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Trade-offs between risk and reward at multiple scales: A state-dependent approach

by

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Ecology is the study of the incomprehensible by the incompetent

- Jan de Wilde

Dedication

For Maia, without whom this thesis would have been completed a year earlier, but without whom life would be half-lived.

Abstract

A ubiquitous problem for all foragers is the trade-off between acquiring food energy while simultaneously avoiding the risk of predation. In central montane Alberta I modelled how ungulate forage changes with succession within cutblocks and the implications for forage availability to ungulates under current harvest regimes. Because cutblocks are discrete patches in space, I developed a dynamic state variable model for an ungulate to explore under what conditions an individual forager could (1) behaviourally avoid predation within a patch through inactivity, (2) overcome patch isolation when confronted with predation during transit between patches, and (3) alter patch use across a home range to optimize fitness. The model includes the requirement to process forage into energy through rumination behaviour that constrains foraging, and compares outcomes under a time-minimizing (sigmoid) and energy maximizing (linear) fitness functions. When an ungulate is in high energetic state, inactivity provides an effective behavioural refuge, or animals prioritize safety over energy gain, individuals avoid predation within patches reducing the need to move between patches. When energy acquisition is prioritized, individuals are at a low energetic state, or within patch anti-predator behaviours are ineffective, individuals move among patches to avoid predators in space, and configuration of the patches influences fitness. When model results were qualitatively compared to activity patterns and cutblock use of female, GPS-collared elk appear to follow a time minimizing strategy in their patch use across the home range and with their activity within riskier patches. I discuss the implications of these findings for the management of elk and cutblocks in west central Alberta.

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Introduction

1.1 Background, observations, and motivation

In the mountainous regions of west central Alberta, forest management results in a landscape consisting of a mosaic of clearcuts (hereafter referred to as cutblocks) within a forested matrix (Timoney & Lee 2001). Past and on-going research has noted that cutblocks play an important role in determining the distribution of ungulate species like elk (*Cervus elaphus*) because of high forage availability associated with the early succession forest communities (Hett et al. 1978, Irwin & Peek 1983, Jenkins & Starkey 1993, 1996, Visscher & Merrill 2009). Evidence also exists that predators use cutblocks, travel along the edges of cutblocks, and avoid humans on roads associated with timber harvest (Kuzyk et al. 2004, Webb 2009). As a result, predation risk among cutblocks also varies across the landscape (Frair et al. 2005, Webb 2009). Within a managed forest, ungulates using cutblocks are therefore faced with making decisions regarding trade-offs between forage acquisition and predator avoidance. Given that the forest harvest is predicted to expand in western Alberta over the next decade (Timoney & Lee 2001), understanding how the number and configuration of cutblocks on a landscape may influence ungulate use of these patches is of practical importance to managers.

The well defined boundaries of cutblocks provide a unique opportunity for exploring the patch-use behaviour of ungulates in a heterogeneous landscape. Optimal foraging theory is the current paradigm for understanding the patch use of individuals (Emlen 1966, MacArthur & Pianka 1966, Charnov 1976, Stephens & Krebs 1986). Applications to ungulates have focused on intake or energy maximization in simplified environments, in the absence of predators (Jiang & Hudson 1993, Langvatn & Hanley 1993, Wilmshurst et al. 1995, WallisDeVries et al. 1999). A ubiquitous problem for foragers in real landscapes is the trade-off between the acquisition of energy through food and avoidance of predators (Lima & Dill 1990). Although the general patterns of ungulate use, including cutblocks, in relation to forage and predation risk have been described (Rettie & Messier 2000, Wolff

& Van Horne 2003, Dussault et al. 2005, Frair et al. 2005, Hamel & Cote 2007), less is known about the behavioural decisions that give rise to these patterns. In particular, large herbivores are known to hierarchically select foraging areas based on the principle of "minimizing the maximum detriment" at each scale of selection (Rettie & Messier 2000, Dussault et al. 2005, Searle et al. 2008, Parker et al. 2009). Yet, even approaches that describe the hierarchical selection of habitats by ungulates represent a static representation of the outcome of behavioural trade-offs between predation risk and reward, providing little understanding of how they would be expected to change among individuals and across varying landscapes conditions.

Furthermore, there is increasing evidence for the importance of individual behaviour in many ecological processes, including foraging and patch use (Mangel & Clark 1986, Roitberg & Mangel 1997, Morales & Ellner 2002, Zollner & Lima 2005). Incorporating individual behaviour into a hierarchical perspective of foraging trade-offs remains difficult. Brown (1999) and Mitchell (2009) have suggested that individuals use different behaviours to trade-off risk and reward between and within patches. At the patch scale, individuals try to minimize exposure to predation while still obtaining adequate forage energy (Gilliam & Fraser 1987), while within a patch they may use behaviours that may increase survival should they encounter a predator (Mitchell 2009). Ungulates possess a rich repertoire of behaviours that can reduce the risk of predation while acquiring energy, including differential patch selection, modification of group size, vigilance, and modification of activity patterns (Hebblewhite & Pletscher 2002, Wolff & Van Horn 2003, Creel & Winnie 2005, Creel et al. 2005, Winnie et al. 2006, Winnie & Creel 2007, Liley & Creel 2008). In some cases, movement behaviours have been used to infer the trade-off between risk and reward by relating distance moved or movement modes, to forage and predation risk (Morales et al. 2004, Frair et al. 2005, Forester et al. 2007, Van Moorter et al. 2010). Yet, these studies also lack a mechanistic framework to understand how individuals can make behavioural trade-offs to meet multiple objectives. Because individuals make decisions at several spatial and temporal scales, a hierarchical patch approach to understanding how individuals may meditate forage acquisition and predation risk, between and within patches within their home range, may improve landscape planning for managing ungulates in an increasingly fragmented landscape.

In my thesis work, I initially investigated the patch use of individuals by trying to relate residence time in cutblocks of elk to forage availability and the risk of predation. However, it became clear that the total time an elk spent in a cutblock followed different patterns. Time in a cutblock was either relatively continuous or spread over multiple visits of varying residency times. This led me to the question, "What was different about cutblocks used for short intervals over multiple visits compared to cutblocks that were used a single time for a long duration, and why were some cutblocks avoided altogether?" Distinguishing why these different strategies of cutblock use existed proved difficult using a statistical approach, given the inter-dependence of the number of visits and the duration of a visit on total residence time. This was the first indication that understanding the behavioural patterns of elk use of cutblocks may be as, if not more, important than determining important cutblock characteristics from total use. Therefore my focus shifted to a behaviour-based modelling approach, in which the goal was to better understand how ungulates make foraging decisions and the implications of within patch behaviours, functional connectivity between patches, and use of patch configurations within a home range.

1.2 Model conceptualization

In the past, there has been some debate as to the usefulness of theoretical exploration and models in ecology (Simberloff 1981, Caswell 1988, Grimm 1994). While "all models are wrong", they do provide understanding of theoretical problems and lend insight into the possibilities that may arise in nature, provided care is taken in their creation and use (Caswell 1988). Grimm (1994) advocated using patterns observed in nature as the starting point for a modelling exercise. Reproducing patterns with the minimum amount of model complexity and the fewest number of assumptions allows us to ask "what if" questions and explore the range of possibilities that may exist in nature (Caswell 1988, Grimm 1994). It is in this vein that I turned my attention away from statistically describing the observed patterns of patch use by elk, to modelling elk decisions based on some simple representations and assumptions of ruminant foraging in a risky environment. Below is a brief description of the modelling process I employed, as well as its development and application to specific questions that formed the basis of my thesis.

One way to incorporate adaptive behaviour at multiple spatial scales is through the use of dynamic state variable models (McNamara et al. 2001). Such models have been used to address a range of ecological questions (e.g., when to feed, where to feed, what to eat, when to migrate, when to abandon mates, and how much to invest in raising offspring) from a behavioural perspective across many species (Kelly & Kennady 1993, Newman et al. 1995, Houston 1998, Houston & McNamara 2000, Nonacs 2001, Barta et al. 2002, Peterson et al. 2007). Kie (1999) suggested that dynamic state variable models might allow for more realistic foraging models for large herbivores by incorporating behaviour, potentially explaining the discrepancies that are observed between current models and empirical observations. However, there has been relatively little research with large ungulates using behaviourally based models, particularly in a landscape context (but see Noonburg et al. 2007). While Noonburg et al. (2007) explicitly incorporated the constraints of an animal that is located in a landscape into the decision making process of individuals, their model was focused on the movement of elk with the onset of winter, which reduced foraging opportunities at higher elevations and did not explicitly model how behaviour may mitigate trade-offs between forage acquisition and safety from predators behaviourally.

I used dynamic state variable models and simple assumptions about the physiology and behaviour of ruminant species to gain insight into how trade-offs in forage acquisition and predator avoidance give rise to patterns of optimal behaviour and space use. I used principles of optimality, despite past criticism, because alternative research programs with definable models and testable hypotheses are still lacking (Pierce & Ollason 1987, Ward 1992, Nonacs & Dill 1993, Ward 1993). However, satisficing, in terms of meeting a minimal requirement, could be an alternative goal of the forager that could still be considered in an optimality framework (Ward 1992). I developed a dynamic state variable model and applied it to different questions in three steps, each building on the previous, to answer some of the following questions that arose when exploring the patterns of cutblock use by elk. First, how does state-dependence interact with the specific form of the fitness function to determine optimal activity patterns when intake rate and predation risk vary? Second, how does increased patch-based motivation to move and in-transit behaviour promote connectivity between patches? Third, how does the spatial configuration of patches influence the variability of patch use within the home range and how does the form of the fitness function and the effectiveness of anti-predator behaviours influence the trade-off between risk and reward within and between patches?

1.3 Thesis overview

1.3.1 Chapter 2: Modelling secondary succession of forage availability in cutblocks

The rapid conversion of lodgepole pine (*Pinus contorta*) dominated landscapes in western Alberta to a mosaic of successional stand ages has long-term implications for elk populations in the region that have not been fully assessed. In my initial approach to statistically link elk locations to forage abundance and predation risk, it was necessary to quantify the availability of forage across the landscape base on stand age and harvest treatments. To determine the successional change in forage availability for ungulates with time since felling, I described and modelled the secondary succession of available forage, both herbaceous and browse, in cutblocks. I developed stand-level models of forage succession using data from 159 cutblocks to simulate forage and cover availability within the home range of an elk under "even-flow" and "pulsed" timber cutting scenarios that are common in this area. The models were used to describe patterns of forage availability at both the stand (through succession) and landscape (through harvest regimes) levels.

1.3.2 Chapter 3: Optimal activity: State-dependence and the tradeoff between risk and reward

Most herbivores continually face trade-offs between foraging opportunities and predation risk, due to the spatial overlap between forage resources and predators (Lima & Dill 1990). The threat of predation has the potential to impact ecological processes as much as the direct effect of predation (numerical removal of individuals; Schmitz et al.

2004). The purpose of this chapter was to better understand the options a ruminant herbivore may have for altering activity patterns to mitigate both direct and indirect effects of predation. In Chapter 3, I used a dynamic state variable model and stochastic dynamic programming to develop a behavioural model that incorporated the need to ruminate, which was a mutually exclusive behaviour from foraging, and to assess activity patterns in terms of trade-off between the reward of further foraging and the risk of predation when inactivity provided a predation refuge (Houston & McNamara 1999, Clark & Mangel 2000).

1.3.3 Chapter 4: Moving between patches: State-dependent functional connectivity

In Chapter 4, I extended the model of optimal behaviour to include movement between a pair of patches separated in space. This simulation was used to investigate the extent to which rewards and risks influenced the functional connectivity among patches (Taylor et al. 1993, Belisle 2005). I measured functional connectivity as the proportional use of a second patch at varying distances from the patch of origin, as a function of conditions within patches and transit between patches. Motivation to move between patches was determined by making the foraging conditions favourable or predation risk low in the second patch. Further I showed how the model could be used to titrate the cost of patch isolation, not unlike a giving up density (GUD) experiment (Brown 1988).

1.3.4 Chapter 5: Trading-off predation at two scales: Anti-predator behaviour within the patch and movement between patches

Hierarchy theory has been used to explain patterns of selection for foraging sites at multiple scales by large herbivores (Senft et al. 1987, Bailey et al. 1996, Searle et al. 2008), but mechanistically do not directly address the behavioural trade-offs of individuals at these different scales (Rettie & Messier 2000, Dussault et al. 2005). Brown (1999) suggests that individuals have two major approaches for reducing the risk of predation each used at a different scale: anti-predator behaviours while within a patch and differential use among patches. In this chapter I extended the models of the last two chapters to investigate trade-offs for individuals in deciding to move among patches or alter behaviours within patches under different patch configuration and variation in forage and predation risk among patches. I investigated how the effectiveness of anti-predator behaviours and the form of the fitness function interact to produce shifts in within- and between-patch foraging strategies.

1.3.5 Chapter 6: Elk in west central Alberta: Cutblock use as a function of trade-off between risk and reward

In this chapter I applied the model presented in Chapter 5 to the specific case of elk using cutblocks in west central Alberta. The model is parameterized to reflect an adult, female elk during summer when forage depletion is minimal. The variation in patch use within the home range was simulated and compared qualitatively to data collected from GPS telemetry of free-ranging elk using cutblocks in west central Alberta. I tested, at two scales, whether female elk in summer were best represented by a linear or sigmoid fitness function, representing an energy maximizing or time minimizing foraging strategy, respectively. Lastly, I discussed potential reasons and implications of the discrepancies between model predictions and observed patterns in elk when forest harvest is expected to continue to produce landscape heterogeneity through the creation of cutblocks.

1.3.6 Chapter 7: Synthesis

In my closing chapter, I (1) give an overview of the ideas and work presented in the previous chapters in the context of previous literature, (2) provide a critical assessment of the short comings of this modelling approach and suggest future improvements that should be pursued, and (3) discuss the advancements to our understanding of behavioural trade-offs between risk and reward and how these results may be used by managers in planning additional harvesting in western Alberta.

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Temporal dynamics of forage succession for elk at two scales: Implications of forest management [1]

2.1 Introduction

In northern temperate forest landscapes, the major disturbance historically has been fire (Johnson et al. 1990, Andison 1998), while today timber harvest shapes many forested landscapes. The removal of trees and the creation of timber harvest units (hereafter cutblocks) stimulates secondary succession that results in changes in forage abundance for elk in both space and time. Because elk use has been related to forage availability (Frair et al. 2005), models of understory succession following timber harvest have become common (Halpern & Spies 1995, Roberts & Gilliam 1995, Nilsson & Orlander 1999, Sutherland & Foreman 2000, Frey et al. 2003, Clark et al. 2003, Corns & LaRoi 1976, Boring et al. 1981, Brakenhielm & Liu 1998, Hunt et al. 2003). However, only a few studies have used succession models to show the long-term implications of timber harvest regimes on forage abundance for elk (Jenkins & Starkey 1996, Bainbridge & Strong 2005).

Forest managers typically use multiple-objective planning techniques to manage both timber harvest and wildlife habitat requirements across a landscape (Rempel & Kaufmann 2003). This approach involves managing timber supply and wildlife habitat simultaneously by determining the priority of a spatial location (i.e. a stand) for one of these two objectives. However, multiple-objective approaches that assume mutually exclusive benefits of stand ages for meeting timber supply and ungulate habitat requirements may not be accurate. For example, after timber harvest the same forest stand that initially provided key forage resources for ungulates will eventually meet other

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[1] This chapter was originally published in January 2009 (vol. 257, pages 96-106) in Forest Ecology and Management by Visscher, D.R. & Merrill, E.H.

habitat requirements such as thermal and hiding cover (Irwin & Peek 1983). In fact, most management guidelines for elk (*Cervus elaphus*) indicate that coniferous stands will provide hiding cover once in the sapling-pole stage, while thermal cover and adequate snow interception typically occurs when stands are $\approx$ 10 m tall and canopy closures reaches 70% (Thomas 1979, Nyberg & Janz 1990).

I use a strategic modelling approach to illustrate the long-term effects of several forest cutting regimes on the dynamics of forage availability at the scale of an elk's home range. I focus on lodgepole pine forest in the central east slopes of the Rocky Mountains of Alberta, where timber harvest has become wide-spread. I start by developing a model of forage succession for coniferous forest in this area from field data and then model changes in forage following several harvesting scenarios, including an "even-flow" of timber harvest and a "pulsed" timber harvest. Even-flow timber harvest is currently the prevailing harvest paradigm in the study area while a "pulsed" harvest scenario has been proposed for mountain pine beetle (*Dendroctonus ponderosae*) management in the area to minimize the risk of an outbreak. For my purposes, I assume animals have full access to forage within a home range so that the spatial arrangement and distribution of forage is less important than the amount of forage in the home range (Boutin & Hebert 2002). Although simplified, this approach provides long-term perspectives on the dynamics of landscape conditions that are important not only for evaluating forest plans where elk are a featured species, but also for anticipating changes in elk populations where they are not a management priority.

2.2 Methods

2.2.1 Study area

The study area is located in the central east slopes of the Rocky Mountains in Alberta (52° 27′ N, 115° 45′ W) and ranges in elevation from 850 to 3300 meters; however, cutblocks were found at elevations below 1750 meters. Summer and winter temperature average 12°C and -7°C, respectively, and precipitation is approximately 500 mm year, with approximately 175 mm of snow falling primarily in the winter months (Strong 1992).

From satellite imagery (Thematic Mapper 5) classification of in the vegetation the study area consisted of approximately 62% conifer forest (consisting primarily of lodgepole pine and white spruce (*Picea glauca*) in the uplands and black spruce (*Picea mariana*) in wetter areas), 4% deciduous forest, and 3% mixedwood forest. Nonforested vegetation types include 5% dry herbaceous (including subalpine herbaceous), 2% shrublands, 2% wet meadow, and 2% treed bog. The remaining 14% is composed of agricultural land, water, roads, bare soil and rock (Frair et al. 2005, Visscher et al. 2006). In 2004, approximately 5% of the area consisted of cutblocks < 40 years of age. Ungulate species inhabiting the area include elk, moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. heminous*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and feral horses (*Equus caballus*; Salter & Hudson 1980, Telfer 1994). Cattle grazing occurs during summer. Major predators include cougar (*Puma concolor*), wolves (*Canis lupus*), and bears (*Ursus arctos* and *U. americanus*).

The area is actively managed for timber harvest and oil and gas exploration, which is expected to increase over time (Timoney & Lee 2001), as well as hunting and other recreational activities. Timber harvest focuses on lodgepole pine stands, where cutting occurs in a two-pass harvest fashion. Typical cutblocks are clearcuts of ≈ 27 hectares (D.R. Visscher, *unpublished data*) although forest managers are beginning to use in-block retention (Kohm & Franklin 1997). Site preparation practices include dragging and burning of residual slash and various forms of micro-site preparation, including mounding and trenching. The study area is also thought to be susceptible to mountain pine beetles, which have reached outbreak conditions in nearby British Columbia forests (Watson 2006). This threat has prompted a number of *ad hoc* policies, in anticipation for when mountain pine beetle reach this area, including the widespread preventative harvesting to reduce the overall susceptibility of the forest by reducing the average age class of forest stands (Anonymous 2006).

2.2.2 Cutblock sampling and characteristics

I sampled 159 cutblocks during the summers of 2001-2002, from 25 July until 10 August, corresponding to peak production of understory biomass. Cutblocks were selected from a GIS of road-accessible sites (road within 1 km of the cutblock) within the combinations of three strata: two elevations (900-1200 m, 1200-1700 m), age since cutting (0-3, 4-7, 8-11, 12-19, and 20+ years), and the presence of mechanical site preparation (0 or 1), including dragging, trenching, and mounding. Transects were established completely within a single cutblock and were a total length of 240 m or 120 m, contingent upon cutblock size. Each transect was divided into 8 sections of 30 m or 15 m depending on total transect length. Because commercial forestry is a relatively new phenomena in this landscape, the oldest cutblock sampled was 37 years old. Therefore, to calculate the forage biomass for a full rotation (100 years) we sampled 15 previously uncut, mature-stands ($>$ 100 years), and linearly interpolated the herbaceous and shrub biomass between our cutblocks of $>$ 37 years and these mature, uncut stands.

Environmental and topographic characteristics of cutblocks were measured on-site or calculated using a digital elevation model (DEM) with a pixel size of 30 m. Canopy closure was calculated as the mean spherical densiometer reading taken in the four cardinal directions from the centre of each sampled section. Mean cutblock slope and aspect (degrees) were derived directly from the DEM. Other measures derived from the DEM included compound topographic index (CTI), a wetness index based on ratio of the catchment area of a given pixel and its slope (Burrough & McDonnell 1998). Similarly, sediment transport index (STI) was calculated as a proxy for soil nutrients and site quality, based on sediment flow (and the nutrient they may contain) and catchment area of all cells upslope of the pixel of interest (see Burrough & McDonnell 1998 for further details). In both cases these indices were used to reflect the potential site quality of a cutblock given its topographic location within a mountainous landscape. The distance (m) to neighbouring deciduous forest patches (d2d) was also calculated, as a proximate measure of the potential propagule availability of understory herbs and shrubs.

