecundity of browsed saplings (Crawley, 1983; Brandner et al, 1995; Gill and

Beardill, 2001). The magnitude of the interaction between hind density and sapling density seems implausible, but the studies that explore interaction of these rates focus more on the effect of sapling density on browse severity (Andren and Angelstam, 1993; Brandner et al, 1995), so direct comparisons are not possible.

Sapling growth is comparatively unresponsive to changes in hind density, with a reduction in hind density of $1/\text{km}^2$ corresponding with an increase in sapling height of just 0.85cm. Reported natural growth rates for Scots pine vary between 7.5cm/year (Beaumont et al, 1995) and 3.5cm/year (Scott et al, 2000). Sapling growth rates within Mar Lodge estate are closer to 1cm/year (Rao, 2008, unpublished data), which can probably be attributed primarily to heavy browsing (Gill and Beardill, 2001; Zamora et al, 2001). Based on the data range modelled in this study, browsing is likely to result in sapling growth suppression even at low hind densities. There is presumably a threshold in hind density, outside the data range modelled in this study, below which sapling growth becomes more responsive to hind density change. This notion is supported by Brandner et al (1990) and Rao (2008, unpublished data).

Calving rate was found to be an additional significant correlate of sapling density. As already discussed in the results, this interaction is more plausible with sapling density as the explanatory variable. Inversion of this causal pathway predicts that an increase in sapling density of 2669/ha would result in an increase in calving rate of 10%. The literature does not discuss this specific interaction, but does conclude that an improved habitat quality, when not offset by elevated deer densities, can result in higher reproductive success in Red deer hinds (Conradt et al, 1999).

Lastly, both Scots pine sapling density and growth showed temporal determination in their interaction with year. This could relate to temporal fluctuations in climate (Forchammer et al, 1998) or additional temporal variation in management.

5.1.3: Model series 3

This aim of model series 3 was to examine the interactions determined in Model series 1 and 2 to elucidate any synchrony in hind population parameters implicated in both model series (pathway A and F, figure 4). Synchrony between model series

would equate to indirect interaction between hind density and Scots pine regeneration by way of density-dependant shifts in hind population parameters. Calving rate was the only parameter that showed synchrony between these models. However, its interaction with sapling regeneration is better placed along pathway G (figure 4). As such, the interaction between hind density and Scots pine regeneration operates exclusively via direct hind density dependence (pathway D, figure 4). The literature exploring plant-herbivore interaction focuses principally on the effects of direct density dependence in determination of plant regeneration rates (e.g. Brander et al, 1990; Andren and Angelstam, 1993; Augustine and Jordan, 1998; Rooney and Waller, 2003). Based on the conclusions of this study, direct density dependence probably encapsulates most of the density-dependant interaction between herbivores and plants.

5.1.4: Model series 4

Model series 4 attempts a coupled projection of hind density (based on hind demographic rates) with a projection of Scots pine regeneration (based on hind density) under disparate culling regimes.

Model 4a shows that a high cull results in a steady decrease in hind density. This decrease in hind density consequently results in a steady increase in hind immigration (positive transience) which progressively compensates for the high cull. This progressive compensation leads to a reduction in the rate of increase in sapling density and height. Model 4a illustrates that the time necessary for saplings to attain a threshold height to escape browsing of apical shoots (approximately 2m) (Zamora et al, 2001) could be several decades, due to the low sensitivity of sapling growth to changes in hind density. Conversely, model 4a shows that sapling density will show significant positive response to reductions in hind density, due to the high sensitivity of sapling density to changes in hind density. Model 4a shows that a sustained high culling effort is required to permit continued Scots pine regeneration to compensate for calf recruitment and hind immigration.

Model 4b shows that a zero cull results in a steady increase in hind density due to calf recruitment. This increase in hind density consequently results in a steady increase in hind emigration (negative transience). At the hind densities modelled, this emigration

is insufficient to compensate for calf recruitment and hind density continues to rise. Model 4b shows that an increase in hind density will result in a drastic reduction in sapling density and a steady reduction in sapling height (due to the disparate sensitivity of these rates to changes in hind density). Steady increase in hind emigration will result in a reduction in the rate of decrease of sapling density and height. Model 4b confirms that a continued culling effort is required to permit both maintenance of and increase in Scots pine sapling density and height.

5.2: Evaluation of methodology and results

The interactions elucidated in model series 1, 2 and 3 are analogous to those elucidated in similar yet more exhaustive studies (Clutton-Brock et al, 1987; Albon et al, 1987; Welch et al, 1999; Gill and Beardill, 2001; Clutton-Brock et al, 2002). Further to this, all multivariate models performed well in the description of their response variables. As such, it can be assumed that the definition of parameters and method of analysis were appropriate for modelling these interactions. Model series 4 incorporates all the complexities of parameter interaction elucidated in the previous models to permit visual appraisal of the influence of hind density on Scots pine regeneration. In this respect at least, the model performs well.