Herbaceous vegetation

Herbaceous species composition and biomass (vascular plants) was sampled within four of the eight sections along each transect. Four plots (0.25 m^2) within a section were placed 1 m off the actual transect line at 2 m or 5 m intervals depending on transect length for a total of 16 plots. At each plot a double-layered mesh grid was used to visually identify plant species composition from 36 grid points. Species of each plant directly under a grid point was recorded. All plots were clipped to ground level, after which the biomass within the plot was dried to a constant weight (50°C for 48 h) and weighed to the nearest 0.01 g. An estimate of available biomass for a cutblock was calculated as the mean of the sampled plots within each cutblock. Species-specific biomass for forbs and graminoids in a plot was considered to be proportional to the observed species composition, estimated from the grid points. Thus, a species comprising 25% of the total herbaceous composition (i.e. observed in 9 of 36 grid points), also comprised 25% of the biomass measured at the plot.

Woody forage

Woody plants within a browse stratum of 0-2.5 m in height (Bobek & Bergstrom 1978, Newton et al. 1989) were surveyed in 2 x 4 m (8 m^2) plots, centred within each of the transect sections for a total of 4 plots within each cutblock. All shrub stems (defined as rooted below ground) within the plots were identified to species and their basal diameter measured using calipers. Woody forage availability (g/m^2) of each species was derived from stem counts and stem-biomass relationships for each plot (see Visscher et al. 2006 for full details and models). Biomass of each species on a transect was the average of the four sampled plots. Shrub composition cover was summarized as one of two food categories: nonbrowse (ranking = 1; Kufeld 1973, Cook 2002) and browse forage (ranking > 1), and species in each group are given in Visscher et al. (2006).

2.2.3 Data analysis

Successional trends in mean herbaceous and woody biomass at a site were modelled through time using non-linear regression and maximum likelihood parameter estimation. Akaike's Information Criterion adjusted for small sample sizes (AIC_c) was used to select the most parsimonious model from a candidate set of biologically meaningful models using model weights (w_i; Burnham & Anderson 2002). Model selection was done in two steps. First an appropriate "base" model form was selected to represent the temporal change in forage biomass since cutting (i.e. assigning a functional "shape" to the model). Second, I added environmental covariates to the base model to investigate which variables best explained the variance in the data around the base model. I restricted *a priori* the candidate set of models to represent specific hypotheses about environmental variables known to influence forage succession. Because model selection using AIC is known to be biased towards overfitting models (i.e., variables not in truth are included in the approximation or model) I removed variables from the final model if the confidence interval around the parameter estimate included zero (Bozdogan 1987).

The impact of site preparation on the development of herbaceous and browse biomass was expected to be greatest in the youngest age classes, while for the older age classes, the effect could be hidden in the natural variation over time. Therefore, a Bonferroni corrected ANOVA was used to compare the effects of site preparation on the availability of both herbaceous and browse biomass within and between age classes (0-3, 4-7, 8-11, 12-19, and 20+ years) while controlling for topographic covariates. I compared the composition of graminoids and forbs across age classes using nonparametric bootstrapped confidence intervals (Efron & Tibshirani 1993). Because total (proportional) composition is the sum of graminoids and forbs, I used the composition of graminoids in my comparison (forbs $= 1-$ graminoids). I tested for deviation from an even composition, as well as changing composition through time (age classes became more or less skewed to graminoids). I created 95 percent confidence intervals using a nonparametric bootstrap and considered a test nonsignificant if there was an overlap in values. Conversely, if the groups did not display any overlap in their respective confidence intervals I determined them to be significantly different ($p \leq 0.05$).

2.2.4 Landscape Modelling

I used a Markov model of forest succession to investigate the effect that cutting scenarios would have on elk forage. Markov models assume a probabilistic transition from one successional state to the next described by a transition matrix. I used this model not to describe species succession in vegetation communities (as in Horn 1974), but rather to model the availability of forage over time (Usher 1979). Unlike some size-structured Markov models that allow individuals to remain in the same class in the next time step with some probability, I required that cutblocks age progressed with each time increment.

I used yearly time increments with a probability of a cutblock transitioning each year into the next age as 1.

I used the continuous function of forage development derived from the field data to determine the biomass available at each year of succession and to model forage availability in a 10×10 km (100 km^2) area, equivalent to the size of an elk's home range (93.5 ± 41.1 km^2; D.R. Visscher, *unpublished data*). I incremented the amount of forage within a stand age yearly and applied cutting regimes only to areas of 100 years old to coincide with the typical rotation length in the study area. I assumed home ranges were completely vegetated (i.e., I excluded rock, ice, water, and anthropogenically built-up areas), when in reality, non-forest cover types constituted approximately 8% of the naturally vegetated landscape in the study area. As such the outputs of our simulations are adequate to depict successional dynamics but not necessarily specific forage availability in the area. Unless otherwise stated, initial conditions (t=0) in the home range include 90% mature forest (100 years old), which is the landscape composition of an average elk home range in this area (i.e., 90% ± 8%; D.R. Visscher, *unpublished data*) and for simplicity dividing the remaining 10% of the area evenly among the cutblock ages (i.e., each age from 0 to 99 comprised 10 ha).

Using this modelling framework I modelled forage abundance, amount of hiding and thermal cover (stand ages 30 to 100 yrs old, Thomas 1979, Nyberg & Janz,1990), and the amount of mature forest (100 years old) for three harvest scenarios. The harvest scenarios included: (1) a constant amount harvested each year ("even-flow"), (2) an episodic harvest strategy where large amounts of timber are cut in a short time ("pulsed"), as proposed for prevention of a mountain pine beetle in Alberta (Anonymous 2006), and (3) a dynamic cutting strategy that combines an episodic and a constant amount of cutting after a lag period to achieve a landscape with a low proportion of forest that eventually maintains a constant flow of timber. For the constant amount harvest strategy, I first simulated seven levels of constant cutting (0, 10, 20, 40, 60, 80, 100 ha/year) starting from a single initial condition (90% forested). I also simulated a single harvest amount (40 ha/year) across a range of initial conditions (10, 20, 40, 60, 80, 90, and 100% forested). For the second scenario, I simulated a harvest to achieve a forest composition of 25, 50, and 75% of initial forest conditions (90%) over one, five, and 10 years with no further logging (Anonymous, 2006). Finally, the dynamic cutting strategy was based on an initial episodic cut of 75% of the exisiting forest over 5 years, followed by a constant harvest regime of 75 ha/year after a 65 year lag (see below for full details).

2.3 Results

2.3.1 Biomass

Herbaceous vegetation

The available herbaceous vegetation over time was best described by the log-normal model form (Table 2.5, Fig. 2.1). The model also included elevation (elev), distance to deciduous forest (d2d), and compound topographic index (CTI; Table 2.5). However, upon inspection, confidence intervals of the parameter estimates for all additional variables encompassed zero. As result, I used the base log-normal form only to model the change in herbaceous biomass after harvesting in the simulations (Table 2.5). Using a Bonferroni corrected ANOVA, I found that site preparation stimulated herbaceous biomass production in the youngest age class (0 to 3 years) when controlling for elevation, CTI, and distance to deciduous patches (df=4, F=3.438, p=0.01).

Herbaceous biomass (consisting of forbs and graminoids) recovered rapidly following felling. Herbaceous biomass peaked at $\approx$8 years and then slowly declined as the cutblocks aged and the canopy closure increased. Herbaceous biomass in mature forests averaged 43.02 ± 15.85 g/m^2 and was lower than in the model estimate for the oldest cutblock sampled (37 yrs, 65.10 g/m^2). Therefore I used the relationship: F_h (g/m^2) = -0.3505 (age) + 78.068 to interpolate the abundance of total herbaceous forage (F_h) for stand ages between 38 to 100 years (mature forest) for which I had no data, as the oldest commercial cutblock in the study area was harvested 37 years ago.

Up to peak biomass at $\approx$8 years, forbs and graminoids comprised approximately equal proportion of herbaceous biomass (Fig. 2.2) after which the proportion of forbs increased, as shade-tolerant forest species replaced pioneer species (Fig. 2.3). For example, I found a higher abundance of early successional species such as bluejoint (*Calamagrostis canadensis*) and fireweed (*Epilobium angustifolium*) while the percent cover of hairy-wild rye (*Elymus innovatus*) and bunchberry (*Cornus canadensis*) dominated in older cutblocks and mature forest (Fig. 2.3).

Woody forage

Changes in the abundance of palatable browse shrub species over time was best described by a log-normal model (Table 2.5, Fig. 2.1), with elevation (elev), distance to deciduous (d2d), and compound topographic index (CTI) explaining additional variation (Table 2.5). Upon inspection, only the confidence intervals of parameter estimates for elevation and distance to deciduous did not include zero and were therefore kept in the final model for simulating changes in shrub biomass over time. Using a Bonferroni corrected ANOVA I found that site preparation had no effect on the production of shrub biomass in any age class (df=4, F=0.812, p=0.52).

Browse abundance developed at approximately the same rate as herbaceous biomass, peaking in the same year, and then declined 30 years following felling (Fig. 2.1). For approximately the first 20 years, palatable browse species comprised the majority ($>$90%) of the available shrub biomass, but then declined rapidly, and by $\approx$ 40 years post-cutting the abundance of browse and non-browse species were roughly equal (Fig. 2.3d). Mature, uncut forests had more browse biomass (66.75 $\pm$ 46.02 g/m^2) than the model estimate for the cutblocks of 37 years (50.32 g/m^2). As a result, I used the equation: B$_p$ (g/m^2) = 0.2608 (age) + 40.671 to interpolate palatable browse abundance (B$_p$) for forest stands of 38 to 100 years of age (mature forest stands). When simulating changes in browse abundance with this model I assumed average landscape conditions (elev=1200 m and d2d=200 m).

2.3.2 Landscape simulations

“Even-flow” harvest

Starting from a heavily forested home range (90%), any timber harvest subsequently increased forage availability (Fig. 2.5). In my scenarios, a full harvest rotation (100 yrs) was required before the landscape reached an equilibrium in forage availability, and all landscapes converged after 100 years if the same amount of forest was harvested each year, regardless of initial conditions (Fig. 2.5b). Over the rotation, total forage availability in a home range increased as the equilibrial proportion of forest was reduced (Left column; Fig. 2.5a). Increasing harvest rates from 10 ha/year/home range to 20 ha/year/home range, resulted in increases of approximately 250 metric tonnes of forage if integrated over a typical home range (100 km^2). The amount of herbaceous forage followed a more consistent increase or decrease from initial conditions than browse. In no even-flow scenarios did I find that either hiding or thermal cover (30 to 100 year old stands; Fig. 2.4) dropped below 60% of the home range over the rotation (Fig. 2.5).

“Pulsed” and dynamic harvest

Pulsed harvesting to reduce old pine stands on the landscape to 25, 50, and 75% of current composition over 1-10 years resulted in a large “cohort” of similar even-aged timber that increased forage for $\approx$40 years before returning forage availability to current (initial) conditions (Fig. 2.6). Even though the initial pine beetle threat was reduced, wide-spread, old-age conditions that likely promote beetle outbreak were found to return before the end of the 100-year rotation.

To minimize the risk of a mountain pine beetle outbreak over long time spans, I found additional cutting was required following the initial forest reduction. Cutting 75 ha per year after a 65-year lag resulted in an equilibrial home range composition of 25% mature forest. This level of harvest resulted in 5% of the landscape being comprised of mature forest (Fig. 2.7a). In the latter harvest scenario, herbaceous and shrub biomass abundance were equal (Fig. 2.7b). Cover provided by stands 30 years or older was not limiting in this scenario. At a minimum, 29% of the home range provided stands that were suitable as hiding or thermal cover.

2.4 Discussion

Successional patterns of ungulate forage in western Alberta were similar to trends reported for this community elsewhere in the Rocky Mountains (Alldredge et al. 2001, Bainbridge & Strong 2005, Strong & Gates 2006). Forage availability peaked approximately a decade following harvest, and even after 40 years herbaceous forage abundance was 50% higher than biomass estimates for mature forest stands. In contrast, by 40 years following felling, palatable browse biomass was only 75% of the palatable browse biomass found in mature conifer stands. A number of studies have reported that site preparation significantly increases forage availability during the first two years following felling (Roberts & Zhu 2002, Frey et al. 2003) and the effect lasts up to ten years following felling (Haeussler et al. 2004). I found that herbaceous biomass was stimulated by site preparation up to 4 years following felling by approximately 40 g/m^2 where some form of site preparation was employed. However, I found no effect of site preparation on palatable browse biomass at any stand age.

The long-term development of forage (both herbaceous and browse) was determined primarily by the time since felling of a cutblock; however elevation, site quality (CTI) and distance to aspen types also had some influence. The elevational effect reflects the increasing productivity of the lower and wetter forests (Visscher et al. 2004). In addition, a higher component of deciduous trees typically occurs in low-elevational lodgepole stands than at high elevational stands in this area (Beckingham et al. 1996), although the cutblocks themselves remained pine dominated and were typically replanted with pine seedlings. As a consequence, the observed increase in browse at lower elevation resulted from the increased number of small aspen and balsam poplar saplings. Likewise, the variable “distance to deciduous” (d2d) indicated that neighbourhood effects may exist that influence the re-establishment of shrubs from adjacent patches of deciduous forest after felling. At high elevations, contiguous lodgepole pine forests provided relatively low forage availability, whereas cutblocks in this context provided increased forage availability for elk (Visscher et al. 2004). Conversely, at low elevations, cutblocks are often found adjacent to mixed species forest types, which provide much more forage than contiguous lodgepole pine forests found at higher elevation. In this context, cutblocks at lower elevation are less important as foraging patches given the smaller difference in relative forage between cutblocks and the adjacent mixed forest, despite having more forage than cutblocks at higher elevations (Visscher et al. 2004). However, in both situations, as new cutblocks are added the relative importance of the cutblock will depend on the forage availability in the current home range.

Few studies have shown that an increase in forage directly translates into increased ungulate numbers. However, there is evidence that through forest maturation, ungulate populations decline (Peek et al. 2002). Likewise, when forage is provided during times of food limitation, population numbers can be maintained or increased (Boyce 1988). Thus, the addition of forage through felling is particularly important in landscapes dominated by conifer forest, as in the northern temperate forests (Irwin & Peek 1983, Jenkins & Starkey 1993, D.R. Visscher, *unpublished data*). It is not surprising then that in forested landscapes ungulates use cutblocks (Lyon & Jensen 1980, Collins & Urness 1983, Irwin & Peek 1983, Jenkins & Starkey 1993, 1996, Frair 2005). However, the landscape context of cutblocks is critical for determining elk use in home ranges effected by forestry (Yeo & Peek 1992, Farmer et al. 2006).

The use of cutblocks by elk results from a number of factors including the presence of foraging opportunities and cover habitat, as well as the risk of mortality associated with increased road access (Hershey & Leege 1976, Lyon & Jensen 1980, Irwin & Peek 1983, Yeo & Peek 1992, Jenkins & Starkey 1996, Farmer et al. 2006, Frair et al. 2008). At the scale of an elk home range, timber harvest regimes can create a shifting mosaic of stand ages (Bormann & Likens 1979, Kohm & Franklin 1997) in which the overall dynamics and forage availability depends on both initial conditions and cutting regimes. I have shown that in the lodgepole pine forests of my study area, successive cutting that manages for an even-flow of timber supply results in fluctuations in total forage availability during approximately the first 30 years, after which a stable forage base is maintained, assuming no other major disturbances occur. The equilibrium forest condition results in a higher overall forage availability because the proportion of the home range that is forested decreases under most even-flow cutting regimes, but not to a level where thermal and hiding cover fall below the recommended guidelines for elk ($<60\%$, Thomas 1979, Nyberg & Janz 1990). The increase in forage reflects a shift from mostly unpalatable shrubs (which are associated with mature forests) to an herb and palatable shrub-dominated forage base that is associated with the reduction in average stand age across the home range.

In contrast to even-flow harvesting, pulsed cutting, which has been proposed to minimize the risk for mountain pine beetle outbreaks, may have major implications for the long-term forage base for elk in many of these areas. First, in the initial post-cutting years (approximately 5 years), forage availabilities in cutblocks, on average, will remain below 40 g/m^2, which is similar to the surrounding conifer forests. This may cause a reduction in elk numbers from present conditions given the reduction in available forage within a typical home range (Peek et al. 2002). Second, even though forage availability will increase rapidly following felling, forest cover is likely to become limiting. On the extreme, if pulse harvesting results in $<25\%$ of current forested conditions, thermal and hiding cover will be below recommended guidelines for approximately the next 30 years.

While increased harvesting may result in higher forage availability, there is a balance that must be struck between cutblock creation and maintenance of mature stands. Adequate mature forest for hiding cover is of particular importance where elk populations are hunted, as is the case in this study area (Hershey & Leege 1976, Lyon & Jensen 1980, Farmer et al. 2006). In addition increased roads associated with timber harvest not only remove suitable habitat but also increase human access, which reduces habitat effectiveness and creates attractive sinks (Hershey & Leege 1976, Lyon & Jensen 1980, Lyon 1983, Farmer et al. 2006, Nielsen et al. 2006, Frair et al. 2008). While road closures can minimize human access, strategic planning for retaining residual patches of mature forest can promote elk use while minimizing the spread of mountain pine beetle through the landscape. By maintaining mature patches of trees in the home range of an elk at a distance no greater then 600 meters from one another, an elk is never more than 300 m from potential cover (Bettinger et al. 1997), but patches are greater than the dispersal distance (60 m) needed to impede mountain pine beetle spread (Robertson et al. 2007).

Therefore, the potential benefits of increasing forage availability from timber harvest will depend not only on landscape context, but also planning for the spatial integration of early and late seral stages at the scale of an elks home range.

The goal of providing an adequate forage base, both temporally and spatially, for elk need not be mutually exclusive from the goals of timber harvest. Where elk management is prioritized, I have shown that careful planning of timber harvest can result in an increased forage base. However, elk are often subject to management practices that prioritize other objectives, as in the case of minimizing the risk of mountain pine beetle outbreaks. My simulations reveal the implications of several different harvest scenarios on the forage base for elk in Alberta. Whether or not elk are prioritized for management or not, the presence of variably aged cutblocks increases the overall landscape forage availability from current conditions and provides a spatial mosaic of distinct forage patches (Hett et al. 1978, Lyon & Jensen 1980, Jenkins & Starkey 1996). However, ensuring that elk benefit from the increased forage availability following timber harvest requires long-term perspectives on the placement of new clearcuts in a landscape context, juxtaposition of clearcuts and cover patches, and attention to access created by road development (Frair et al. 2008).

2.5 Tables

Forage type	Rank	Model	LL	K	AIC_c	ΔAIC_c	w_i
Herbaceous	1	log-normal	-839.91	4	1687.82	0.00	0.90
	2	polynomial	-841.31	5	1692.62	4.92	0.08
	3	gamma	-843.70	4	1695.40	7.57	0.02
Shrub	1	log-normal	-852.19	4	1712.64	0.00	0.63
	2	gamma	-853.20	4	1714.66	2.02	0.23
	3	polynomial	-852.60	5	1715.60	2.95	0.14

Table 2.1: Model selection from candidate models for estimation of herbaceous and forage shrub biomass as a function of cutblock age (x). Values for model log-likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion for small samples (AIC_c), AIC_c difference (ΔAIC_c), and model weight (w_i). The top ranked model form the base model in further analysis including environmental variables. Candidate models included log-normal ($a\exp[-0.5(\frac{\ln[\frac{x}{b}]}{c})^2]$), gamma ($ax^b\exp[-cx]$), and polynomial ($a\ln[x] + bx^2 + cx + d$) forms.

Forage type	Rank	Variables	LL	K	AIC_c	ΔAIC_c	w_i
Herbaceous	1	elev, d2d, CTI	-784.50	7	1583.7	0.00	0.69
	2	elev, d2d, CTI, site	-784.27	8	1585.5	1.76	0.29
	3	elev, d2d, CTI, STI, aspect, slope, site	-783.99	11	1591.8	8.03	0.01
	4	elev, d2d	-789.95	6	1592.4	8.71	<0.01
	5	d2d	-794.80	5	1600.0	16.25	<0.001
Shrub	1	elev, d2d, CTI	-784.33	7	1583.4	0.00	0.65
	2	elev, d2d, STI	-785.55	7	1585.8	2.44	0.19
	3	elev, d2d, CTI, STI, aspect, slope, site	-781.25	11	1586.3	2.89	0.15
	4	elev, d2d	-790.51	6	1593.6	10.17	<0.01
	5	elev, d2d, site	-789.97	7	1594.7	11.28	<0.01

Table 2.2: Model selection from candidate models for estimation of herbaceous and shrub biomass as a function of the base model (log-normal, based solely on cutblock age) and additional environmental variables. Models are shown in decreasing rank, with values for model log-likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion for small samples (AIC_c), AIC_c difference (ΔAIC_c), and model weight (w_i). For brevity only representative one and two covariate models (plus the base model) are given. In all cases, models with less variables (K=<6) resulted in very low model weights (<0.01). Environmental variables (x_n) were added to the log-normal model as: $(a + d_1 x_1 \ldots d_n x_n) \exp[-0.5(\frac{\ln[\frac{age}{b}]}{c})^2]$. Environmental variables included elevation (elev), distance to a deciduous forest patch (d2d), compound topographic index (CTI), sediment transport index (STI), aspect, slope, and the presence of site preparation (site).

Forage Type		Best Model			Collapsed Model		
	Variable	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Herbaceous	a	226.03	80.65	371.77	131.11	119.31	143.34
	b	8.02	6.71	9.56	8.43	7.15	10.04
	c	1.21	1.02	1.49	1.25	1.06	1.53
	elev	-0.025	-0.099	0.051	-	-	-
	d2d	-0.034	-0.085	0.016	-	-	-
	CTI	-4.77	-13.04	3.43	-	-	-
Shrub	a	394.32	253.57	540.47	304.21	218.92	393.15
	b	9.23	6.77	13.48	9.24	6.79	13.63
	c	1.33	1.02	1.97	1.34	1.02	1.98
	elev	-0.186	-0.259	-0.115	-0.171	-0.241	-0.102
	d2d	-0.059	-0.108	-0.011	-0.065	-0.113	-0.018
	CTI	-6.27	-14.25	1.56	-	-	-

Table 2.3: Parameter estimates and confidence interval of best (top ranked model from Table 2) and collapsed model for prediction of herbaceous and shrub biomass. Variables (from the best model) with confidence intervals that encompassed zero were not included to reduce the risk of overfitting. Parameter estimates were then calculated for this collapsed model, which was subsequently used for prediction. Environmental variables (x_n) were added to the log-normal model as: $(a + d_1x_1 \ldots d_nx_n)\exp[-0.5(\frac{\ln[\frac{age}{b}]}{c})^2]$.

2.6 Figures

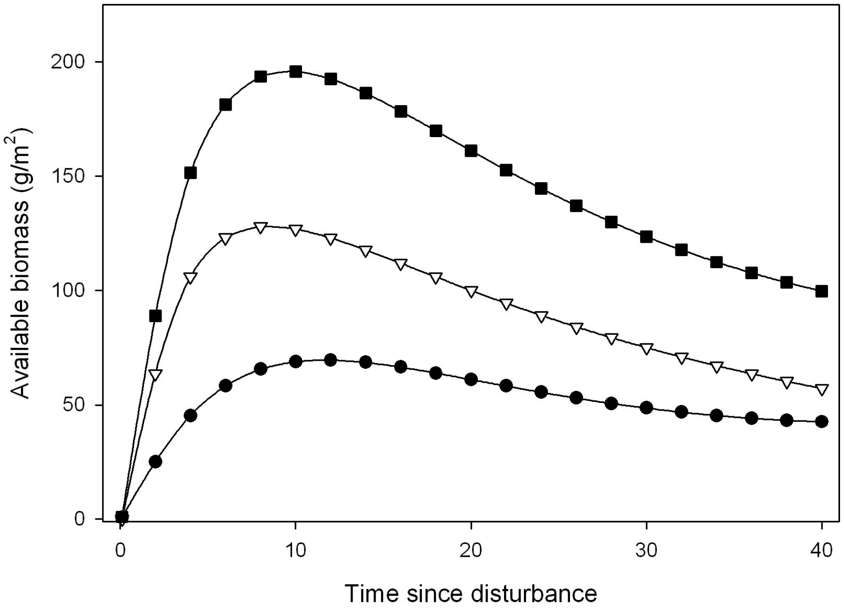


Figure 2.1: Available biomass (g/m^2) as a function of time since disturbance (felling) in years. Models were calculated from the collapsed models selected for both herbaceous (open triangles) and forage shrub species (solid circles), the total available biomass (herbaceous+shrub; solid squares) is also given. For forage shrub biomass, which depended on elevation and distance to a deciduous forest patch average values were assigned (1200 m and 215 m, respectively).

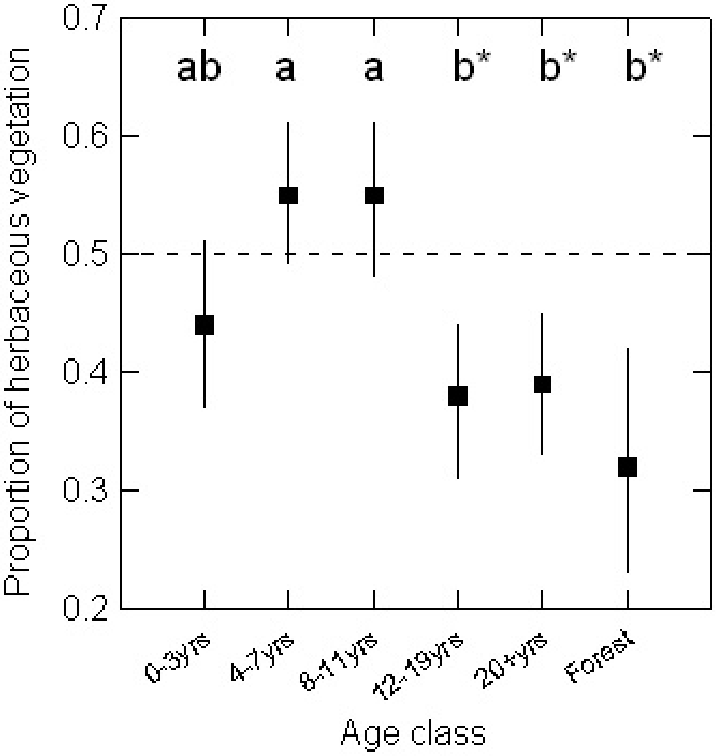
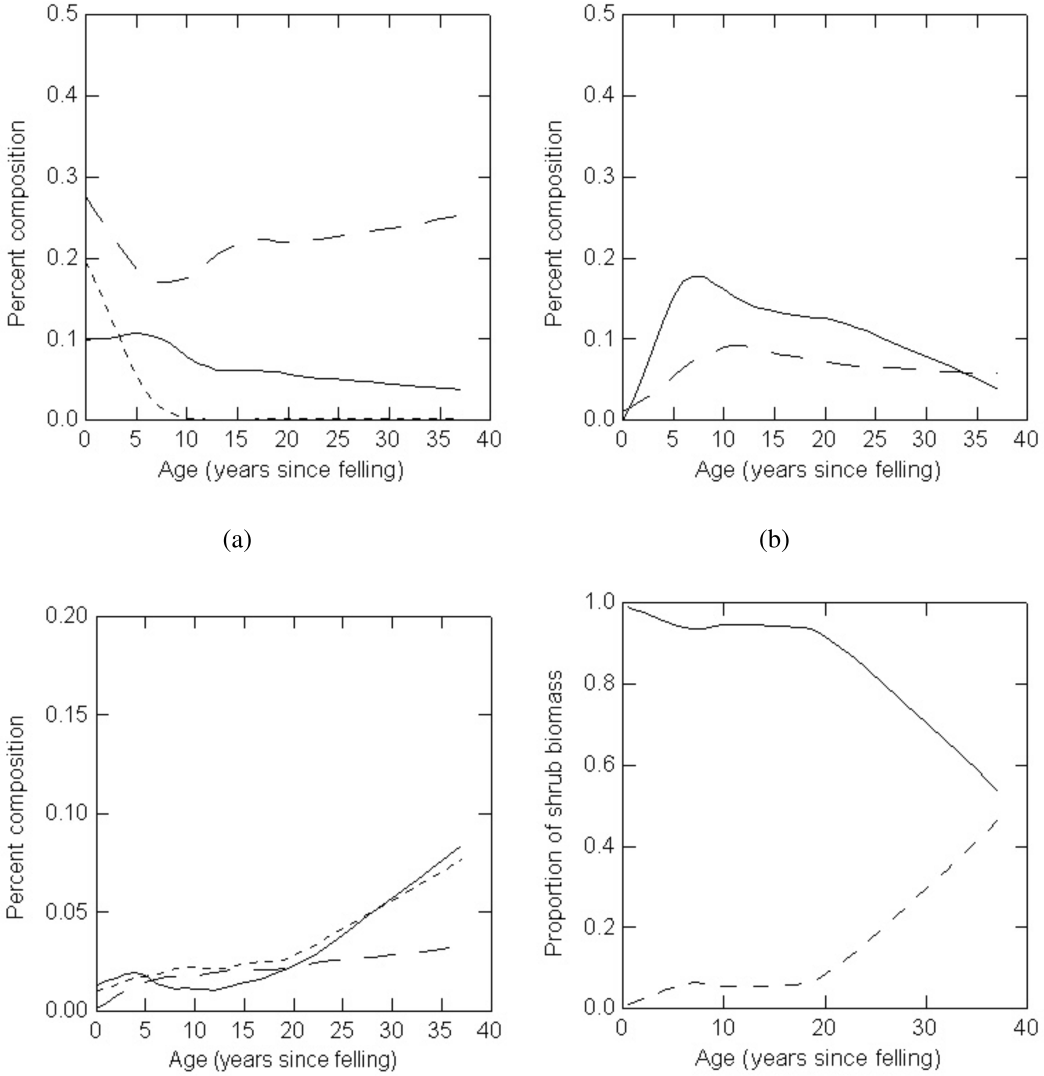


Figure 2.2: Bootstrapped mean (and 95% confidence intervals) proportion of total herbaceous vegetation composition that is comprised of graminoids (forbs therefore equal 1-graminoids) for cutblocks 0-3 (n=35), 4-7 (n=36), 8-11 (n=26), 12-19 (n=29) and 20+ (n=33) years since felling and the reference mature forest (n=15). Similar letters indicate a lack of significant difference between age classes while asterisks indicate a significant deviation in the composition of herbaceous biomass away from 50% graminoids and 50% forbs.



(a)

(b)

(c)

(d)

Figure 2.3: Percent composition of total cover for three nonvegetative cover types in relation to time since felling using a LOWESS smoother. (a) Artifacts of disturbance, including coarse woody debris (solid line), litter (long dashed line), and bare ground (short dashed line). (b) Two “pioneer” type species, *Calamagrostis canadensis* (solid line) and *Epilobium angustifolium* (dashed line). (c) Three forest species, including *Elymus innovatus* (solid line), *Cornus canadensis* (short dashed line), and moss (long dashed line). (d) Percent composition of forage shrubs (solid line) and nonforage shrubs (dashed line) of total shrub biomass. Note the change in scale of the y-axis in the different panels.

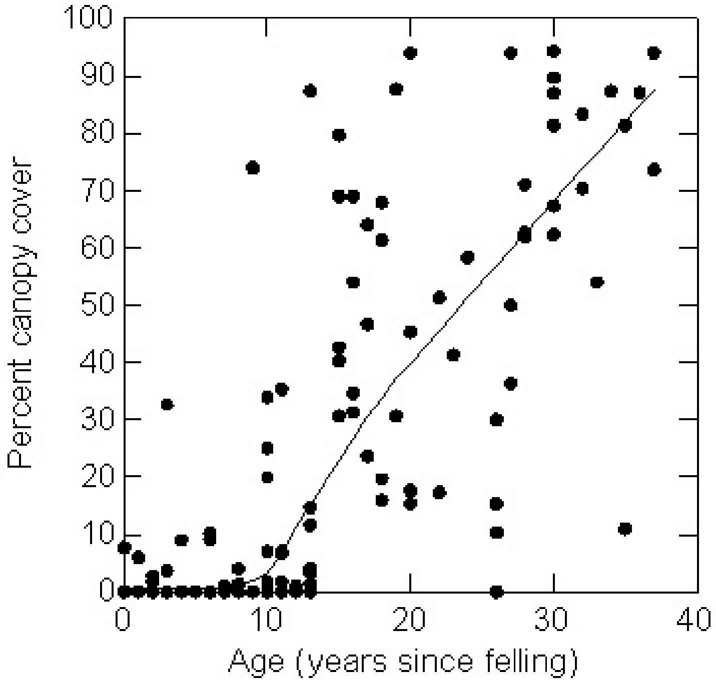
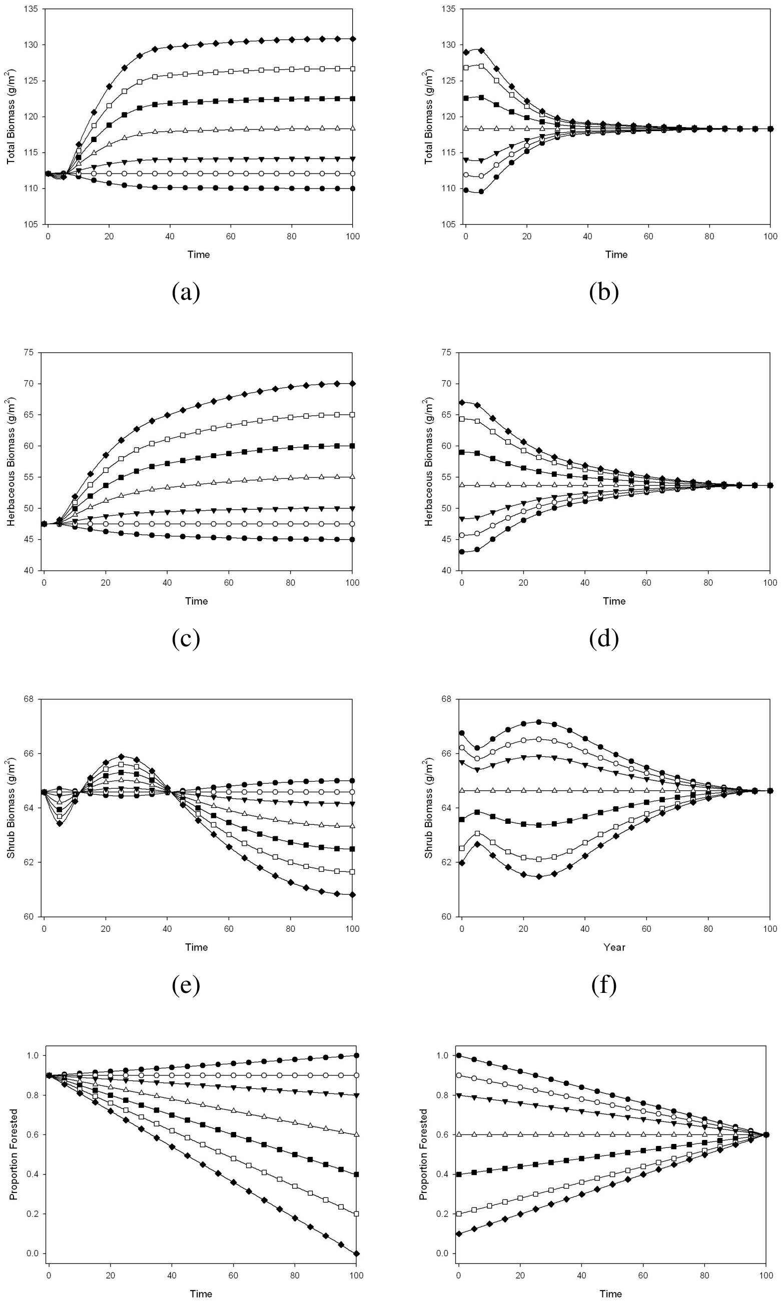


Figure 2.4: Percent overstorey canopy cover as a function of time since felling. Canopy closure was measured using a spherical densiometer with readings taken in the four cardinal directions at each surveyed shrub plot. Values for each cutblock are the mean densiometer reading across all plots. A LOWESS smoother indicates the two stage nature of development: cutblocks below approximately ten years of age have virtually no overstorey canopy that can be read by the densiometer, while in older cutblocks (>10 years) canopy coverage increases approximately linearly. By 30 years the canopy has filled in enough to constitute hiding and thermal cover, as defined by Thomas (1979) and Nyberg & Janz (1990).



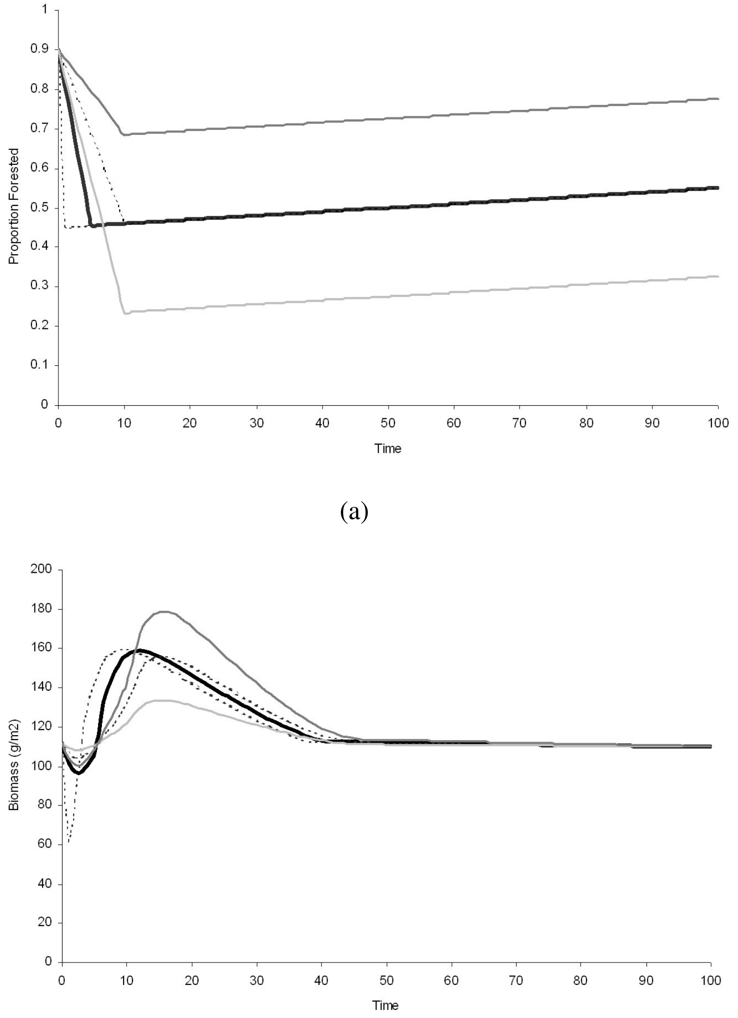
(a) (b)

(c) (d)

(e) (f)

(g) (h)

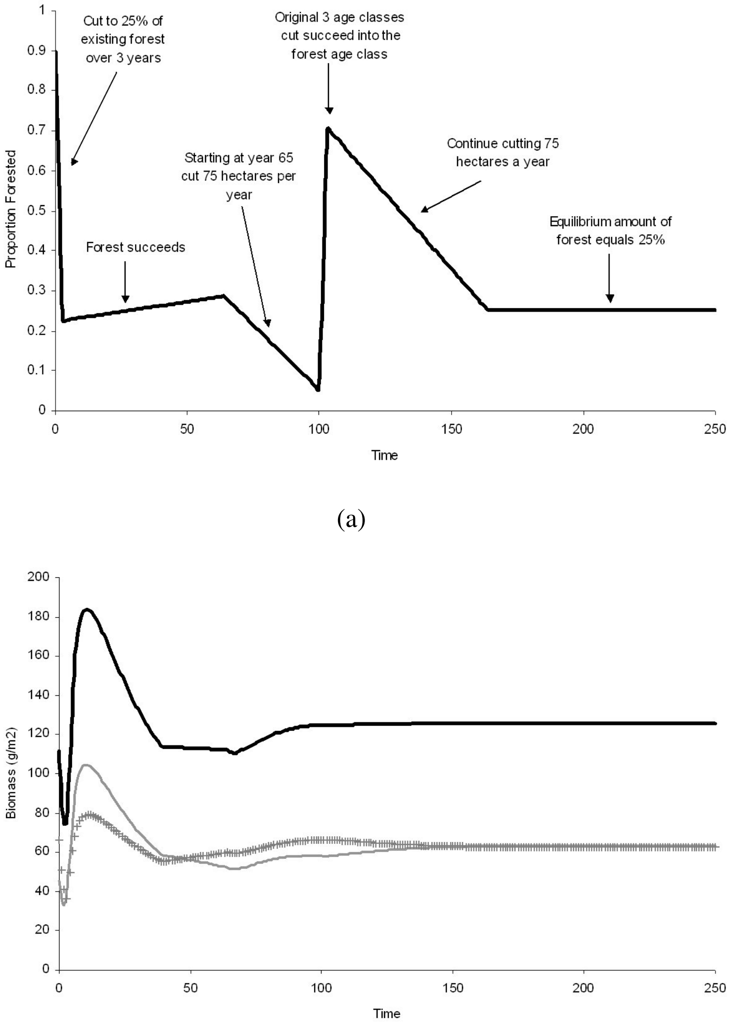
Figure 2.5: The changes in forage availability and forest cover as a function of various even-flow harvest scenarios, where time is given in years. The first column (a, c, e, g) holds the initial conditions constant (90% forested) and harvest amount is varied (0 ha, solid circle, 10 ha, open circle, 20 ha, solid triangle, 40 ha, open triangle, 60 ha, solid square, 80 ha, open square, 100 ha, solid diamond). In the second column (b, d, f, h) harvest amount is held constant (40 ha) and initial conditions varied (100% forest, solid circle, 90% forest, open circle, 80% forest, solid triangle, 60% forest, open triangle, 40% forest, solid square, 20% forest, open square, 10% forest, solid triangle). First row (a, b) is total biomass. Second row (c, d) is herbaceous biomass. Third row (e, f) is shrub biomass. Fourth row (g, h) is the proportion of mature forest.