However, the process inevitably suffers from data bias, parameter and model assumption and inaccuracy and omission of additional explanatory variables. Data bias can succinctly be attributed to inaccuracies in count data (in delineating hinds from calves and yearling stags (Luxmoore, 2002, unpublished data) and in the inevitable selectivity of cull data (Martinez et al, 2005). In the case of the latter, lactating hinds are selected against, which could disrupt inferred levels of fecundity and any other intercorrelated demographic rates, such as weight (Luxmoore, 2002, unpublished data; Kruuk et al, 1999). Further inaccuracy can infiltrate the process in parameter definition. For this study, the majority of parameters were directly inferred from the raw data. Transience rate and calving rate were also inferred from the raw data, but their calculation was based on discretion. The main point of discretion in calculating transience rate was in assuming a sex ratio of 1:1 in counted calves.

The main assumptions of linear modelling are that interactions are linear (or log linear) and that causal relationships are unambiguous (Crawley, 2007). Causal relationship between most of the parameters utilised in this study is likely to be highly ambiguous, with mutual determination operating between deer density and deer population parameters (Albon et al, 1987; Coulson et al, 1997) and deer density and plant regeneration parameters (Brandner et al, 1990; Pettorelli et al, 2002). It is therefore necessary to use discretion in delineating explanatory variables from response variables. In this study, hind density was assigned as the principal explanatory variable in accordance with the preponderance of other studies (e.g. Clutton Brock et al, 2002; Rooney and Waller, 2003).

Model inaccuracy can largely be attributed to poor and limited choice of explanatory variables. The interactions within herbivore populations and between herbivores and plants are functionally complex and include multiple factors (Crawley, 1983; Clutton Brock et al, 2002). Roughly speaking, for this study, there are two principal sources of explanatory power that further residual variation in the data can be attributed to. Collection of data on these variables would improve the accuracy in determining the variation in Scots pine regeneration exclusively attributable to changes in hind density.

Firstly, further intrinsic explanation of residual variation. For Red deer, this may pertain to the influence of the stag counterpart of the population (Smart et al, 2007), the influence of age-specific demographic rates (Albon et al, 2000; Coulson et al, 2004) or the influence of density dependence operating at multiple temporal and spatial scales (Coulson et al, 1997; Coulson et al, 2004).

Secondly, further extrinsic determination of residual variation. For Scots pine saplings, this may pertain to variation in canopy cover and soil wetness (Vickers and Palmer, 2000), climatic variation (Forchhammer et al, 1998) or the constraint on growth determined by the height of adjacent vegetation (Zamora et al, 2001; R. Luxmoore, pers comm, 04/07/2009). Adjacent vegetation height is reported to be a significant constraint on Scots pine sapling growth within Mar Lodge estate, where any emergent Scots pine saplings are subsequently browsed (Rao, 2008, unpublished data). The assumption within this study is that hind density constitutes a hierarchal

constraint on both general vegetation height and Scots pine sapling height, making it a valid explanatory parameter. However, it is likely that the interaction rate between hind density and Scots pine growth rate elucidated in this study will shift markedly once deer densities are reduced below a threshold level (Rao, 2008, unpublished data).

The coarse scale of data analysis is likely to further confound the integrity of modelled interactions. This study used time series data, with data resolved at the scale of year and beat, giving a maximum sample size of 40. With this low scale of data resolution, the spatial and temporal intricacies of parameter interaction may be overlooked or even misinterpreted. Bastrenta et al (1995) stress the particular importance of finer temporal scale data collection when assessing plant-herbivore interactions.

Model series 4 accounts for an additional array of assumptions and inaccuracies. The assumptions include: that the interaction between hind density and Scots pine regeneration rate is the same for an increase in hind density as it is for a reduction in hind density; that the interaction between hind density and Scots pine regeneration is exclusive (the doubtless numerous other explanatory variables are omitted). In addition to this, the model can only predict the degree of interaction between parameters as opposed to the exact numeric correspondence of demographic rates. These limitations are significant, but the model still provides a good visual summary of the interactions elucidated in the previous models and acts as a platform for further discussion of these interactions.