(a)

(b)

Figure 2.6: Changes in the proportion of the landscape that is (a) forested and (b) total biomass (herbaceous + shrub; g/m^2) for differing cutting scenarios to minimize the risk of mountain pine beetle outbreak, where time is given in years. The solid lines represent the changes that occur when the landscape is reduced to 25% forest (light gray), 50% (black), and 75% (dark gray). The dashed lines show the effect of harvesting down to the respective percents (25, 50, and 75) over 1 year (left dashed line), 5 years (solid black line) and 10 years (right dashed line).



(a)

(b)

Figure 2.7: Cutting scenario and timing of events to reach and maintain the landscape that is 25% forested, in order to minimize the risk of mountain pine beetle outbreak now and in the future. (a) the proportion of the landscape that is forested through time with the key events occurring including the initial cut, lag, and start of the cutting (year 65) to maintain a low forested equilibrium. (b) the corresponding changes in total (solid black line), herbaceous (solid grey line), and shrub biomass (grey crosses), as a result of cutting. Time is given on the x-axis in years.

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Ungulate state-dependent behaviour: Trading-off risk and reward with optimal activity patterns

3.1 Introduction

Animals adjust their behaviours to the threat of predation (Sih 1980, Lima & Dill 1990, Brown et al. 1992). Given that such trait-mediated or non-consumptive effects (NCEs) of predators may have a large effect on prey populations, it is important to identify when NCEs are likely to have pronounced effects on the fitness of an individual (Trussell et al. 2008, Preisser et al. 2009). Optimal foraging theory has long provided a framework for examining the trade-offs between the risk of predation and potential foraging opportunities (Stephens & Krebs 1986, Gilliam & Fraser 1987, Houston et al. 1993). If the risk of predation overlaps either spatially or temporally with potential foraging opportunities, foragers will need to delay present foraging for the sake of remaining unavailable for predation (Lima & Dill 1990). While optimal foraging models have addressed the effect of predation risk on patch selection, there has been less focus on examining the trade-offs in behaviours to evade predation once in a patch. For example, individuals may form large foraging aggregations or synchronize their activity with conspecifics, effectively diluting the per-capita risk, or alternately, they may increase the rate of vigilance when exploiting a risky foraging opportunity (Brown 1999, Mitchell & Lima 2002, Fortin et al. 2004, Caro 2005, Rands et al. 2003, 2008). Such trade-offs may be crucial when energetic costs preclude movement or shuttling behaviour to a suitable refuge. Reducing foraging activity itself to diminish the threat of predation is another important behaviour, since many predators detect prey based on movement (Caro 2005). Indeed, field studies have shown that, typically, prey reduce their activity levels when predators are present (Anholt & Werner 1995, 1998, Anholt et al. 2000, Wolff & van Horn 2003, Biro et al. 2004, Winnie & Creel 2007).

Given that minimizing short-term predation risk may have long-term energetic costs (Lima 1998, Banks et al. 2000), it is useful to identify situations when consequences to fitness are expected. For easily manipulated species, trade-offs can be quantified by assessing the cost of predation in the same currency as foraging, namely, energetics. Brown and Kotler (2004) review methods for titrating the additional rewards necessary to incur an increased risk of predation. For example, giving up density experiments are a well-known example of a titration method. For large, free-ranging herbivores not easily manipulated in the lab or field (but see Altendorf et al. 2001, Hochman & Kolter 2007), studies often depend on radio-telemetry data to infer behavioural decisions in the past, unaware of the motivation for the behaviours. However, it may be difficult to determine when the consequences of predation risk constrain activity of free-ranging herbivores because of the multitude of compensatory behaviours available to herbivores (Caro 2005) and because the NCE of predation may be contingent on resource availability (Lind & Cresswell 2005, Preisser et al. 2009). Further, it is often assumed that behavioural decisions and outcomes of trade-offs are based on the average individual, but the importance of state-dependent behaviours may be crucial for the interpretations we make about observed trade-offs from wild populations (McNamara & Houston 1990, Houston et al. 1993, Nonacs 2001).

Dynamic state variable models and stochastic dynamic programming have been used to address complex behavioural decisions, by modelling the essential components of the trade-off in terms of fitness (Houston & McNamara 1999, Noonburg et al. 2007). As models of behaviour, they have been applied primarily to parasite and bird systems (Houston & McNamara 1986, Fenton & Rands 2004). Ruminant herbivores likely face unique challenges in trading-off foraging opportunities and predation risk because they are required to ruminate (regurgitate and re-masticate) food gathered during distinctive behavioural bouts prior to foraging further (van Soest 1984). Rumination constraints have been incorporated into previous models of optimal foraging, but rarely have been included in state-dependent models of behaviour (Belovsky 1978, Owen-Smith 1993, Houston & McNamara 1999, Bergman et al. 2001, but see Bednekoff & Houston 1994, Newman et al. 1995, Burrows et al. 2000). Also, since foraging and rumination are mutually exclusive behaviours, rumination itself may not be costly but rather provide potential “free time” in which ruminants may engage in anti-predator behaviour by becoming inactive, whereby they become less detectible to predators either individually or among conspecifics.

In this chapter, I assess the adaptive behaviour of ruminants in making trade-offs between foraging and being inactive in response to the threat of predation, when spatial refuges are unavailable or too costly to move to. I used a state-based behavioural model that was designed to optimize the trade-offs between energy acquisition and safety, in terms of fitness. The model was used to investigate changes in activity budgets, in the face of variable predation risk under differing resource availabilities, reflected by the ratio of intake to rumination rates. Although the model is developed for a ruminant herbivore, it can be applied to other species with handling constraints during foraging.

3.2 The model

Following Clark and Mangel (2000), I developed a dynamic state variable model. Generally, this modelling technique comprises four main components. First, states are defined as a representation of the model organism or system. Second, a limited set of decisions available to the individual are defined. Third, how the states change as a result of a decision (state dynamics) are formulated. Last, a currency is defined to assess which decision is optimal at the individual’s current state. My description of the model follows these general steps and is used to represent a ruminant’s activity budget and state-based decision making.

3.2.1 State variables and behaviours

I model an ungulate defined by it’s gut fill (g) and energy reserves (e) as state variables. These states update as the individual behaves. I assumed that the behaviours (b) of a ruminant forager include ruminating (1; converting gut contents into energy reserves), resting (2; engaging in no foraging or ruminating activity), and foraging (3; actively filling the gut). I assumed that these activities are mutually exclusive (Lundberg & Palo 1993) and that there is no cost for switching behaviours as they occur in the same patch. For simplification, I assume there is no predation risk when ruminating or resting, as the individual becomes undetectable due to its inactivity or increased anti-predator behaviour (i.e. vigilance). In contrast, the forager obtains forage only while foraging, and thus, upon exposing itself, this behaviour necessarily leads to a greater risk of predation. All activities incur some metabolic cost, incremented as a loss of m for active foraging and $\frac{m}{2}$ energy units per time for ruminating and resting (Moen 1973). Forage intake, resulting in increased gut contents, g was modelled as a constant addition of β forage for each unit of time spent foraging. I assumed that a β amount of forage was obtained with a probability λ (set to 0.95 for the remainder of the analysis). Thus, with probability 1-λ, no forage was found and the gut contents remained unchanged while the individual incurred the metabolic cost of foraging. Similarly, rumination was modelled as a constant removal or conversion, α, of gut contents into energy reserves during the time spent ruminating. I assume that the individual died if either state, energy reserves or gut contents, reached a value of 0, additionally I set the maximum values of gut fill or energy reserves high enough to not act as a constraint.

3.2.2 Fitness functions

The appropriate fitness currency to maximize has been debated and at present, no consensus has been reached due to the individuality of the questions being addressed (McNamara & Houston 1986, Clark & Mangel 2000). While Clark and Mangel (2000) have suggested that mixing fitness currencies may be inappropriate, the time scale in question requires consideration of both survival and energy reserves. The obvious termination of future fitness as the result of a predation event ensures that foragers should benefit from avoiding risky areas (Lima & Dill 1990). Similarly the deposition of additional energy reserves (via fat) has been implicated in increased probabilities of pregnancy, earlier parturition dates, and subsequent calf survival and condition in ruminants, thus contributing directly to fitness (Cook et al. 2004). Therefore fitness is modelled as a function of the behaviour selected and the state of the individual (gut fill and energy reserves) in time and the optimal decision is given as:

$$F(b, g, e, t) = \max\{V_1, V_2, V_3\} \tag{3.1}$$

where

$$V_1 = F(1, g-\alpha, e+\alpha-\frac{m}{2}, t+1)$$

$$V_2 = F(2, g, e-\frac{m}{2}, t+1) \tag{3.2}$$

$$V_3 = \begin{array}{c} (1-p)(\lambda)F(3, g+\beta, e-m, t+1)+ \\ (1-p)(1-\lambda)F(3, g, e-m, t+1) \end{array}$$

where V_1 refers to the fitness accrued by ruminating, V_2 refers to the fitness accrued from being behaviourally inactive, and V_3 refers to fitness accrued through active foraging. p is the probability of a predation event (and therefore survival is $1-p$). Predation was modelled as a binomial process with the probability of a predation event (p) occurring at any time unit (t). Thus the fitness function for any unit time is calculated as:

$$F(b,g,e,t) = \begin{cases} F(b,g,e,t) & \texttt{if}\ t < T \\ \Phi(e,T) & \texttt{if}\ t = T \end{cases} \tag{3.3}$$

To ensure that the form of the fitness function did not affect the outcome of the model, as suggested by Burrows & Hughes (1991) and Burrows et al. (2000) for a digestively constrained model, terminal fitness, $\Phi(e,T)$, was calculated two different ways. In the first situation, terminal fitness as a product of increasing energy reserves was calculated as:

$$\Phi(e,T) = e_T \tag{3.4}$$

I additionally defined terminal fitness with a sigmoid function as:

$$\Phi(e,T) = \frac{exp(-rep + e_T)}{1 + exp(-rep + e_T)} \tag{3.5}$$

where rep is some reproductive threshold that must be met by the energy reserves in order to increment fitness. The shape of the fitness function describes the utility of additional energy stores for the individual, given its current energetic state, and as such represents the prioritization of the fitness benefits of additional energy and remaining safe from predation. Fitness as a linear function of energy reserves tends to prioritize gaining additional energy reserves over avoiding predation, until high levels of energy are reached.

Conversely, fitness as a sigmoid function prioritizes remaining safe over gaining additional energy reserves, when above some reproductive threshold rep. The reverse occurs when below the threshold. Notice that in both cases, when $t = T$ fitness is dependent only on energy reserves, not gut fill. I assume that any remaining forage in the gut at the end of the time horizon is no longer useful for an individual.

3.2.3 Monte Carlo forward iterations

The stochastic dynamic programming algorithm (eq. 3.1) provides the state-dependent decision array. This array is the optimal policy and can be thought of as the “road map” or “rule book” an individual must conform to to behave optimally (Clark & Mangel 2000). In order to generalize to free-ranging individuals (for which we do not know the state), I used the Monte Carlo forward iteration procedure (Clark & Mangel 2000), and simulated 100 individuals starting at each possible combination of states for gut fill and energy reserves up to 100 state units. Individuals followed the optimal policy as they updated their state at each time interval. A random number was selected at each time period and if greater than $1 - p$, a predation event occurred. I assumed that the predation events always resulted in the death of the forager if it were detectable to the predator (which only occurred when the individual was active). As simulated, the probability of predation was a memoryless function, where the probability of predation in each time unit is independent of previous predation events. Simulations are conducted across a range of risk of predation and ratios of intake rates and digestion rates. For each simulation, I recorded the average number of foraging bouts and time spent ruminating, resting or actively foraging only for surviving individuals. Baseline conditions and parameter values are given in Table 6.1.

3.3 Results

The behavioural decision of an individual in these simulations was driven by three factors: 1) the specific form of the terminal fitness function, 2) the relative risk of predation, and 3) the need to maintain a positive gut fill, as influenced by the ratio of intake to rumination rate. As such, these three factors influenced the behavioural decisions of a forager, the potential for the forager to remain inactive and avoid exposure to predation (i.e., employ a behavioural refuge).

3.3.1 Form of the fitness function

The specific form of the fitness function determined how the acquisition of additional energy reserves was prioritized, relative to avoiding predation. When the fitness function was based on a linear increase in energy reserves, individuals risked predation to acquire forage and tended not to rest until they reached a very high energetic state (Fig. 3.1a-c). Once at a high energetic state, the net gain in fitness obtained by acquiring additional forage, discounted by the risk of predation, was no longer greater than the net loss in fitness resulting from inactivity. This trade-off between foraging with predation and being safely inactive resulted in a time minimization strategy due to the inclusion of resting behaviour into the behavioural repertoire. However, over the majority of state space and time, individuals behaved as energy maximizers, alternating between foraging and ruminating to achieve ever increasing energy reserves.

Conversely, when fitness was defined by a sigmoid function an individual's use of resting was determined by whether or not its energy level was above or below the reproductive threshold. When below the reproductive threshold the individual behaved as an energy maximizer foraging and ruminating to achieve an energetic state in excess of the reproductive threshold (Fig. 3.1d-f). Once above the reproductive threshold, foraging did not warrant the exposure to predation because fitness depended solely on survival. Resting behaviour was used to minimize exposure to predation and the individual started to forage only when its reserves fell below the reproductive threshold due to the metabolic costs associated with resting. This pattern of resting and foraging (with subsequent rumination) close to the reproductive threshold resulted in a time minimizing strategy. The average final energy reserves, for individuals starting at all initial conditions, corresponded to the reproductive threshold plus some additional amount to cover the possibility of finding no food during a foraging bout (Fig. 3.2).

3.3.2 Effect of predation risk

The effect of predation risk on fitness was to devalue the potential energetic gains of foraging by the expectation of survival. As foraging became increasingly risky, the fitness benefits of remaining inactive outweighed the benefit of foraging at the cost of potential death. The particular value where there was a switch in behaviour from an energy-maximization to time-minimization strategy depended on the form of the fitness function and the metabolic cost of resting. When modelled as a linear fitness function, after reaching a high energetic state, individuals changed their behaviour to a time minimizing foraging strategy when under increased predation (Fig. 3.1a,b,c). Conversely with a sigmoid function the behavioural strategy was less influenced by increasing predation risk because this function already prioritized safety (Fig. 3.1d,e,f). Rather, the behavioural strategy was influenced only by the *presence* of predation risk as evidenced in the final energy states of simulated individuals (Fig. 3.2). Overall, resting behaviour became increasingly common as predation rate increased and this can be attributed to two main factors. First, resting provided a behavioural refuge from predation for the individual. Second, as resting did not reduce gut fill it did not hasten gut depletion, necessitating foraging (to prevent emptying of the gut) at the risk of predation. As would be expected, an increased predation rate reduced the overall survival of individuals in the simulation (Fig. 3.3).

3.3.3 Relative rate of intake to rumination

When I varied the ratio of intake rate (α) to rumination rate (β), I found that the average length of foraging bouts changed because activity was constrained by the need to prevent a complete emptying of gut contents. Thus, when the rumination rate was greater than intake rate, individuals required more foraging time per bout to ensure sufficient forage in the gut for subsequent processing (Fig. 3.4). This combination resulted in lower survival rates. Conversely, when intake rate exceeded rumination rate, individuals spent more time ruminating because rapid gut fill required rumination (Fig. 3.4). Individuals were able to acquire forage rapidly in short bouts, gaining enough gut contents that required multiple time steps to ruminate, which increased survival. The final energy state that individuals could achieve was dependent on the relative rate of intake as well as its absolute value (Fig. 3.2). The effect of the ratio of intake to rumination rate on bout length and dynamics was the same for both fitness functions regardless of predation risk. Increasing the absolute values of intake and rumination rates resulted in fewer foraging bouts because individuals could sooner reach the threshold reproductive value (sigmoid fitness function) or the point at which predation made further foraging less beneficial than remaining at rest (linear fitness function). Likewise, a reduction in the absolute rates increased the number of bouts required to reach a time minimizing strategy.

3.3.4 Phases in behaviour through time

Following the behavioural trajectory of an individual through simulation time, I observed three distinct phases, which, to a greater or lesser extent, occur with both forms of the fitness function (Fig. 3.5). These phases represented shifts in the dominant factor(s) influencing the pattern of observed behaviour and the time-specific ability of an individual to use inactivity to reduce exposure to predation. The first phase is the result of the individual's initial states of both gut fill and energy reserves. Individuals that are able to ruminate or rest immediately because their state was above the reproductive threshold are able to reduce exposure to predation until the metabolic cost of remaining inactive brings their energetic state below the reproductive threshold (i.e. a "silver spoon" effect). Likewise since fitness was calculated solely on energy reserves, the only behaviour that increases fitness is ruminating. Individuals tended to ruminate whenever their gut contents were higher than the amount removed in a single time step of rumination. The duration of this phase was dependent on the individuals initial state and the metabolic cost associated with resting or ruminating.

The second phase was influenced by the dynamics of foraging bouts. No resting occurred during this phase because individuals, modelled with either fitness function, behaved as energy maximizers. Individuals increased their reserves to the point where it is no longer beneficial to forage, relative to the risk of predation or the reproductive threshold. The ratio of intake to rumination rate determined the local proportion of time spent foraging and therefore exposure to predation (see above). The duration of this phase was dependent on the absolute values of both intake and rumination. The faster the individual foraged for food (and subsequently processed it into energy), the sooner it reached (or exceeded) the threshold energy level where resting behaviour is beneficial due to an increased risk of predation, as dependent upon the form of the fitness function.

The third phase was characterized by a time minimizing foraging strategy. It occurred when energy reserves were above the switch point in the fitness function, where safety was prioritized. This switch point was given by the inflection point of the sigmoid fitness function, representing the reproductive threshold. When fitness was modelled as a linear function, the switch point occurred when the expectation of survival multiplied by the gains of foraging was less than the net loss of remaining inactive, which depended on the particular parameter values for net energetic gain and predation risk. Individuals actively foraged only when energy levels fell below some critical value due to metabolic costs. The onset of this phase is determined by the level of predation and/or the threshold value of the sigmoid fitness function. The activity pattern that arose in this phase was the long-term stable activity pattern.

3.4 Discussion

The non-consumptive effects (NCE) of predation are known to be important determinants for individual behaviour, leading to population- and ecosystem-level consequences (Brown 1999, Ripple et al. 2001, Trussell et al. 2008). Typically, NCE of predation occur when individuals are unable to forage maximally and suffer reduced growth and reproduction because of anti-predator behaviours. I show situations where forage conditions may mitigate these detrimental effects and individuals may meet a reproductive threshold in spite of the risk of predation. The ability to “pay down” the cost of the NCE of predation by reducing activity is dependent on the specific form of the fitness function and the ratio of intake to rumination rate. The ability to efficiently acquire energy and high energy state both allow for an increase in inactive behaviours, thus avoiding predation while still meeting the specified fitness goals in a state-dependent fashion.

Prioritization of either energy acquisition or safety through the fitness function promotes (or discourages) the use of inactive behaviours and directly influences the potential for NCE of predation to occur. When inactivity is linked to a reduced risk of predation through anti-predator behaviours, the model outcomes show that prioritizing safety results in increased survival while still meeting some minimal reproductive threshold. These results are consistent with the asset protection principle and reflect a time minimizing foraging strategy (Schoener 1971, Clark 1994). In contrast, when individuals are modelled with a linear fitness function, they follow an energy maximization strategy (Schoener 1971) and are most susceptible to NCE of predation as predation risk increases. As a result, they not only suffer decreased survival due to the direct effect of predation, but also a reduced fitness, which is proportional to the rate at which they can acquire energy. The fitness functions represented here are ends of a continuum and the activity budgets of individuals employing a sigmoid fitness function may approach that of individuals employing a linear fitness function when intake is low or the reproductive threshold is very high. In both cases individuals are required to spend more time foraging and cannot afford inactive behaviours.

In free-ranging herbivores the ability of individuals to pay down the NCE of predation may depend on which foraging strategy they follow and the most appropriate strategy may vary seasonally or by sex, due to differences in energetic requirements and life history traits (Barboza & Bowyer 2001, Ruckstuhl & Neuhaus 2002, Bonenefant et al. 2004, Main 2008). For example, a female's lifetime reproductive value may increase by adapting predator avoidance behaviours that ensure the safety of a calf (Main 2008). Bull moose (*Alces alces*) may minimize foraging activity to engage in other fitness related activities during the rut (Miquelle 1990). Conversely, after the rut males may prioritize rapid acquisition of energy to replace energy stores needed to survive the winter (Main 2008). Similarly, Hay et al. (2008) found that male buffalo (*Syncerus caffer*) in bachelor herds in Africa had rates of mortality that were four times higher than in mixed groups, but also had higher diet quality as indexed by faecal nitrogen, which leads to larger body size and presumably, increased reproductive success. However, foraging strategies also have short-term constraints, such as the minimal energy reserves of small-bodied birds needed to survive overnight in winter (Houston & McNamara 1999). In the case of my model, I assumed that to maintain rumen functioning ruminants could not allow their gut to empty (Spalinger et al. 1993, Gross et al. 1996, Gordon et al. 2002). Nonetheless, the particular value of minimal gut fill does not change the model dynamics, but rather the average gut fill of an individual (D. Visscher, *unpublished data*).

The potential for NCE of predation is also contingent on environmental factors, specifically foraging conditions (Trussell et al. 2008). When constraints on acquiring forage are minimal (i.e., high ratio of intake to rumination rate) individuals have the potential to mediate the NCE of predation. Trussell et al. (2008) found that the type of foraging resource plays an important role in mediating the influence of predation risk. They found that snails foraging in barnacle beds had twice the NCE of predation, relative to those foraging in mussel beds. These results were attributed to the structural refuge that mussel beds provide, lowering the snails perceived risk of crab predation (Trussell et al. 2008). In contrast, I found that when the rate of processing forage (rumination) is relatively high compared to intake, individuals are required to actively forage for longer periods of time resulting in lower survival rates regardless of the risk of predation. Owen-Smith (1994, 1997) found that foraging times of kudu (*Tragelaphus strepsiceros*) during the dry season were higher than the wet season, which he attributed to compensation for longer search times for less available forage. Kudu were exposed to an increased risk of predation during at this time in part due to their reduced nutritional state and a lack of forage and suitable cover (Owen-Smith 2008). Similarly, I found that when intake rates become too low, individuals were not able to meet the fitness threshold (for sigmoid fitness) or had very low final energy reserves (for linear fitness) and were unable to compensate for the NCE of predation through inactive behaviours. In these cases, individuals modelled with either fitness function suffer low fitness resulting from both a reduction in survival due to increased activity and low energy reserves.

If prey are informed about the temporal pattern in risk of predation, they may be at an advantage because they may be able to match their inactivity to the periods of highest predation risk and consequently, there will be little cost to anti-predator behaviour (Lima

& Bednekoff 1999). While many field studies of the risk allocation hypothesis (Lima & Bednekoff 1999) are inconclusive due to difficulty in testing, Brown et al. (2006) found that juvenile cichlids modified their area use, foraging activity, and time spent moving, relative to their previous exposure to temporal variation in risk (Ferrari et al. 2009). However, if this potential to match behaviour to risk exists, it is expected that the requirement to ruminate may, in fact, help the ungulate forage efficiently under the risk of predation. It is possible that individuals informed about the timing of a predation event may adaptively fill their guts to varying levels of fill (dependent on perceived risk) during low risk situations, before retreating to ruminate when the predation risk increases above some acceptable level. In accordance with Bednekoff & Houston (1994), I found that individuals tend to maintain low levels of gut fill where the additional capacity could be adaptively filled in response to predation risk. Free-ranging ungulates may have access to this potential, as relatively low rumen fill is observed in both free-ranging browsing and grazing ruminants (Hofmann 1973, Owen-Smith 1994). In this situation the presence of a predator may constitute more of an interruption to foraging than a risk of death and an ungulate could potentially use its gut as a short term cache, storing up potential energy for future conversion at a time when active foraging would incur an increased predation risk (Pravosudov & Lucas 2001). This phenomenon has been noted in birds, which use their crops in this way to mitigated the overnight energetic costs when unable to forage (Evans 1969). There is also evidence that dairy cattle increase their rumen fill in the evening, relative to morning and mid-day foraging bouts, to ensure energy conversion when foraging is not possible (i.e. nighttime; Taweel et al. 2004).

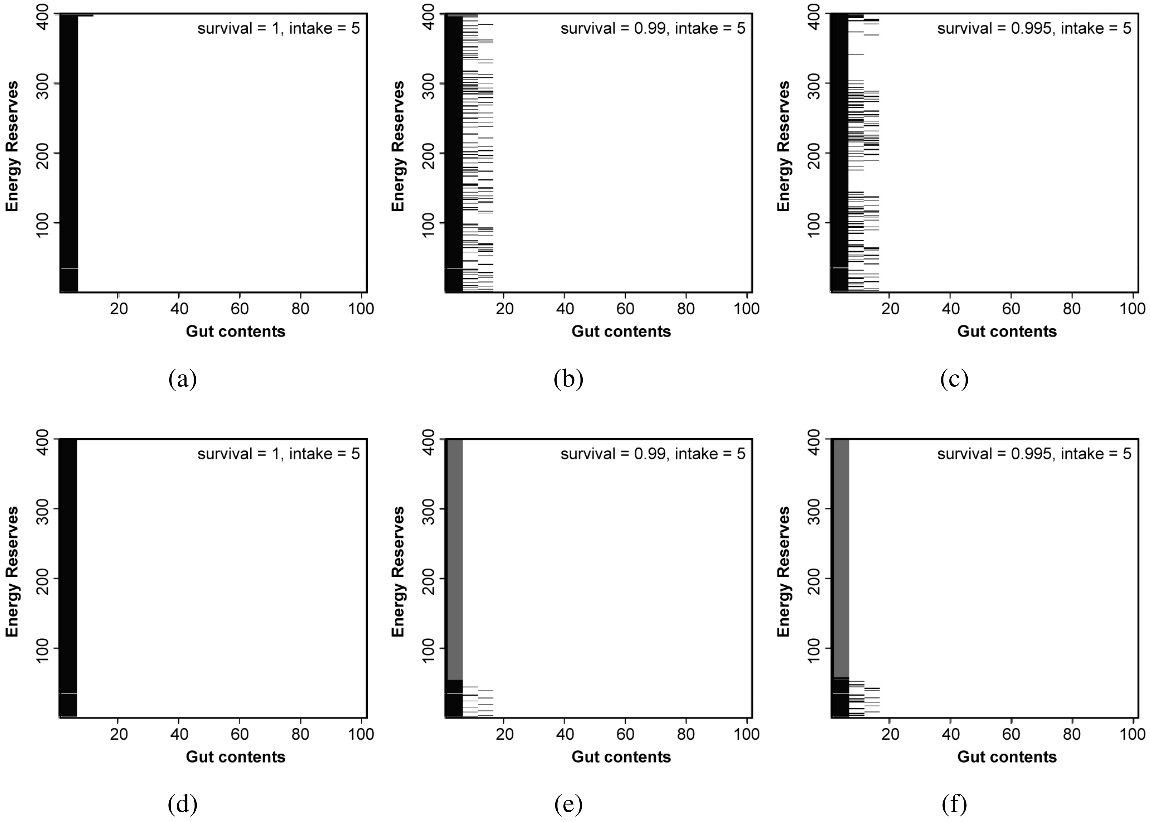
The ability to afford inactive behaviours through high energetic states, high intake rates, or reduced reproductive requirements, provides individuals with “free time” allowing them to match their behaviour to perceived predation risk. I found that when individuals are able to maintain high rates of intake or are above a critical reproductive threshold, they can afford the costs of inactivity to avoid predation. I assumed that inactivity conveys an anti-predator benefit by allowing individuals to cope with increased risk by remaining behaviourally unavailable to predation (i.e., a behavioural refuge *sensu* Banks et al. 2000). Inactivity has been linked to reduced predation risk in numerous field studies, resulting from reduced detectability, increased vigilance, or the ability to form groups (Anholt & Werner 1995, 1998, Anholt et al. 2000, Childress & Lung 2003, Wolff & van Horn 2003, Biro et al. 2004, Winnie & Creel 2007). Conversely, individuals that are in a low energetic state or unable to maintain a high rate of intake do not have access to this same “free time” due to a need to forage to maintain a positive gut fill or meet a target energy requirement. As a result, they cannot afford to match their behaviour to the increased risk and subsequently suffer from increased NCE of predation. The ability to match a behavioural response to risk, through changes in inactivity, may be similar to what has been described for the overlap in food processing (i.e., chewing) and vigilance in handling-limited foraging where ungulates can take advantage of “spare time” to be vigilant when processing only if the they are efficient at matching vigilance with chewing (Fortin et al. 2004).

3.5 Tables

Variable/Parameter	Description	Units	Baseline value	Range
b	behaviours	-	-	1-3
g	gut fill	state units	-	0-100
e	energy reserves	state units	-	0-400
m	metabolic cost	state units/time	2	-
α	conversion rate for gut contents to energy reserves	state units/time	5	-
β	intake rate	state units/time	5	2-10
rep	reproductive threshold	state units	50	-
p	probability of a predation event occurring in time t		0.005	0.0001-0.01
λ	probability of finding food		0.95	-
T	final time horizon	time units	200	-

Table 3.1: List of model variables and parameters including a description and the baseline conditions used for simulation purposes in the dynamic state variable model.

3.6 Figures



(a) (b) (c)

(d) (e) (f)

Figure 3.1: The influence of the predation rate and the form of the fitness function on the optimal policy, determined using the stochastic dynamic programming algorithm. The optimal policy is a function of an individual's accumulated gut fill (x-axis) and energy reserves (y-axis). The optimal policy is displayed for fitness defined as increasing energy reserves (upper row, a-c) and when fitness is defined as a sigmoid function (lower row, d-f). Grey areas indicates the state space where an individual should rest, the black area indicates the range of states for which an individual should actively forage, and white area indicates the state space where an individual should ruminate. Predation (1-survival) increases from 0 (left column, a and d), 0.005 (middle column, b and e), and 0.01 (right column, c and f). Intake rate is set equal to rumination rate $\beta = 5$ and the probability of finding food $\lambda = 0.95$. All other values are given as the baseline values in Table 1 unless otherwise noted on the figure. Note that the optimal policy is solved for values of gut fill from 0-100 and energy reserves from 0-400 to ensure that maximum values do not act as a constraint; however individuals, are simulated from 0-100 for both gut fill and energy reserves for the Monte Carlo iterations.

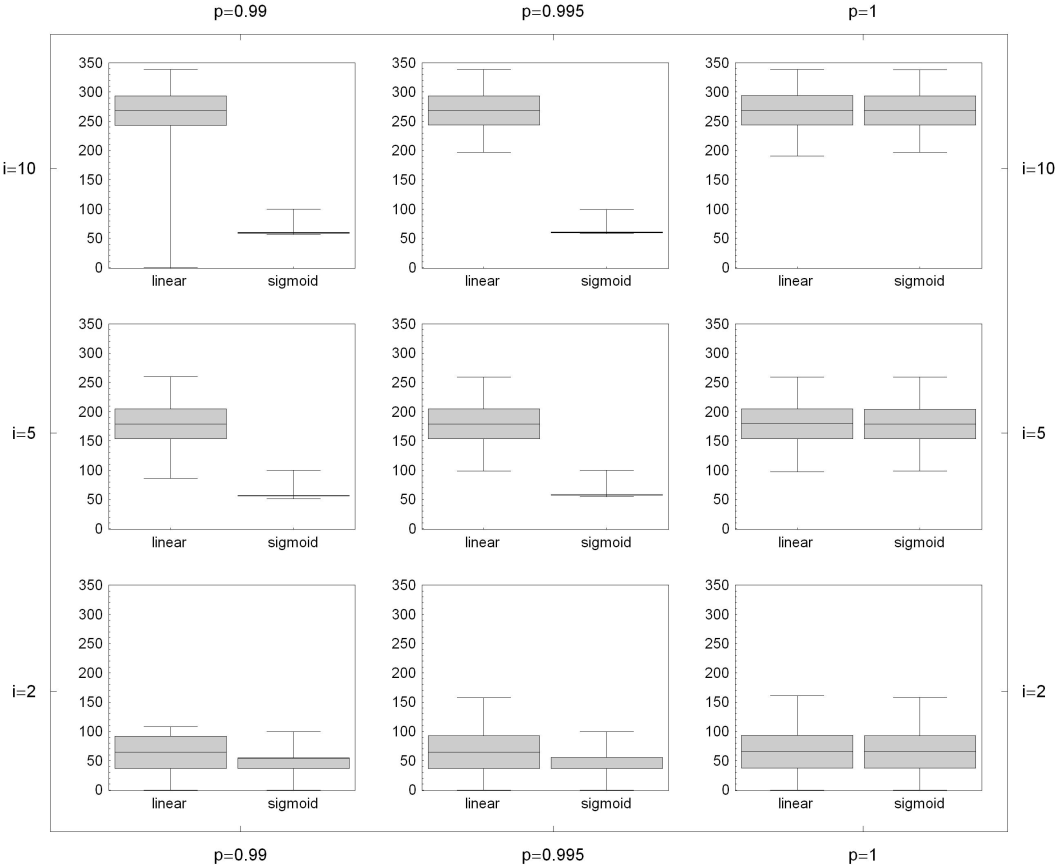
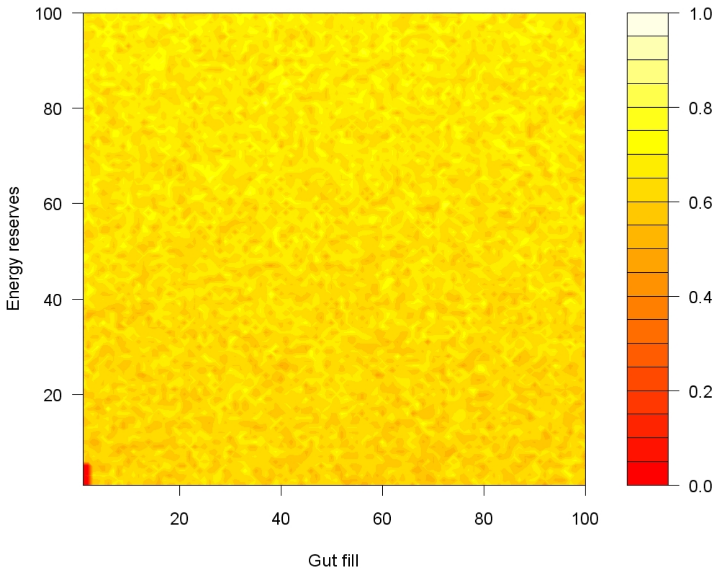
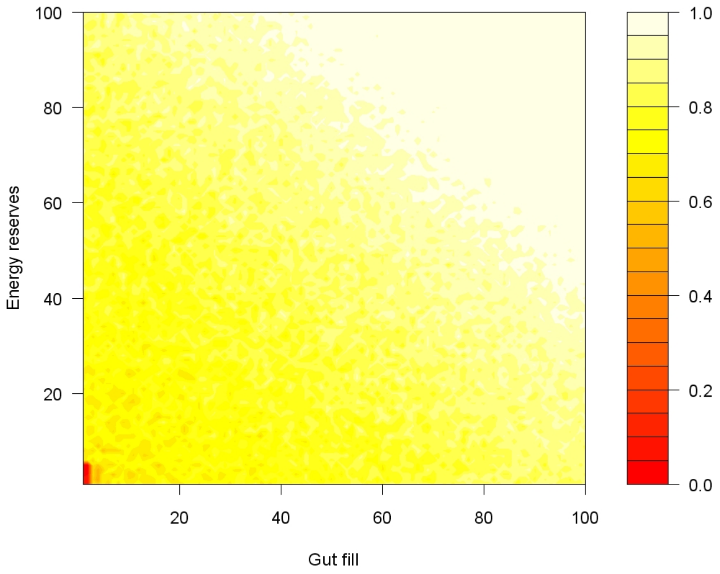


Figure 3.2: Boxplots of the final energy state of 100 replicate individuals starting at every combination of gut fill (0-100) and energy reserves (0-100). Only surviving individuals are plotted from the potential 1,000,000 individuals total. Results are given for individuals simulated with both linear and sigmoid fitness functions. Columns represent the influence of the risk of predation (1-p) ranging from risky (p=0.99) on the left to completely safe (p=1) on the right. Rows represent the influence of the relative rate of intake to rumination rate (set to 5) ranging from twice as fast (i=10; top row) to 2.5 times as slow (i=2; bottom row). Notice that in the absence of predation both fitness functions result in the same final energy conditions, the result of a predominantly rate maximization foraging strategy. Also note that across all predation levels, under poor foraging conditions (i=2), a number of individuals are unable to achieve the reproductive threshold (*rep*) defined in the sigmoid fitness function.

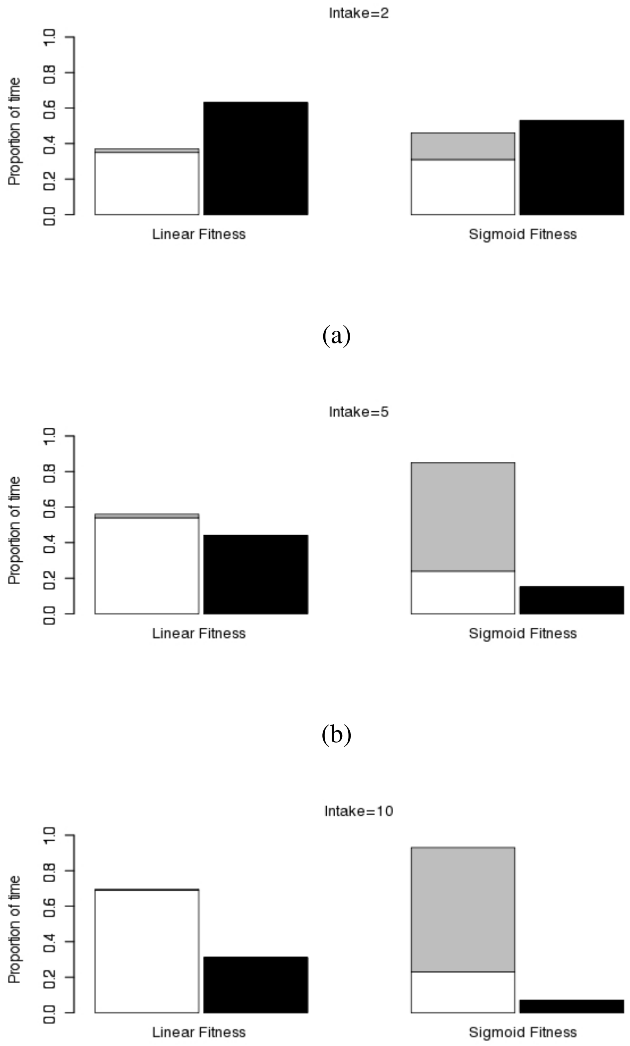


(a)



(b)

Figure 3.3: Rates of survival for individuals as a function of initial conditions (gut contents, x-axis and energy reserves, y-axis) when fitness is modelled as a linear (a) and sigmoid function (b) of energy reserves. Intake rate is held at the baseline value (β=5, equal to rumination rate). For reference, the average survival for individuals modelled with a linear fitness function and p=0.99 is 63.4%, while the average survival of individuals modelled with a sigmoid fitness and p=0.99 is 86.8%.



(a)

(b)

(c)

Figure 3.4: Overall mean activity budget for 100 simulated individuals initialized with a gut content of 50 units and an energy content of 50 units. The left side of each panel contains the activity budget of individuals simulated with a linear fitness function while the right side represents those simulated with a sigmoid fitness function. The white region is the time allocated to ruminating behaviour, the grey area represents the proportion of the simulation time devoted to resting, and the black region represents the time spent actively foraging. Resting and ruminating behaviour are stacked on one another to represent the total "inactive" time that may be observed under field conditions. Panel (a) represents the case when intake is 2 units per foraging time step, (b) represents an intake of 5 units per foraging time step, and (c) represents an intake of 10 units per foraging time step. In all cases rumination rate is held constant at 5 units per time step during ruminating activity. For comparison individuals simulated with a linear fitness function survived at a rate of 0.59, 0.52, and 0.54 for intake rates of 2, 5, and 10, respectively, while individuals simulated with a sigmoid fitness function survived at a rate of 0.69, 0.85, and 0.90 for intake rates of 2, 5, and 10, respectively.