The hind data utilised in this study permits estimation of parameter interaction at the hind population level with reasonable success. However, collection of data on marked individuals, through an observation based study, would improve the accuracy in determination of sex and maturity (in comparison to rough count data) and the estimation of other demographic rates, such as calving and transience (Coulson, pers comm). In addition to this, data collected at a higher resolution, both spatially and temporally, would permit greater accuracy and confidence in modelling interactions between hind density and Scots pine regeneration (Coulson, pers comm.). For this study, count data was limited in its resolution both spatially and temporally and

regeneration data was limited in its resolution temporally. Improvement in data accuracy (through collection of individual observation data) and resolution would allow for greater insight into the feedback between management inputs (reducing deer densities) and output (achieving Scots pine regeneration). From the research perspective, experimental manipulation (within discrete spatial and temporal scales) of deer density and other constraints on Scots pine regeneration, such as adjacent vegetation height, would further improve the capacity to model Scots pine - Red deer interaction.

5.3: Implications in policy and research terms

5.3.1: Policy implications

One of the principal objectives in the management of Mar Lodge estate is the reduction of deer numbers to permit natural regeneration of Scots pine (Luxmoore, 2002, unpublished data). This study has affirmed the validity of this management approach and has ascertained the approximate degree of interaction between management input and the desired output. As such, the NTS can be confident that a continuation of their deer reduction program will improve on regeneration rates and this can also be communicated to associated stakeholders. It is also of use to recognise the degree of variation in Scots pine regeneration rate that is independent of fluctuations in deer density. Based on the univariate models (models 2a and 2b), 64% of variation in sapling density and 36% of variation in sapling growth can be attributed to factors other than hind density.

The study also revealed the importance of a continued high cull in controlling for immigration and in surpassing the assumed threshold in hind density required for growth of saplings above the adjacent vegetation height. Such efforts have already been resolved upon, whereby the NTS have adopted a zero tolerance policy for deer within the Regeneration zone (Rao, 2008, unpublished data). Despite this, extension of this study would allow continued critical appraisal of NTS management efforts in achieving Scots pine regeneration. It is also hoped that other Scottish highland estates may adopt a similar rigorous long-term appraisal of their deer reduction programs.

5.3.2: Research implications

There are fewer research implications, owing to the vast wealth of existing literature on deer population dynamics and plant-herbivore interactions. Many of these studies are more rigorous and use more advanced means of exploring parameter interaction than this study (e.g. Bastrenta et al, 1995; Coulson et al, 2004). However, there is one avenue of investigation in this study that may warrant inclusion in future studies. Despite the lack of significance elucidated, the inclusion of additional herbivore demographic rates in modelling plant demographic response permitted greater potential insight into the complexities of plant-herbivore interaction. Studies incorporating these rates would gain a greater appreciation of the multiple causal pathways and direct and indirect effects implicated in plant-herbivore interaction.

5.4: Summary

The principal aim of this study was to elucidate, through logical progression, the cumulative effect that hind density has on the regeneration of Scots pine within Mar Lodge estate. This was achieved through a series of models exploring the multiple interactions between and within hind demographic rates and Scots pine demographic rates. The main conclusion of these analyses is that a reduction in hind numbers, exclusive of the consequent intrinsic demographic shifts, is the main determinant of Scots pine regeneration rate. This confirms the validity in reducing hind density to achieve Scots pine regeneration. Scots pine sapling density shows a high degree of sensitivity to changes in hind density whereas, for the data range modelled, Scots pine sapling growth shows little response to changes in hind density. Projection of the interaction between hind density and Scots pine regeneration shows that to achieve continued sapling regeneration, a sustained culling effort is required to compensate for calf recruitment and hind immigration. Experimental manipulation of deer density, accompanied by observations of marked individuals, would permit elucidation of the finer-scale interactions between hind density and Scots pine regeneration. This would allow Mar Lodge estate to set cull quotas and anticipate regeneration rates with greater accuracy and confidence.

6: References

- Albon, S. D., Coulson, T., Brown, D., Guinness, F. E., Pemberton, J. M. and Clutton-Brock, T. H. (2000) Temporal Changes in Key Factors and Key Age Groups Influencing the Population Dynamics of Female Red Deer. *Journal of Applied Ecology*, 69, (6), 1099-1110
- Albon, S. D. and Clutton-Brock, T. H. (1988) Climate and the population dynamics of Red deer in Scotland. *Ecological Change in the Uplands*, (Ed. Usher, M. B. and Thompson, D. B. A.) British Ecological Society Special Publication No. 7, 93-107, Blackwell Scientific Publications, Oxford
- Albon, S.D., Clutton-Brock, T. H. and Guinness, F. E. (1987) Early Development and Population Dynamics in Red Deer. II. Density-Independent Effects and Cohort Variation. *Journal of Animal Ecology*, 56, (1), 69-81
- Albon, S. D., Mitchell, B. and Staines, B. W. (1983) Fertility and Body Weight in Female Red Deer: A Density-Dependent Relationship. *Journal of Applied Ecology* 52, (3), 969-980
- Alverson, W., Waller D. S. and Solheim, S. L. (1988) Forests too deer: edge effects in Northern Wisconsin. *Conservation Biology*, 2, 348-358
- Anderson, R. C. (1994) Height of White-Flowered Trillium (*Trillium Grandiflorum*) as an Index of Deer Browsing Intensity. *Ecological Applications*, 4, (1), 104-109
- Andren, H. and Angelstam, P. (1993) Moose Browsing on Scots Pine in Relation to Stand Size and Distance to Forest Edge. *Journal of Applied Ecology*, 30, (1), 133-142
- Augustine, D. J. and Jordan, P. A. (1998) Predictors of White-Tailed Deer Grazing Intensity in Fragmented Deciduous Forests. *The Journal of Wildlife Management*, 62, (3), 1076-1085