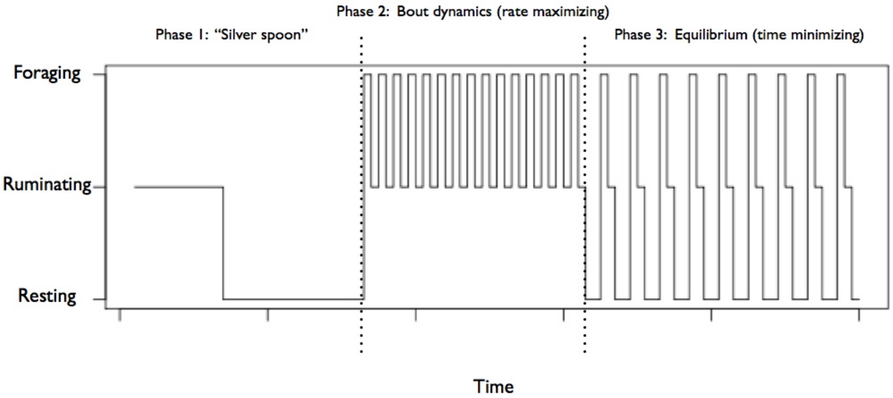


Figure 3.5: Hypothetical representative trajectory of activities for a simulated organism following the optimal policy through time (based on a sigmoid fitness function). The overall trajectory can be divided into 3 phases. The first, "silver spoon" phase is marked by rumination and resting behaviour only. The length of this phase depends on the initial conditions of the simulated individual and the absolute metabolic cost of these activities. The second phase is characterized by the bout dynamics of foraging. During this phase, simulated individuals act as rate maximizers, foraging and ruminating in turn until they reach some fitness threshold (in terms of energy reserves) or the risk of foraging out weighs the costs. The "rhythm" of this phase (duration of each half of the bout) is determined by the relative ratio of intake to rumination rate. The duration of this phase is determined by the speed at which the individual can achieve the fitness threshold (absolute rate of intake and rumination). Lastly, the equilibrium phase is the long term time minimizing strategy in which the simulated individual adopts to "hover" around the fitness threshold, foraging and ruminating as needed (i.e., foraging when metabolic costs push it below the threshold, and resting when above the threshold).

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Functional connectivity: A state-dependent approach

4.1 Introduction

Animal behaviour is regarded as an increasingly important process in landscape ecology, particularly the interaction of movement behaviour and landscape pattern. Quantification of the structural connection of patches is no longer considered adequate for assessing the connectivity among patches. Rather, an assessment of why animals are motivated to move to a new patch, and the degree to which landscapes both facilitate or impede animal movement among resource patches, is required to determine functional connectivity among patches (Taylor et al. 1993, With et al. 1997, Belisle 2005). By differentially distributing individuals on the landscape, functional connectivity directly influences population growth and trophic dynamics (Senft et al. 1987, Bailey et al. 1996, Holyoak 2000, Swihart et al. 2001, Matter et al. 2009), and is critical for conservation and management of animal populations (Frank & Wissel 1998, Chetkiewicz et al. 2006, Rouquette & Thompson 2007, Graham et al. 2009, Pinto & Keitt 2009). The motivation to move among patches comes in the form of trade-offs between rewards, such as gaining access to forage resources or mates, and avoiding the risks of predation or the uncertainty in future reward. Thus, the task facing landscape ecologists who are interested in the functional connectivity of landscapes and its implications for animal populations, is to identify and understand which factors influence how animals view trade-offs, in term of both staying in a patch or moving through a matrix to different patches.

Optimal foraging models (OFM) have often been used to address the trade-offs in spending time in discrete patches within heterogeneous landscapes (MacArthur & Pianka 1966, Emlen 1966, Charnov 1976). Recent advances in OFM include incorporating state-based decision making, predation risk, and errors in the decision making process of the forager (Sih 1980, McNamara & Houston 1990, Houston et al. 1993, Nonacs 2001, Richards 2004, Noonburg et al. 2007). Despite these improvements, the use of OFM continues to focus primarily on within patch processes, or has been limited to using time to evaluate trade-offs for moving among patches, even though the risk of mortality and energetic costs of moving between patches has been show to influence animal decisions (Ricketts 2001, Johnson et al. 2002, Revilla et al. 2004, Rizkalla & Swihart 2007, Frair et al. 2008, Gillies & St. Clair 2008). Therefore, incorporating the other costs associated with moving through a matrix to a patch could improve our understanding of the functional connectivity in heterogeneous landscapes (Lima & Zollner 1996, Zollner & Lima 2005, FitzGibbon et al. 2007, Ovaskainen et al. 2008).

Belisle (2005) highlighted two additional hurdles that potentially impede the efforts of landscape ecologists to model landscape connectivity based on animal behaviour: (1) variation in the motivation among different individuals to leave a patch and (2) variation in the connectivity between patches once they leave. Despite being widely applied to a variety of ecological questions (see Houston & McNamara 1999), state-dependent behavioural models have not been used to investigate functional connectivity. Yet, their potential usefulness seems clear: they can specifically incorporate an individual's motivation to leave a patch based on its current state and future fitness and the trade-offs in future fitness for moving to another patch, given the costs and risks of moving to other patches. While these models will not replace the need for empirical measures of connectivity (reviewed in Kindlmann & Burel 2008), they will provide insight into the range of possible responses that may be observed in nature and could further unify the disciplines of animal behaviour and landscape ecology (Lima & Zollner 1996).

In this chapter, I use a dynamic state variable model of a ruminant to assess the functional connectivity between two patches, based on trade-offs between within-patch rewards and risks and the costs of moving to another patch (Houston & McNamara 1999, Clark & Mangel 2000). I start by assessing functional connectivity only between pairs of patches separated in space to avoid the confounding nature of landscape configuration (Gustafson & Gardner 1996, Gardner & Gustafson 2004), but a multiple-patch landscape is addressed in chapter 4. Using pairs of patches, I determine over what distances functional connectivity between patches is maintained when individuals are motivated to move to a new patch but are also confronted by risks of predation and energy expended in movement while in transit. For this assessment, all individuals are motivated to move to the second patch because of a positive difference in foraging rewards or a negative difference in predation risk between the patch of origin and the distant patch; however, whether or not they move depends on their state and costs related to transit. The energetic cost of transit between the patches is positively related to distance, as is the risk of predation due to increased exposure (Parker et al. 1984, McAdam & Kramer 1998, Zollner & Lima 2005). Connectivity between patches is indexed as the proportional use by individuals of a second (distant) patch after multiple time steps. Finally, I show how my approach can be used to titrate the cost of isolation of a patch from a functional perspective based on animal behaviour, not unlike giving-up density experiments (Brown 1988).

4.2 Methods

I extend the dynamic state variable model of ungulate foraging reported in chapter 2 to examine the trade-offs in moving between two foraging patches to address the functional connectivity of patches in a landscape. Whether an ungulate moved from its current patch (patch 1) to the second patch (patch 2) during a simulation was dependent on the state of the ungulate, the difference in the patch-specific intake, rumination, and predation rates, and the energetic costs and predation risk associated with movement between patches. I used the proportion of time steps spent in patch 2 as the metric of functional connectivity between patches because it removed the effect of predation in patch 1 while incorporating the risk of in-transit predation.

4.2.1 Patch structure and transit costs

Foraging patches differed in the intake (β) and rumination (α) rates they offered the ungulate and the predation risk (p) to which it was exposed. All simulated individuals started in patch 1 (Fig. 4.1) and I imposed a motivation to move from patch 1 to patch 2 by independently setting the foraging rewards in patch 2 higher and predation risk lower than in patch 1. Cost of transit (c) between patches was related to the distance between patches (d) such that the energetic cost for a simulated individual increased with distance, as did their exposure to predation during transit (u; Table 4.5). In each simulation I used baseline values for patch 1 and iteratively varied the values in patch 2, for a total of 5 simulations (Table 4.5) over increasing inter-patch distances (given in distance units; DU). If the state-dependent rewards of moving to patch 2 was sufficient to overcome the transit costs (energetic cost and predation risk) then the individual would subsequently be found in patch 2. Once an individual moved to patch 2 there was no motivation to move back to patch 1. For simplicity, movement between patches was instantaneous, as such costs of transit between patches influenced the decision to move to a new patch but not the time spent in the two patches. The baseline, patch-based and in-transit energetic costs and predation rate are given in Table 4.5.

4.2.2 Ungulate behaviours and state variables

I model an ungulate defined by it's gut fill (g), energy reserves (e), and current location (i; patch 1 or 2) as state variables. As in chapter 2, behaviours (b) of a ungulate forager included rumination (1; converting gut contents into energy reserves), resting (2; not engaging in either foraging or ruminating), and foraging (3; actively filling the gut). Behaviours were assumed to be mutually exclusive in time. The forager could select between any of the behaviours in either of the two patches, but in doing so exposed itself to a patch specific predation risk (p), intake (β), and rumination (α). Inactive behaviours (resting and ruminating) formed a behavioural refuge and did not incur a risk of predation (chapter 2). The inactivity of rumination and resting incurred a metabolic cost of half the metabolic cost of active foraging (m). During each time step spent foraging, there was a probability of 0.95 (λ) that the ungulate found forage, and when it did, forage was added to the gut contents (g) at a constant rate (β). Gut depletion during rumination was modelled as a constant conversion (α) of gut content into energy stores (e). If either gut contents or energy reserves fell to 0 I assumed that death occurred.

4.2.3 Fitness functions

The optimal fitness of an individual, based on the state of the individual (location, gut fill, and energy reserves) in time, depends on the behaviour which maximizes fitness as:

$$F(i,b,g,e,t) = max \left\{ \begin{array}{l} max(V_{1,1}, V_{1,2}, V_{1,3}) \\ max(V_{2,1}, V_{2,2}, V_{2,3}) \end{array} \right. \tag{4.1}$$

where

$$\begin{gathered}
V_{1,1} = F(1,1,g-\alpha_1, e+\alpha_1-\frac{m}{2}, t+1) \\
V_{1,2} = F(1,2,g,e-\frac{m}{2},t+1) \\
V_{1,3} = \begin{array}{c} (1-p_1)(\lambda)F(1,3,g+\beta_1,e-m,t+1)+ \\ (1-p_1)(1-\lambda)F(1,3,g,e-m,t+1) \end{array} \\
V_{2,1} = (1-ud)F(2,1,g-\alpha_2,e+\alpha_2-\frac{m}{2},t+1)-cd \\
V_{2,2} = (1-ud)F(2,2,g,e-\frac{m}{2},t+1)-cd \\
V_{2,3} = (1-ud)\left[\begin{array}{c} (1-p_2)(\lambda)F(2,3,g+\beta_2,e-m,t+1)-cd+ \\ (1-p_2)(1-\lambda)F(2,3,g,e-m,t+1)-cd \end{array} \right]
\end{gathered} \tag{4.2}$$

where $V_{i,b}$ refers to the fitness accrued in the i^{th} patch (i=1 or 2) by selecting the b^{th} behaviour (1; ruminating, 2; resting or 3; foraging) and p_i is the probability of a predation (and therefore survival is $1-p_i$) occurring in patch i. Additionally, I allowed the individual to incur a risk of predation (u) when making the decision to travel from patch 1 to patch 2, which increased with inter-patch distance d. Likewise energy reserves were decreased by a cost (c) accrued when traveling over the inter-patch distance upon reaching the new patch. While transit between patches occurred instantaneously, the costs and risks associated with it were incorporated into the individual's decision to make use of a new patch by discounting its potential gains and adding to its patch-specific costs.

Thus the fitness function at any time is calculated as:

$$F(i,b,g,e,t) = \begin{cases} F(i,b,g,e,t) & \texttt{if } t < T \\ \Phi(e,T) & \texttt{if } t = T \end{cases} \tag{4.3}$$

where terminal fitness, $\Phi(e,T)$, was calculated as either linearly increasing energy reserves, given as:

$$\Phi(e,T) = e_T \tag{4.4}$$

or defined as a sigmoid fitness function as:

$$\Phi(e,T) = \frac{exp(-rep + e_T)}{1 + exp(-rep + e_T)} \tag{4.5}$$

where rep is a reproductive threshold that must be met by the energy reserves to gain a fitness benefit. In all cases when $t = T$, fitness was dependent only on energy reserves and not gut fill. I assumed that any remaining forage in the gut at the end of the time horizon did not convey a fitness benefit. A full list of parameters and variables, their description and values are given in Table 4.5.

4.2.4 Monte Carlo forward iterations

I used the Monte Carlo forward iteration procedure (Clark & Mangel, 2000), simulating 100 individuals, starting at each possible combination of gut fullness and energy reserves (100 x 100 state combinations) for the same time period ($T = 100$). Each individual followed the optimal policy (calculated from eq. 4.1) and updated its state at each time step unless it died. With a set of five simulation scenarios, I investigated the trade-offs in foraging opportunities within patches and the costs for between patch transit. In all cases, patch 1 had baseline characteristics (Table 4.5) and only patch 2 was altered. In the first three simulations I either increased intake or rumination rate, or lowered the predation risk of patch 2 and kept transit costs constant at baseline values (but dependent on inter-patch distance). In the last two scenarios I kept patch 2 characteristics constant (but with increased intake) and varied transit costs. In these cases, I assumed that the in-transit predation costs were inversely related to the in-transit energetic costs. This assumption was made because the cost of predation incurred while moving to patches depends not only on the magnitude of the risk but also the duration of risk exposure. For example, an individual may move more quickly among patches to minimize predation exposure, but it will incur higher energy costs (Parker et al. 1984, McAdam & Kramer 1998, Frair et al. 2005, Zollner & Lima 2005). The patch values and transit costs for each scenario are given in Table 4.5 and a representation of the patches is illustrated in Fig. 4.1.

For each simulation I recorded the proportion of time surviving individuals spent in patch 2. I used the average proportion of time spent in patch 2, from the 1000 simulations at each combination of states, as a metric of functional connectivity between patches because it reflected only those individuals that lived long enough to decide to leave patch 1 based on state-dependence, thereby eliminating the effects of predation in patch 1 itself (but not the effect of predation risk in patch1 on the decision to leave the patch). Because the initial distribution of individuals, in terms of energetic and gut-fill states was the same among simulation scenarios, a high mean proportion of time spent in patch 2 reflected high patch connectivity or little resistance to moving among patches due to low transit costs.

4.3 Results

Overall connectivity declined with increasing distance between the patches, but the rate at which this occurred was influenced by the form of the fitness function. As shown in chapter 2, the different forms of the fitness function explicitly prioritized different aspects of fitness. When a linear fitness function was used, energetic gain was prioritized above predation risk for a majority of states, and subsequently, connectivity was maintained over relatively large distances compared to when fitness was modelled with a sigmoid function (Fig 4.2a & 4.3a). When the fitness function was linear, connectivity between relatively distant patches was maintained because individuals were motivated to move to a new patch, particularly when intake rates were high. The difference in intake rates between patches had the biggest impact on connectivity relative to an increase in rumination rate or a decrease in predation rate (Fig. 4.2a). When modelled with a linear fitness function individuals were able to reduce one of the transit costs (either energetic cost or predation risk) at the expense of the other through transit behaviour. Behaviours that resulted in a decreased transit cost facilitated connectivity over larger inter-patch distance over-and-above patch based motivation (dark shaded boxes; Fig. 4.3a). Conversely, individuals who reduced the transit predation risk at the expense of increased energetic cost reduced the connectivity relative to the baseline patch-based motivation (light shaded boxes; Fig. 4.3a).

In the case of individuals modelled with a sigmoid fitness function, safety was prioritized over the acquisition of energy for any individuals exceeding the reproductive threshold (chapter 2). As a result, when connectivity was modelled with a sigmoid fitness function, individuals ceased to move to patch 2 over shorter distances relative to those modelled with a linear fitness function (Fig 4.2b & 4.3c). Instead, individuals tended to "make ends meet" in the patch of origin. This was possible because the patch of origin was sufficient for maintaining their state at the baseline reproductive threshold. If the reproductive threshold had been raised, the motivation to move would have increased, resulting in more individuals moving to patch 2. Likewise, if the baseline conditions in patch 1 had been poorer such that the reproductive threshold could not be maintained (e.g., intake was below metabolic costs) more movement to patch 2 would have occurred. As mentioned above, individuals maintained connectivity over the greatest inter-patch distances when intake rates were increased in patch 2 (Fig. 4.2b). A decrease in patch-specific predation or an increase in rumination rate had very little effect on connectivity (Fig. 4.2b). When either the energetic cost or predation risk during transit was reduced, at the expense of the other rate, there was no change in connectivity over-and-above that produced by the baseline patch-based motivation (Fig. 4.3b).

When the costs and risks associated with transit between the patches was modified to represent situations where transit was either energetically "costly" or incurred an increased risk of predation ("risky") the maintenance of connectivity depended on the unique trade-off between transit costs and risks. In this situation, use of patch 2 was highest in the costly scenario when individuals were able to reduce the cost of movement at the expense of predation risk (Fig. 4.4). Conversely, when movement was risky, individuals able to trade-off predation risk at the expense of energetic cost maintained connectivity and use of patch 2 (Fig. 4.4).

4.3.1 Behavioural refuge and connectivity

The extent to which safety during inactive behaviours (rumination and resting) influenced connectivity was assessed for the situation only where movement to patch 2 was motivated by increased intake. Further, I compared outcomes only between individuals modelled with a linear and sigmoid fitness function at 2 DU. I found that the effectiveness of within patch anti-predator behaviours (i.e., inactivity) had little to no effect on the functional connectivity of patches for individuals modelled with a linear fitness function (white boxes; Fig. 5.3). For individuals modelled with a sigmoid fitness function (shaded boxes; Fig. 5.3) there was a large difference in connectivity. When individuals could use inactivity to form a complete behavioural refuge (i.e., through effective anti-predator behaviours) high levels of patch connectivity were maintained. When inactivity was ineffective and individuals were exposed to the same patch-specific risk of predation, as when actively foraging, connectivity ceased completely (Fig. 5.3).

4.3.2 State-dependence and connectivity

Transit to patch 2 occurred in individuals of all initial states when modelled with a linear fitness function (Fig. 4.6a). In contrast, when modelled with a sigmoid fitness function only individuals in a “poor” state made significant use of patch 2 (Fig. 4.6b). In addition, individuals with high gut fill and energy reserves most often choose not to move because they were able to meet their fitness goals in patch 1. Conversely, when individuals were modelled with a linear fitness function they moved to patch 2 when it provided a quicker means of increasing the energy reserves. At a distance of 2 DU between patches, individuals modelled with a linear fitness function had a lower average rate of survival (86%) than individuals modelled with sigmoid fitness functions (96%). The difference in survival was not soley due to the risk associated with transit between patches but was also the result of these individuals rarely employing resting behaviour, thus decreasing their overall inactive time and exposing them to predation through an increase proportion of time foraging (see chapter 2). However I was limited to comparing the results from the two types of fitness models over relatively short inter patch distances (i.e., 2 DU) because when the inter-patch distance exceeded this value, there was virtually no use of patch 2 by individuals modelled with a sigmoid fitness function.

4.3.3 Titrating the cost of isolation

Using my approach, I was able to assess how willing a ruminant was to accept the costs of transit by determining the additional rewards necessary to increase use of the patch 2. I conducted this assessment by initially assuming that animals prioritized safety (i.e., sigmoid fitness function) and employed patch conditions that represented when individuals ceased to be motivated to move to patch 2 (i.e., 4 DU; energetic cost of 4 and an in-transit predation risk of 0.004). I then iteratively increased the intake level in patch 2 to determine at what intake value at least 50% of the individuals were motivated to overcome the costs of transit to move to patch 2. I found that intake rates had to be increased approximately 2.5 times before individuals spent over 50% of their time in patch 2 (Fig. 4.7). In the same assessment assuming a linear fitness function, a less than 2-fold increase in intake in patch 2 resulted in over 50% of an individual's time being spent in patch 2. Individuals modelled with a linear fitness required less motivation to use patch 2 as they prioritized energetic gain and already used patch 2 approximately 30% of the time under these conditions (Fig. 4.2a)

4.4 Discussion

Maintaining or restoring landscape connectivity is an important component of conservation (Haddad et al. 2003, Chetkiewicz et al. 2006). The use of dynamic state variable models in this application has shed light on the motivations and behaviours that lead to enhanced landscape connectedness and how to improve management and conservation of species in fragmented landscapes. I found that the state of the animal, and whether or not individuals followed a strategy of maximizing energy intake (linear fitness function) or minimizing foraging time to avoid predation (sigmoid fitness function), influenced the functional connectivity between two patches. The influence of foraging strategy and current energetic condition is not surprising considering that energy reserves form the basis for individual fitness and the quick acquisition of these resources allows individuals not only to replenish energy reserves, but as observed in my simulations, to safely ruminate or rest resulting in increased survival rate (chapter 2). Patch enhancement through forage improvements, such as forage seedings, burning, or selective forest cutting, is a common management strategy to encourage the use of areas for many ruminant species (Reynolds 1969, Short & Knight 2003, Genghini & Capizzi 2005, Edwards et al. 2004). Yet even when there is high motivation to move between patches, movement results in a reduction in energetic state, particularly if foraging opportunities in the matrix are minimal. A reduction in energetic state therefore requires additional foraging activity once in the patch to recoup the cost of moving. When foraging incurs an increased risk of predation, it could result in lowered survival, reflecting an attractive sink (Delibes et al. 2001). However, unlike the attractive sinks reported by Delibes et al. (2001) and Kristan (2003), reduced survival is not the result of poor perception or suboptimal decision making resulting in poor patch selection, but rather the legacy of an individual's previous energetic state compounded by the cost of movement. In this case, the attractive sink may be a temporary condition as individuals subsequently forage to increase their current energy reserves when the patch provides higher intake (Wairimu et al. 1992, Radder et al. 2007). As a result, how an individual starts a simulation reflects a "silver spoon" effect, wherein individuals with initially high reserves gain a fitness benefit in the future. Field studies exaiming how condition interacts with movement among patches remains largely unexplored (Stamps 2006), but there is accumulating evidence from simulation studies it is an important factor. For example, Zollner & Lima (1999, 2005) also showed a strong effect between the amount of energy reserves and the probability of successful dispersal of an individual, where individuals with higher reserves were able to sustain the cost of anti-predator defences during dispersal and able to move for longer to locate a patch.