Augustine, D. J. and McNaughton, S. J. (1998) Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance. *The Journal of Wildlife Management*, 62, (4), 1165-1183

Baines, D., Sage, R. B. and Baines, M. M. (1994) The Implications of Red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology*, 31, (4), 776-783

Bastrenta, B., Lebreton, J. and Thompson, J. D. (1995) Predicting Demographic Change in Response to Herbivory: A Model of the Effects of Grazing and Annual Variation on the Population Dynamics of *Anthyllis Vulneraria*. *Journal of Ecology*, 83, (4), 603-611

Beaumont, D., Dugan, D., Evans, G. and Taylor, S. (1995) Deer management and tree regeneration in the RSPB reserve at Abernethy Forest. *Scottish Forestry*, 49, 155-161

Brandner, T. A., Peterson, R. O. and Risenhoover, K. L. (1990) Balsam Fir on Isle Royale: Effects of Moose Herbivory and Population Density. *Ecology*, 71, (1), 155-164

Cameron, A. G. (1923) Cameron, A. G. (1923) *The Wild Red Deer of Scotland, Notes From the Inland Forest On Deer, Deer Stalking And Deer Forests In The Scottish Highlands*. 1st Edition. William Blackwood and Sons

Canham, C. D., McAninch, J. B. and Wood, D. M. (1994) Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. *Canadian Journal of Forest Research*, 24, (4), 817-825

Carranza, J., Alarcos, S., Sánchez-Prieto, C. B., Valencia, J. and Mateos, C. (2004) Disposable-soma senescence mediated by sexual selection in an ungulate. *Nature*, 432, 215-218

Catchpole, E. A., Morgan, B. J. T., Coulson, T., Freeman, S. N. and Albon, S. D. (2000) Factors Influencing Soay Sheep Survival. *Journal of the Royal Statistical Society series C (Applied Statistics)*, 49, (4), 453-472

Caughley, G., and Lawton, J. H. (1981) *Plant-Herbivore Systems*. In: *Theoretical Ecology*. 2nd Edition (Ed: May, R. M.), 132-166. Blackwell Scientific Publications, Oxford

Cermack, P. (1998) The influence of ungulates on forest ecosystems in Moravia. *Lesnictvi-Forestry*, 44, 278-287

Clutton-Brock, T. H., Coulson, T. and Thomson, D. (2002) *Red deer on Rum: a 20-year study of the ecological consequences of changes to male and female numbers*. Scottish Natural Heritage Commissioned Report F99AC417

Clutton-Brock, T. H., Rose, K. E. and Guinness, F. E. (1997) Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society of London, series B*, 264, 1509-1516

Clutton-Brock, T. H. and Albon, S. D. (1989) *Red Deer in the Highlands*. Oxford, UK. Blackwell Scientific Publications

Clutton-Brock, T. H., Albon, S. D. and Guinness, F. E. (1987) *Reproductive success in male and female Red deer*. (Ed. Clutton-Brock, T. H.) Chicago. University of Chicago Press,

Clutton-Brock, T. H., Major, M. and Guinness, F. E. (1985) Population regulation in male and female Red deer. *Journal of Animal Ecology*, 54, 831-846

Clutton-Brock, T. H., Guinness, F. E., Albon, S.D. (1982) Red deer: behaviour and ecology of two sexes. In *University of Chicago Press*, Chicago: University of Chicago Press

Conradt, L., Clutton-Brock, T. H. and Guinness, F. E. (1999) The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia*, 120 (2), 218-224

Coulson, Tim. Professor of Population Biology, Imperial College London. (Personal communication 28th August 2009)

Coulson, T., Guinness, F. E., Pemberton, J. M., and Clutton-Brock, T. H. (2004) The demographic consequences of releasing a population of Red deer from culling. *Ecology*, 85, (2), 411–422

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. and Grenfell, B. T. (2001) Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. *Science*, 292, (5521), 1528–1531

Coulson, T., Albon, S. D., Guinness, F. E., Pemberton, J. M., and Clutton-Brock, T. H. (1997) Population substructure, local density, and calf winter survival in Red deer (*Cervus elaphus*). *Ecology*, 78 (3)

Crawley, M. J. (1983) *Herbivory: the dynamics of animal plant interactions*. Oxford. Blackwell Scientific Press.

Crawley, M. J. (1989) *The relative importance of vertebrate and invertebrate herbivores in plant population dynamics*. (Ed: Bernays, E. A.) Insect-plant interactions. Florida. CRC Press, Boca Raton, pp 47-71

Crawley, M. J. (2007) *The R Book*. Chichester, England. John Wiley & Sons Ltd

Forchhammer, M. C., Stenseth, N. C., Post, E. and Langvatn, R. (1998) Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proceedings of the Royal Society of London, series B*, 265, 341-350

Forsyth, D. M., Parkes, J. P. and Hickling, G. J. (2000) A case for multi-species management of sympatric herbivore pest impacts in the central Southern Alps, New Zealand. *New Zealand Journal of Ecology*, **24**, 97–103

Fowler, C. W. (1981) Density Dependence as Related to Life History Strategy. *Ecology*, **62**, (3), 602-610

Frelich, L. E. and Lorimer, C. G. (1985) Current and Predicted Long-term Effects of Deer Browsing in Hemlock Forests in Michigan, USA. *Biological Conservation*, **34**, 99-120

French, D. D., Miller, G. R. and Cummins, R. P. (1997) Recent development of high-altitude *Pinus sylvestris* scrub in the Northern Cairngorm mountains, Scotland. *Biological Conservation*, **79**, (2-3), 133-144

Gill, R. M. A., Beardall, V. (2001) The impact of deer on woodlands: The effect of browsing and seed dispersal on vegetation structure and composition. *Forestry*, **74**, (3), 209-218

Gill, R. M. A., Webber, J. and Peace, A. (2000) *The economic implications of deer damage*. The Deer Commission for Scotland, contract report

Gonzalez-Martinez, S. C. and Bravo, F. (2001) Density and population structure of the natural regeneration of Scots pine (*Pinus sylvestris* L.) in the High Ebro Basin (Northern Spain). *Annals for Science*, **58**, 277-288

Guisan, A., Edwards, T. C. and Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157** (2-3), 89-100

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton J. M., and Grenfell, B. T. (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, **430**, 71-75

Healy, W. M. (1997) Influence of deer on the structure and composition of oak forests in central Massachusetts. (Ed. McShea, W. J., Underwood, H. B. and Rappole, J. H.). *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA

Holl, W., Frommberger M. and Strassl, C. (2002) Soluble carbohydrates in the nutrition of house longhorn beetle larvae, *Hylotrupes bajulus* (L.) (Col., Cerambycidae): from living sapwood to faeces. *Journal of applied Entomology*, 126, (9), 463-469

Kruuk, L. E. B., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M. and Guinness, F. E. (1999) Population density affects sex ratio variation in Red deer. *Nature*, 399, 459–461

Leirs, H., Stenseth, N. C., Nichols, J. D., Verhagen, R. and Verheyen, W. (1997) Seasonality and non-linearity in an African rodent: determinism and stochasticity. *Nature*, 389, 176-180

Low, A. J. (1988) Scarification as an aid to natural regeneration in the Glen Tanar native pinewood. *Scottish Forestry*, 42, 15–20.

Luxmoore, Richard. Head of Nature Conservation, National Trust for Scotland. (Personal communication, 4th July 2009)

Luxmoore, R. (2002) *Deer management at Mar Lodge Estate: Preliminary analysis of data derived from culls and counts*. National Trust for Scotland (unpublished)

Martin, J. and Baltzinger, C. (2002) Interaction among deer browsing, hunting, and tree regeneration. *Canadian Journal for Research*, 32, (7), 1254-1264

Martinez, M., Rodriguez-Vidal, C., Jones, O. W., Coulson, T. and Miguel, A. S. (2005) Different hunting strategies select for different weights in red deer. *Biology Letters*, 1, (3), 353-356

Martinez-Jauregui, M., San Miguel-Ayanz, A., Mysterud, A., Rodriguez-Vigal, C., Clutton-Brock, T. H., Langvatn, R., Coulson, T., (2009) Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? *Global Change Biology*, 15, 1727 - 1738

McCullough, D. R. (1999) Density Dependence and Life-History Strategies of Ungulates. *Journal of Mammalogy*, 80, (4), 1130-1146

McInnes, P. F., Naiman, R. J., Pastor, J. and Cohen, Y. (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, 73, 2059-2075