In contrast, reducing the predation risk of the distant patch had the least effect on maintaining connectivity. The small effect was presumably due to the overall low predation risk within the simulated landscapes and, in these simulations, the ability of individuals to use inactive behaviours as predation refuge (Banks et al. 2000). In situations where predation risk is very high in one patch and the other patch acts like a refuge, the willingness to move to the safer patch may extend connectivity over a wider range of inter-patch distances. This is, in fact, one potential reason for the behaviour of resident elk in a partially migratory system (Hebblewhite & Merrill 2007, 2009). Hebblewhite & Merrill (2009) found that by making use of a complete refuge, resident elk were able to mitigate the high risk associated with the presence of wolves due to the wolve's avoidance of human activity. The small influence of predation risk within a patch may also depend on the ability of individuals to modify risk using anti-predator behaviours. In this study I assumed that individuals used inactivity to reduce predation risk while within patches. If anti-predator behaviours during inactivity were ineffective, individuals using a time minimizing strategy (i.e., sigmoid fitness function) gained little anti-predator benefit from inactivity and were able to meet their fitness goals in their initial patch and therefore did not expose themselves to the risk and cost of moving between patches. As with inactivity, the effectiveness of the anti-predator behaviour depends on forage resources. Vigilance has a cost to intake when animals are encounter-limited in their foraging (Fortin et al. 2004) and forming large groups may be possible only where resources are high (Fortin & Fortin 2009). Likewise, I found that the potential for inactivity and anti-predator behaviours increased when foraging conditions facilitated individuals to reach their fitness goals in short order (i.e., intake rates were high), thus allowing them to forage using a time minimizing strategy and avoiding the non-consumptive effects of predation (chapter 2). Incorporating vigilance and grouping behaviour into models of connectivity may be possible given the recent emphasis in field studies to understand the trade-offs of these behaviours (Childress & Lung 2003, Fortin et al. 2004, Winnie & Creel 2007, Liley & Creel 2008, Hay et al. 2008, Robinson 2009).

Matrix conditions also are known to influence functional connectivity between patches (Bowman & Fahrig 2002, Bender & Fahrig 2005, Zollner & Lima 2005, Russel et al. 2007, Revilla & Wiegand 2008), but field studies are often not able to separate the influence of matrix conditions from the motivation to move among patches. Gap-crossing and homing studies involving translocated individuals are used to measure functional connectivity and rely on the motivation that individuals have to return to an established territory (Belisle et al. 2001, Bowman & Fahrig 2002, Belisle 2005, Gillies & St Clair 2008). These studies have added to our knowledge of how certain landscape features or habitat types facilitate or impede movement, but they may provide limited understanding of the trade-offs that most individuals face, except in extreme circumstances. The fitness consequences of not returning to ones territory may be large because home ranges represent a large investment in time and energy in maintenance, as well as an investment in local knowledge. Thus, the consequences of starting from "scratch" may constitute a large motivation, causing individuals to maintain connectivity over distances and topography that would normally not be connected in day-to-day movements (Bowman & Fahrig 2002). Results of homing studies have more in common with dispersal studies where there is a strong fitness motivation to leave a patch to search for another (i.e., the potential to reproduce), rather than a strong motivation to return.

Alternatively, the trade-off between movement rates and the efficacy of anti-predator behaviours, while moving between patches, has not been well documented nor explored in a modelling framework (but see Zollner & Lima 2005). Some field studies have shown movement rates of individual to be higher in areas of increased predation risk (Yoder et al. 2004, Frair et al. 2005), while others suggest that movement rates are decreased in risky areas (Anholt et al. 2000, McAdam & Kramer 1998). Often, movement and vigilance are assumed to be mutually exclusive and the ability to minimize either movement costs or the in-transit risk of predation may form a trade-off (McAdam & Kramer 1998, Sharpe & Van Horne 1998, Kramer & McLaughlin 2001, Zollner & Lima 2005). There is the potential that decreased movement rates may foster anti-predator strategies (Kramer & McLaughlin 2001). For example, McAdam & Kramer (1998) found that squirrels and chipmunks used intermittent pauses when moving into riskier habitats. However, this evidence is not conclusive. I modelled the exclusivity in the movement cost-predation risk trade-off and altered movement costs and predation risk while in transit, and found that functional connectivity was most sensitive to a reduction in the energetic cost of movement. Higher connectivity was maintained when individuals were able to reduce the energetic cost of moving among patches at the expense of increased predation risk. However, the degree to which connectivity was maintained depended on the formulation of the fitness function. Outcomes of the trade-off between movement costs and predation risk will depend on species-specific situations, where either movement is energetically costly or moving incurs a high risk of predation. The ability to match behaviours to prevailing landscape conditions while moving between patches represents an important advantage for an individual and facilitates connectedness in landscapes. Understanding the ability of individuals to perceive the risks and costs of movements and match behaviour to the conditions of the inter-patch matrix remains a fruitful area for study, perhaps leading to a better understanding of the role that behaviour plays in landscape connectivity.

Analyses of patch use in heterogeneous landscapes have typically used an optimal foraging model approach and patch use is often described in terms of the marginal value theorem (MVT; Charnov 1976, Stephens & Krebs 1986). However, these models assume that individuals use an energy-maximization foraging strategy and have typically ignored state-dependence (but see Newman 1991, Nonacs 2001). While the MVT makes broadly applicable predictions of patch use, animals are often observed to have longer patch residence times than predicted from the MVT (Stephens & Krebs 1986, WallisDeVries et al. 1999, Nonacs 2001). Incorporating individual behaviour and state-dependence may help explain deviations between models and observation (Kie 1999, Searle et al. 2005). However, dynamic state variable models may never result in generalizable results, despite the fact that they often bear qualitatively similar results with different (i.e., time minimizing) foraging strategies (Newman 1991, Nonacs 2001). While my model was not meant to test the MVT, some insights may still be applicable. If we assume that increasing the intake of the distant patch is analogous to reducing the intake of the initial patch through depletion (i.e., in either case a motivation gradient is produced resulting in movement) then the proportion of time spent in the distant patch (i.e., patch j) reflects the travel time effect in the MVT. In this situation I observe that the time spent in the original patch increases, reflected by the lower use of the distant patch, in accordance with the MVT (Charnov 1976). However, the relationship between the motivation to move and patch use is dependent on other behavioural factors, in particular an individual's foraging strategy specified by the fitness function and its ability to mitigate predation risk through anti-predator behaviours. Incorporating these effects into foraging models (i.e., giving up density models; Brown 1999) may present researchers with generalizable predictions for testing in the field (Taborsky 2008).

The modelling framework presented here could be modified to investigate the behavioural “permeability” of various routes through the matrix to a distant patch or be used to select the particular corridor location which minimizes the fitness consequences (movement cost and predation risk) of moving between isolated patches. As such, it may be used to rank planned restoration efforts and corridors based on their potential to increase connectivity. Dynamic programming has similarly been used as a tool for determining the optimal allocation of funds to conservation efforts and the optimal use of those funds for reconstructing populations in fragmented landscapes (Westphal et al. 2003, Wilson et al. 2006, McDonald-Madden et al. 2008). However, regardless of the permeability of the matrix or the role that behaviour plays in maintaining functional connectivity it is important to note that critical thresholds in landscape configuration will result, regardless of whether or not movement behaviours mitigate isolation effects or movement costs (With & Crist 1995). Individual behaviour will not remove critical thresholds in landscape use - it can only delay their onset. Researchers concerned with further mitigation of critical thresholds or restoring connectivity may use dynamic state variable models to titrate the motivation to maintain connectivity similarly to using giving up density (GUD) experiments, which titrate the additional food required to equalize use between a safe and risky patch (Brown 1988, Kotler & Blaustein 1995, Brown & Kotler 2004). As such, the additional rewards found in the distant patch represent the marginal rate of substitution of foraging (or fitness) benefits for the transit costs incurred (both energetic and predation risk). The basic titration principle is a potentially useful and relevant tool for landscape ecologists. The model presented here asks: “What additional state-dependent motivation is required to overcome the costs associated with patch isolation?”. It can be used to assess the efficacy of different management strategies for restoring connectivity. Using the model in this way results in a process oriented titration of functional connectivity and provides researchers with greater insights into the behavioural basis for trade-offs in a landscape context, potentially improving management of species in fragmented landscapes (Lima & Zollner 1996, Roitberg & Mangel 1997, Russell et al. 2003, Belisle 2005, Zollner & Lima 2005).

4.5 Tables

Parameter	Description	Units	Baseline value
m	metabolic cost	SU/time	2
T	Total number of time steps	time units	100
u	predation rate in transit	risk/distance units	0.001
c	energetic cost of transit	SU/distance units	1
Variable	Description	Units	Baseline value
α	conversion of gut contents to energy reserves	SU/time	5
β	intake rate	SU/time	5
p	patch-specific probability of predation	risk/time	0.005
d	distance between patches	distance units	-

Table 4.1: List of model parameters including a description and the baseline conditions used for simulation purposes in the dynamic state variable model, where SU are state units.

Motivation	Scenario	Intake	Rumination	Patch predation	Travel cost	Travel predation
Baseline	-	5	5	0.995	0	0
Patch based	Higher intake	10	5	0.995	d	d/1000
Patch based	Higher rumination	5	10	0.995	d	d/1000
Patch based	Lower predation	5	5	0.998	d	d/1000
In-transit	Cost reducer	10	5	0.995	d/2	2(d/1000)
In-transit	Risk reducer	10	5	0.995	2d	(d/1000)/2

Table 4.2: Simulation scenarios for functional connectivity. Patch based motivation investigates the influence of patch enhancement of the distant patch (patch 2) relative to the starting patch (patch 1), this was done by increasing the intake rate and rumination rate, and decreasing the patch specific predation rate, respectively. The remaining simulation scenarios reflected situations where movement behaviour enhanced functional connectivity over and above patch enhancement. I consider when movement and anti-predator behaviour are mutually exclusive to one another. In this situation a reduction either the travel cost or the in-transit predation risk results in an increased cost or risk in the other rate, respectively. *d* is the distance from patch 1 to patch 2. In all cases patch 1 remains at baseline conditions.

4.6 Figures

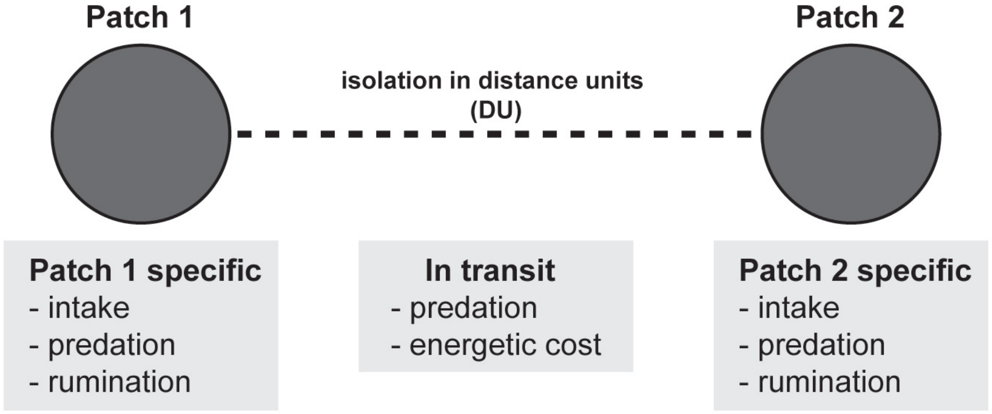
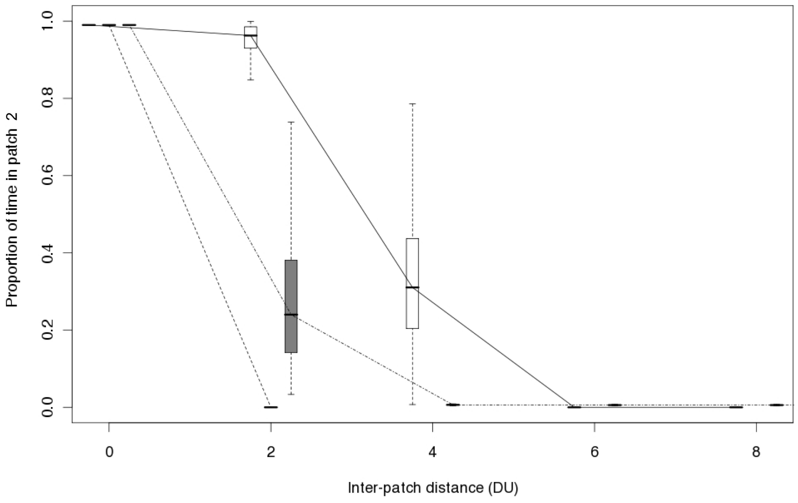
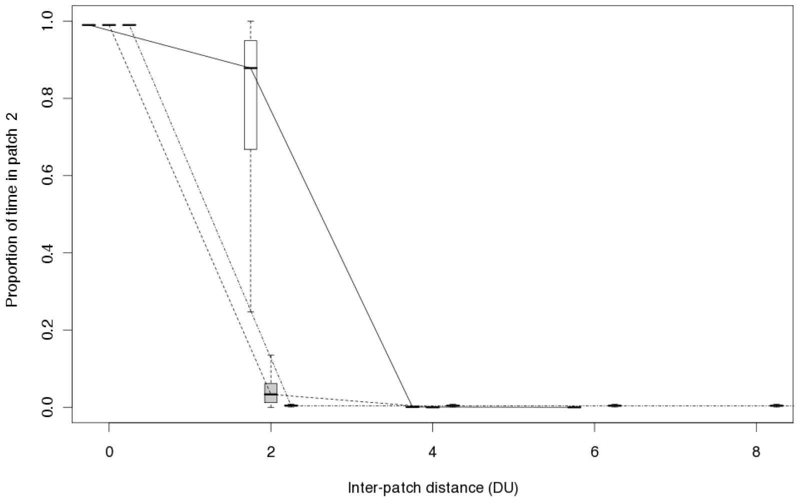


Figure 4.1: The relationship of the pair of patches to one another, as well as the in-transit and patch-specific rates.

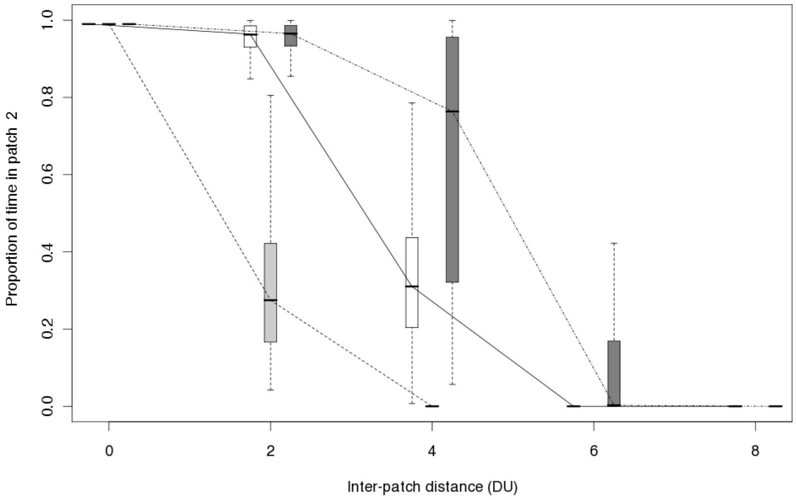


(a)

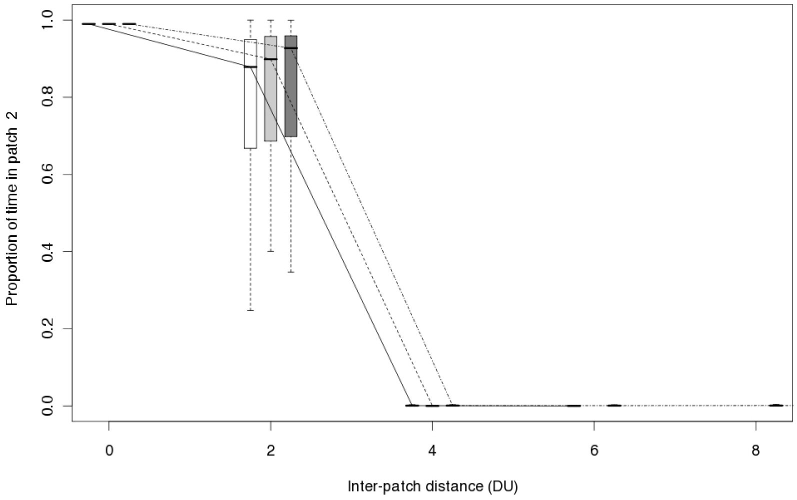


(b)

Figure 4.2: Functional connectivity as a function of patch based motivation and increasing inter-patch distances (DU) for individuals modelled using a linear (a) or sigmoid (b) fitness function. The white boxes connected with a solid line indicate the connectivity due to increased intake in patch 2, the light grey boxes and dashed line refer to the connectivity resulting from a reduction in predation risk in patch 2, and the dark grey boxes and the dotted-dashed line refer to the connectivity maintained by an increased rumination rate in patch 2 for both forms of the fitness function. Within each scenario all other parameters were held constant at baseline values (see Table 1).



(a)



(b)

Figure 4.3: Functional connectivity for in-transit motivation, over-and-above the patch based motivation of increased intake rate, for individuals modelled using a linear (a) or sigmoid (b) fitness function. The white boxes connected with a solid line indicate the connectivity due to baseline increase in intake in patch 2 with the baseline energetic costs and risk of transit, the light grey boxes and dashed line refer to the connectivity resulting from an individual incurring an energetic cost of movement to reduce exposure to predation (1/2 predation risk and 2x energy cost), and the dark grey boxes and the dotted-dashed line refer to the connectivity maintained by an individual reducing its energetic cost at the expense of increasing its exposure to predation (2x predation risk and 1/2 energetic cost). Within each scenario all other parameters were held constant at baseline values (see Table 1).