Miller, G. R. and Cummins, R. P. (1982) Regeneration of Scots Pine *Pinus sylvestris* at a Natural Tree-Line in the Cairngorm Mountains, Scotland. *Holarctic Ecology*, 5, (1), 7-34

Miller, M. W., Wild, M. A. and Williams, E. S. (1998) Epidemiology of chronic wasting disease in captive Rocky Mountain elk. *Journal of Wildlife Diseases* 34, 532-538

Milner-Gulland, E. J., Coulson, T. and Clutton-Brock, T. H. (2004) Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*. *Wildlife Biology*, 10, (3), 167-181

Milner-Gulland, E. J., Shea, K., Possingham, H., Coulson, T. and Wilcox, C. (2001) Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation*, 4, 157-167

Mysterud, A., Langvatn, R., Yoccoz N. G. and Stenseth, N. C. (2001) Plant Phenology, Migration and Geographical Variation in Body Weight of a Large Herbivore: The Effect of a Variable Topography. *Journal of Animal Ecology*, 70, (6), 915-923

Palmer, S. C. F. and Truscott, A. M. (2003) Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and Management*, 182 (1-3), 31-47

Pettorelli, N., Mysterud, A., Yoccoz, N. G., Langvatn, R. and Stenseth, N. C. (2005) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proceedings of the Royal Society of London, series B*, 272, (1579), 2357-2364

Putman, R. J., Langbein, J., Hewison, A. J. M. and Sharma, S. K. (2008) Relative roles of density-dependent and density-independent factors in population dynamics of British deer. *Mammal Review*, 26, (2-3), 81 – 101

Putman, R. J., Edwards, P. J., Mann, J. E. E., How, R. C. and Hill, S. D. (1989) Vegetational and faunal change in an area of heavily grazed woodland following relief from grazing. *Biological Conservation*, 47, 13-32

Rao, S. (2008) *Mar Lodge Estate: Regeneration quadrat monitoring report 2008*. National Trust for Scotland (unpublished)

Rooney, T. P. and Waller, D. M. (2003) Forest Dynamics and Ungulate Herbivory: From Leaf to Landscape. *Forest Ecology and Management*, 181, (1-2) 165-176

Rooney, T. P., McCormick, R. J., Solheim, S. L. and Waller, D. M. (2000) Regional variation in recruitment of Hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecological Applications*, 10, (4), 1119-1132

Scott, D., Welch, D., Thurlow, M. and Elston, D. A. (2000) Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. *Forest Ecology and Management*, 130, 199-211

Scottish Natural Heritage (1994) *Scottish Natural Heritage, Red Deer and the Natural Heritage*. Scottish Natural Heritage, Perth, UK

Shaw, M.W. (1974). *The British Oak*. (Ed. Morris, M. G. and Perring, F. H.), Botanical Society of the British Isles, Edinburgh: Claxson, E. W.

Smart, J. C. R., White, P. C. L. and Termansen, M. (2008) Modelling conflicting objectives in the management of a mobile ecological resource: Red deer in the Scottish Highlands. *Ecological Economics*, 64 (4), 881-892

Steven, H. M. and Carlisle, A. (1996) The native pinewoods of Scotland. *Oliver and Boyd, Edinburgh*

Vickers, A. D. and Palmer, S. C. F. (2000) The influence of canopy cover and other factors upon the regeneration of Scots pine and its associated ground flora within Glen Tanar National Nature Reserve. *Forestry*, 73, (1), 37-49

Vila, B., Torre, F., Martin, J. and Guibal, F. (2003) Response of young *Tsuga heterophylla* to deer browsing: developing tools to assess deer impact on forest dynamics. *Trees- structure and function*, 17, (6) 2003

Virtanen, R., Edwards, G. R. and Crawley, M. J. (2002) Red deer management and vegetation on the Isle of Rum. *Journal of Applied Ecology*, 39, 572- 583

Welch, D., Staines, B. W. Scott, D., French, D. D. and Catt, D. C. (1991) Leader Browsing by Red and Roe Deer on Young Sitka Spruce Trees in Western Scotland I. Damage Rates and the Influence of Habitat Factors. *Forestry*, 64 (1), 61-82

Yoccoz, N. G., Mysterud, A., Langvatn, R. and Stenseth, N. C. (2002) Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society, series B*, 269, 1523–1528.

Zamora, R., Gomez, J. M., Hodar, J. A., Castrop, J. and Gacia, D. (2001) Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. *Forest Ecology and Management*, 144, (1-3) 33-42

7: Appendix 1

7.1: Measures of deer pressure

Model 7a:

| Response variable | | | | | | Explanatory variable | | |
|-------------------|---------------|----------------|----------|------|-----------|-----------------------|------------------|----------|
| Model | Variable name | Transformation | <i>F</i> | d.f. | std error | <i>R</i> ² | Variable name | Estimate |
| 4 | growth (cm) | None | 11.78* | 3,10 | 1.24 | 0.71 | hind density (x) | -1.15* |
| 5 | | | | | | | browse intensity | -0.12 |
| 6 | | | | | | | pellet count | 0.02 |

Table 7: Deer pressure and Scots pine sapling growth

Values for browse intensity and pellet count are taken from Rao (2008, unpublished data). Hind density is measured in hinds/ km² and browse intensity is measured as % saplings browsed. All explanatory and response variables are delineated by beat and by year

Scots pine sapling growth interacts most closely with hind density (significance in trend at $p = > 0.05$). At the resolution modelled, both hind density and browse intensity act as constraints on sapling growth, whereas mean pellet count interacts positively with sapling growth. In the case of the latter, it may be that converting data on pellet counts to beat and year-specific means distorts its true interaction with sapling growth.

Model 7b:

| Response variable | | | | | | Explanatory variable | | |
|-------------------|---------------|----------------|----------|------|-----------|-----------------------|------------------|----------|
| Model | Variable name | Transformation | <i>F</i> | d.f. | std error | <i>R</i> ² | Variable name | Estimate |
| 1 | density/ ha | None | 8.9* | 3,10 | 3434 | 0.65 | hind density (x) | -2282.3* |
| 2 | | | | | | | browse intensity | -352.4 |
| 3 | | | | | | | pellet count | 1267.3* |

Table 8: Deer pressure and Scots pine sapling density

Scots pine sapling density interacts most closely with hind density (significance in trend at $p = > 0.05$) but also shows significance in its interaction with pellet count. At the resolution modelled, both hind density and browse intensity act as a constraint on

sapling density, whereas mean pellet count interacts positively with sapling growth. This disparity in the direction of trend, which is the same as that elucidated in Table 7, could be attributable to the transformation of data on browse intensity and pellet count from quadrat-specific rates to beat-specific rates. For pellet count, this transformation may have disrupted the data integrity, resulting in the implausible interaction observed with Scots pine regeneration in Tables 7 and 8. Irrespective of this, model 6a and 6b support the use of hind density as the principal constraint on Scots pine regeneration rates.

7.2: Calculation of calving rate

Calving rate, as defined in this study, is the estimated ratio of hinds: calves during calving (the period of parturition during spring/summer). It constitutes a rough estimate based on data extracted from the count and cull datasets.

Values for beat and year-specific calving rate are calculated retrospectively by:

$$1) R^{x-1} = (C^x + L^x) / (O^x + M^x)$$

Where R is the estimated calving rate, C constitutes counted calves, L comprises the number of lactating hinds culled, O constitutes counted hinds and M comprises the total number of hinds culled. i.e., the number of hinds potentially calving in year $x-1$ is equal to the number of hinds counted in year x added to the number of hinds culled in year x . The number of calves parturated in year $x-1$ is equal to the number of calves counted in year x added to the number of lactating hinds culled in year x .

7.3: Calculation of transience rate

Transience, as defined in this study, is the addition or subtraction of hinds to the observed population that cannot be attributed to recruitment or mortality. It constitutes a rough estimate, based on known and inferred demographic rates over the year $x-1$.

The calculation for transience rate can be described by:

1) Observed population for year x – Estimated population for year x

An expansion of this can be described by:

2) Observed population count for year x – ((Observed population count for year x^{-1}) + Recruitment leading up to count x – Mortality leading up to count x)

The calculation is run for each beat within each year, to obtain spatially and temporally explicit estimates. Each calculated rate is then divided by the beat-specific winter-limited area, to obtain an estimate/km². Within the equation, recruitment is inferred to be 50% of calves counted in year x^{-1} (the calf count is indiscriminate of sex) that will then be recruited into the adult hind population in year x . Mortality is primarily comprised of the hind cull leading up to the observed population count (year x) but additionally constitutes an estimate of natural over-winter mortality (2% of the adult hind population, as specified in Luxmoore (2002) unpublished data).

Having clarified these demographic rates, the full estimation of transience rate can be described by:

3) $T^x = (H^x - (H^{x-1} + \frac{1}{2} C^{x-1} - M^x - [(H^{x-1} + \frac{1}{2} C^{x-1})/100] * 2)) / A$

Where T is the beat and year-specific transience rate, H is the hind count, C is the calf count, M is the hind cull and A is the beat-specific area. The square brackets enclose the estimate of natural over-winter mortality. The calculated transience rate is only intended as an estimate to make approximate spatially and temporally explicit comparisons.

7.4: Coupled calculation of hind density and Scots pine regeneration rate

These calculations relate to Model series 4. The calculations made towards construction of model 4 are best described in compartments:

1) Transience is calculated by:

$$T^x = T^{x-1} + ((H^{x-1} - H^{x-2}) * Ti)$$

Where T is transience rate, H is hind density and Ti is the estimated interaction between hind density and transience rate. Based on model series 1, transience rate interacts more closely with H^{x-1} , so it is the difference between H^{x-1} and H^{x-2} that determines T^x relative to T^{x-1} . Transience rate is determined by H^{x-1} but will ultimately constitute an addition / subtraction to H^x . If transience rate interacted more closely with H^x , then calculation of H and T would be confounded by mutual determination and construction of this model would not be possible.

2) Calving rate is calculated by:

$$R^x = R^{x-1} + ((H^x - H^{x-1}) * Ri)$$

Where R is calving rate and Ri is the estimated interaction between hind density and calving rate. Calving rate is determined by H^x , but will ultimately constitute an addition / subtraction to H^{x+2} (see figure 4, appendix 1).

3) Hind density is calculated by:

$$H^x = H^{x-1} + T^x + R^{x-2} - C^x$$

Where C is culling rate (hinds/ km²) and H^x is calculated by a series of additions / subtractions to H^{x-1} . Over this period there will be a further subtraction of individuals based on natural mortality. However, for the sake of simplicity, natural mortality is not considered in this model.

4) Scots pine sapling density is calculated by:

$$SD^x = SD^{x-1} + ((H^{x-1} - H^{x-2}) * SDi)$$

Where SD is the sapling density and SD_i is the estimated interaction between hind density and Scots pine density. As with transience rate, Scots pine density interacts more closely with H^{x-1}, so it is the difference between H^{x-1} and H^{x-2} that eventually determines the change in density of SD^x.

5) Scots pine sapling growth is calculated by:

$$SG^x = SG^{x-1} + ((H^x - H^{x-1}) * SG_i)$$

Where SG is the sapling growth and SG_i is the estimated interaction between hind density and Scots pine sapling growth.

The equation in full would be too inelegant to detail. However, for Scots pine growth, the equation can be summarised as:

$$SG^x = SG^{x-1} + ((H^x - (H^{x-1} + T^x + R^{x-2} - C^x)) * SG_i)$$

And for Scots pine density, the equation can be summarised as:

$$SD^x = SD^{x-1} + ((H^{x-1} - (H^{x-2} + T^{x-1} + R^{x-3} - C^{x-1})) * SD_i)$$

Based on the complexity of inter-annual interactions, the model requires initial input of estimates for transience rate, calving rate and hind density. These are taken from the intercept values estimated in model series 1 and 2.

7.5: Grouping demographic rates by year

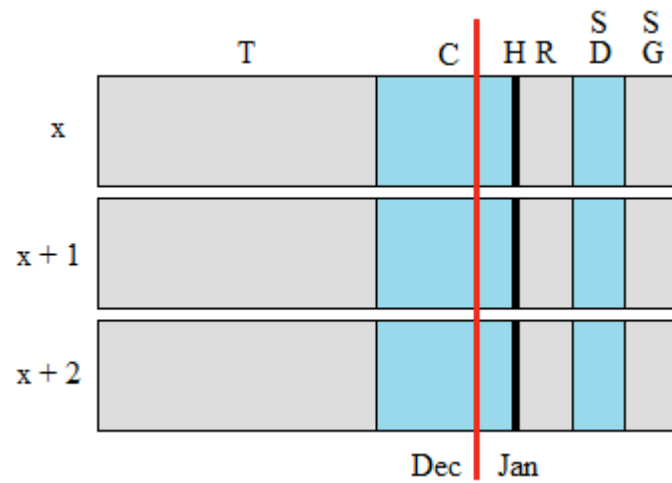


Figure 6: Grouping of demographic rates into discrete years

Figure 6 represents the manner in which demographic rates were grouped when modelling interactions. The letters represent the same demographic rates as outlined in section 6.4. Transience operates over the period $x-1$ to x , but is included in with data from year x . The cull also operates from late $x-1$ till early x , but hind population parameters from this cull period are included with data from year x . Retrospective calculation of calving rate based on data from year $x+1$ is included in with data from year x , as it is with other demographic rates in year x that this retrospective estimate would be expected to interact with. Based on the models of this study, T^{x+1} and SD^{x+1} are determined by H^x . Based on the assumptions of model series 4, R^x (which is determined by C^{x+1} and H^{x+1}) influences H^{x+2} , via the recruitment of calves parturated in year x into H^{x+2} (in H^{x+1} , R^x calves will still be counted as calves).