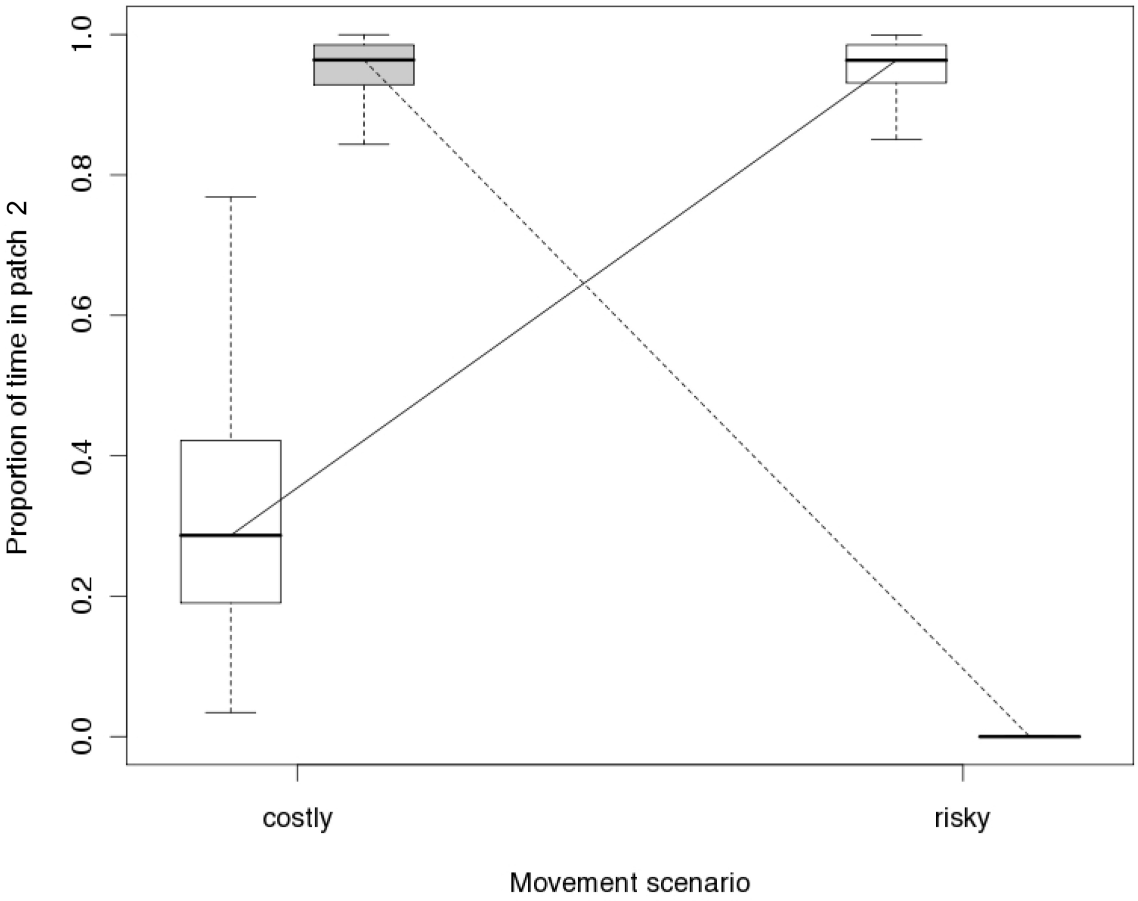


Figure 4.4: The influence of the trade-off between energetic cost and predation risk while in transit on functional connectivity. Two sets of transit conditions are given; one in which travel is relatively costly (has a high energetic cost but low risk of predation) and the other where travel is relatively risky (incurs a high risk of predation but a lower energetic cost). Individuals were able to decrease either predation risk or energetic cost at the expense of the other rate. The baseline cost of movement was 2 and 3 SU for the risky and costly scenario, respectively. Likewise the baseline risk of predation was 0.01 and 0.001 for the risky and costly scenario, respectively. Individuals able to reduce predation risk at the expense of energetic cost (white boxes) increased their baseline cost by 1 SU while reducing their baseline predation by 10. Likewise, individuals able to reduce travel costs at the expense of predation risk (grey boxes) reduced their baseline cost by 1 SU while incurring 10 times the baseline risk of predation. These scenarios highlight the importance of matching one's behavioural strategy to the specific conditions of the matrix encountered in order to maintain connectivity.

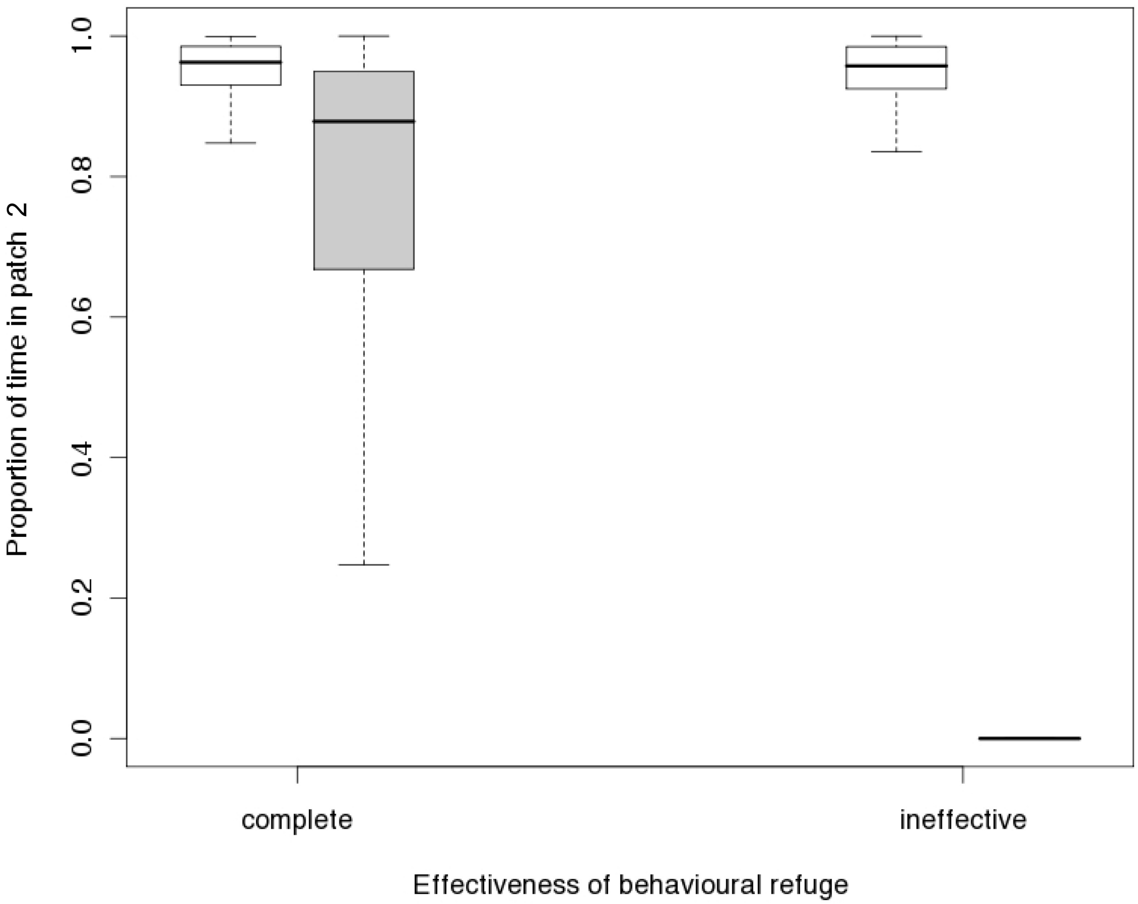
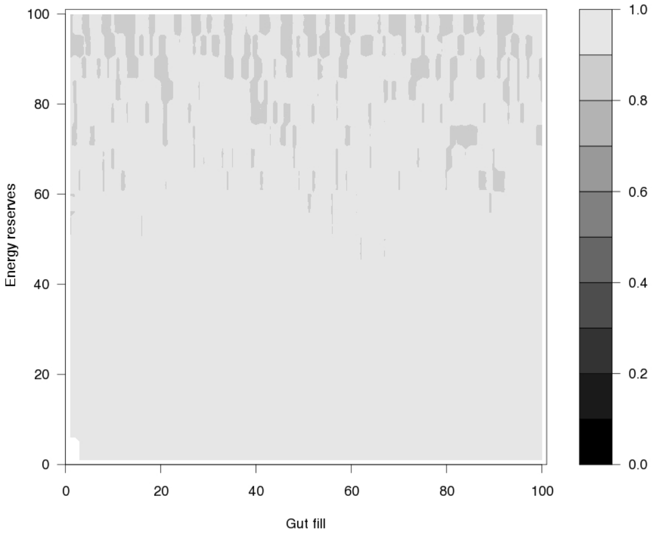
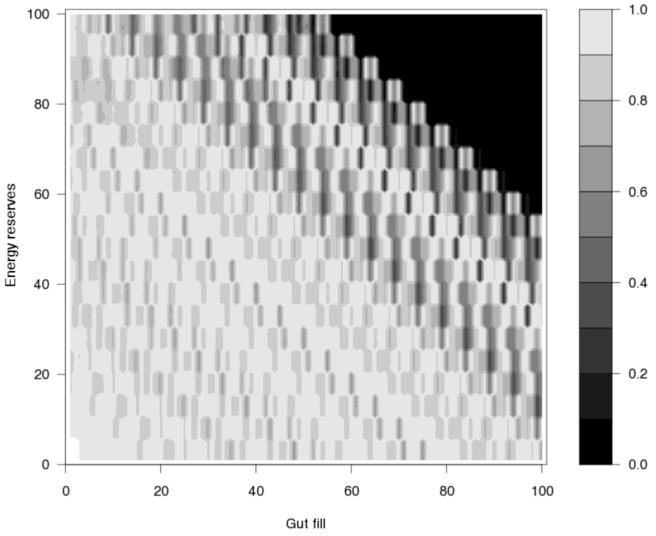


Figure 4.5: The influence of the behavioural refuge (effectiveness of anti-predator behaviour) during inactivity on functional connectivity, measured as the proportion of use of patch 2, when inactivity forms a complete refuge (i.e., predation rate during inactivity = 0) or inactivity conveys no anti-predator benefit (i.e., predation during inactivity = predation risk during foraging). Individuals modelled with a linear fitness function are given in the white boxes, while individuals modelled with a sigmoid fitness function are given in the shaded grey boxes. Inter-patch distance is 2 DU and patch 2 has an increased intake rate relative to patch 1 while all other values remain constant at baseline values.



(a)



(b)

Figure 4.6: Proportional use of patch 2 as a function of initial state (gut fill and energy reserves) for individuals modelled with a linear fitness function (a) or a sigmoid fitness function (b). The inter-patch distance is 2 DU and patch 2 has an increased intake rate relative to patch 1 while all other values remain constant at baseline values. Darker colours indicate less use while lighter colour indicate higher proportional use of patch 2.

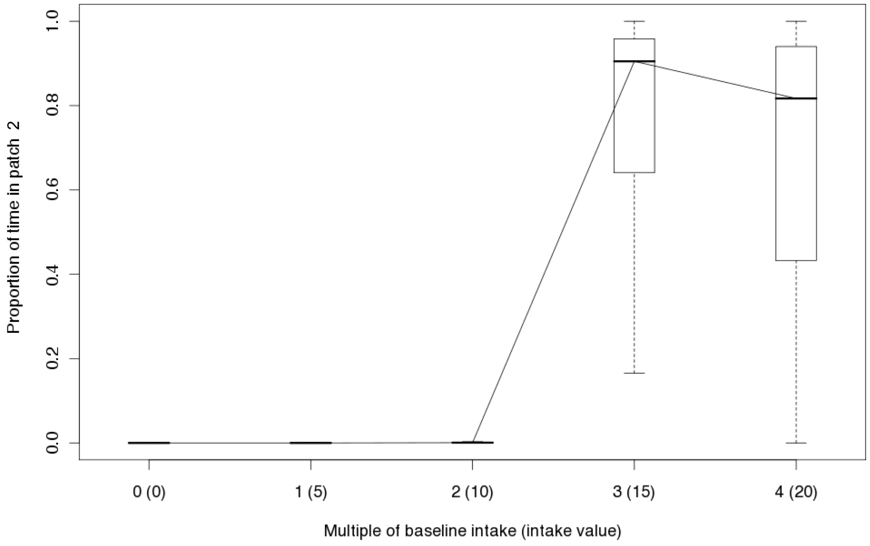


Figure 4.7: Example of a GUD-like titration of isolation costs. This represents the marginal rate of substitution of energy for isolation. At an inter-patch distance of 4 DU, increasing motivation was presented to individuals (simulated with a sigmoid fitness function) in the form of increased intake, given as multiples of baseline values (and absolute intake values). The proportion of time spent in the isolated patch (patch 2) was recorded. There is non-zero use of the patch at an intake of 10 and substantial use at an intake of 15.

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Hierarchical trade-offs between risk and reward mediated by behaviour

5.1 Introduction

A fundamental interest in ecology is the abundance and distribution of individuals on the landscape. Landscapes provide the backdrop for the ecological processes that lead to a distribution of animals (Southwood 1998). Natural landscapes are rapidly becoming fragmented by human activities. To better conserve and manage species inhabiting altered landscapes, an understanding of how patch configuration affects animal distributions is required (Wilcox & Murphy 1985, Saunders et al. 1991, Huxel & Hastings 1999, Palomares 2001). At the same time, ecologists have become aware of the important role that individual behaviour plays in the distribution of populations (Lima & Zollner 1996, Roitberg & Mangel 1997, Russell et al. 2003, Belisle 2005, Zollner & Lima 2005). With an increasing ability to remotely monitor individuals in landscapes with technologies such as global positioning collars, spatial data at the level of the individual animal is now plentiful. However, while we have become very good at saying *where* animals are, we have fallen short of explicitly answering *why* they are where they are. Static species-habitat relationships (e.g., Boyce & McDonald 1999) and utilization distributions (Worton 1989, Marzluff et al. 2004) are often used to infer the reasons for the distributions we observe (Hebblewhite et al. 2005, Wolf et al. 2009, Godvik et al. 2009). However, if we want to truly address the underlying motivations of why animals make particular choices, an approach that explicitly incorporates behavioural decision making is required (Lima & Zollner 1996, Roitberg & Mangel 1997, Zollner & Lima 2005).

A major determinant for the allocation of time by large herbivores within and among patches is determined by foraging opportunities and requirements to avoid predation (Boyce et al. 2003, Mao et al. 2005, Frair et al. 2007). Where forage and predation risk are positively related, herbivores will need to make behavioural choices that reflect trade-offs in net energy acquisition and predator avoidance at several scales (Senft et al. 1987, Bailey et al. 1996, Brown 1999, Rettie & Messier 2000, Dussault et al. 2005, Searle et al. 2008, Hebblewhite & Merrill 2009). Rettie & Messier (2000) argue that avoidance of predation occurs primarily at a large spatial scale and, therefore, necessarily constrains foraging opportunities. This ignores the behaviours that individuals can use to mitigate predation once in a patch (Dussault et al. 2005, Searle et al. 2008) such as inactivity or vigilance (Anholt & Werner 1995, Caro 2005, Fortin et al. 2004, Creel & Winnie 2005, Winnie & Creel 2007). While trade-offs in forage and predation risk have been investigated such studies have focused only on space use, and as such the behavioural ability of large herbivores to trade-off foraging and predation may be under-appreciated. The ability to optimize fitness by moving among patches may be constrained by energetic costs or predation risk (Johnson et al. 2002, Belisle 2005, Zollner & Lima 2005, Frair et al. 2008, Resetarits & Binckley 2009). The cost incurred in moving between patches depends not only the magnitude of the risk, but also the duration of risk exposure. In most cases, individuals that move quickly between patches will minimize predation exposure, but at the same time they will incur higher energy costs (Parker et al. 1984, McAdam & Kramer 1998, Johnson et al. 2001, Zollner & Lima 2005). The real cost of these behaviours depends not only on the immediate consequences to an individual's state but also on their overall fitness goals (Kohler & McPeek 1989, Zollner & Lima 2005, Winnie & Creel 2007, Hay et al. 2008, Wojdak 2009). As a consequence, individuals in patchy landscapes have an array of options for trading-off risks and rewards, both within and between patches, contingent on their cumulative well-being.

To address how individuals make optimal trade-offs between foraging and avoiding predation, I constructed a dynamic state variable model that incorporated the behaviours of a large ruminant herbivore when foraging within a patch and moving among patches on the landscape, following the general approach of Houston & McNamara (1999) and Clark & Mangel (2000). I omitted the effect of conspecifics on the focal individuals because state-dependent, ideal free distributions often do not equilibrate and they require a computationally intensive game-theoretic approach (McNamara & Houston 1990, Noonburg et al. 2007). I investigated how the spatial arrangement of patches influenced the distribution of use among patches within an individuals home range and how limits on anti-predator behaviours (while in patches) influenced the variation in use among patches, all in a state-dependent fashion. I hypothesized that when ruminant herbivores were limited by their ability to engage in anti-predator behaviour within a patch, they were forced to trade-off foraging opportunities and predation risk in space with patch selection. Conversely, when constrained by spatial configuration, individuals were required to "make do" with available patches and relied on anti-predator behaviour to mitigate the risk of predation.

5.2 Methods

I developed a dynamic state model representing a ruminant herbivore moving in a heterogenous environment, within a home range consisting of five patches. The herbivore made decisions that reflected trade-offs in foraging opportunities and predation risk that positively co-varied among patches. At each time step the behaviour influenced the gut-fill and energetic state, which reflected fitness. I refer the reader to chapter 4 for specific details and a mathematical description of the full model, but provide an overview here.

5.2.1 Behavioural model

The simulated individual had three discrete states (g; gut fill, e; energy reserves and i; location) that were updated based on the consequences of the decisions it made. At every time step the individual had the option of three behaviours (b). First, the individual could ruminate ($b = 1$), converting its gut contents into energy reserves. Second, the individual could refrain from either of these two activities and rest ($b = 2$). Third, it could actively forage ($b = 3$), increasing its gut fill but at an energetic (metabolic) cost associated with foraging (m). Intake resulted in gut contents increasing based on intake rate (β_i) with a probability of λ (and increasing by 0 with probability 1- λ), which represented the probability of finding food (set to 0.95 for all simulations) . Both rumination and resting had an associated metabolic cost of activity that was half the cost of active foraging. The simulated individual was able to pursue any of these three behaviours in one of the five patches in the home range. Each patch presented the individual with a unique combination of intake rate and predation risk (p_i; Table 5.5). Rumination (α_i) rates were constant for all patches. In all cases $_i$ indexes the patches and $i = 1, 2, 3, 4, 5$. Patches were assigned intake values and predation rates such that the patch with the highest intake rate also had the highest predation risk and the reverse was true for the safest patch (Table 5.5). This caused the individual to make patch selection decisions that involved trading-off forage and predation risk (Lima & Dill 1990). To move among patches, the simulated individual incurred an energetic cost (c) of movement and an in-transit risk of predation (u), both of which increased with inter-patch distance (d_{ij}; energetic cost = 1 x d and predation risk = d/1000; chapter 4). Where i indexes the current location and j the subsequent patch, thus when $i = j$ the inter-patch distance was 0 (the individual remained in its current location). To explore trade-offs in patch use resulting from anti-predator behaviours (during inactivity) within patches, I simulated the situation where inactivity (resting and ruminating behaviours) formed a complete predation refuge (predation risk = 0), where inactivity formed an incomplete refuge (predation risk during inactivity = predation during foraging - 0.002), and where inactive behaviours incurred the same predation risk as actively foraging (i.e. anti-predator behaviour is non-existent or completely ineffective). The absolute predation risk during inactivity was therefore dependent on the patch specific predation risk assigned to each patch as well as the effectiveness of the behavioural refuge and anti-predator behaviours (Banks et al. 2000, Zollner & Lima 2005).

Stochastic dynamic programming was used to solve for the optimal decisions (both behaviour in the patch and patch selection) through time, based on state as:

$$F(i, b, g, e, t) = max(V_{max(i=1,2,3...n),1}, V_{max(i=1,2,3...n),3}, V_{max(i=1,2,3...n),3}) \tag{5.1}$$

where

$$V_{i,1} = (1 - ud_{i,j})F(i, 1, g - \alpha_i, e + \alpha_i - \frac{m}{2}, t + 1) - cd_{i,j}$$

$$V_{i,2} = (1 - ud_{i,j})F(i, 2, g, e - \frac{m}{2}, t + 1) - cd_{i,j} \tag{5.2}$$

$$V_{i,3} = (1 - ud_{i,j}) \left[\begin{array}{c} (1 - p_i)(\lambda)F(i, 3, g + \beta_i, e - m, t + 1) - cd_{i,j} + \\ (1 - p_i)(1 - \lambda)F(i, 3, g, e - m, t + 1) - cd_{i,j} \end{array} \right]$$

where $V_{i,b}$ refers to the fitness accrued in the i^{th} patch (i=1,2,3...n) by selecting the b^{th} behaviour (1; ruminating, 2; resting or 3; foraging) and p_i is the probability of a predation (and therefore survival is $1 - p_i$) occurring in patch i. Additionally, I allowed the individual to incur a risk of predation (u) when making the decision to travel between patches, which increased with inter-patch distance $d_{i,j}$. Likewise energy reserves were decreased by a cost (c) accrued when traveling over the inter-patch distance upon reaching the new patch. While transit between patches occurred instantaneously, the costs and risks associated with it were incorporated into the individual's decision to make use of a new patch by discounting its potential gains and adding to its patch-specific costs.

Thus the fitness function at any time is calculated as:

$$F(l_i, b, g, e, t) = \begin{cases} F(l_i, b, g, e, t) & \texttt{if}\ t < T \\ \Phi(e, T) & \texttt{if}\ t = T \end{cases} \tag{5.3}$$

where the terminal fitness function $\Phi(e, T)$ of an individual serves as the goal of the forager, prioritizing safety or the acquisition of energy. As such, it was expected to affect patch use and behaviour in a state-dependent fashion. I simulated all scenarios with both a linear and sigmoid fitness function. The linear fitness function prioritized the acquisition of energy until the fitness of gaining additional forage multiplied by the risk of predation was less than the fitness of resting behaviour, given as:

$$\Phi(e, T) = e_T \tag{5.4}$$

or defined as a sigmoid fitness function as:

$$\Phi(e, T) = \frac{exp(-rep + e_T)}{1 + exp(-rep + e_T)} \tag{5.5}$$

where rep is a reproductive threshold that must be met by the energy reserves to gain a fitness benefit. The goal of an individual modelled with a sigmoid fitness was determined by where it was located along the sigmoid curve, based on state. While in the convex portion of the sigmoid curve, the individual prioritized forage acquisition, much like a linear fitness fitness. However, in the concave portion of the curve, individuals prioritized safety (Stephens & Krebs 1986). Over the long term individuals modelled with the sigmoid fitness function minimized their exposure to predation. In all cases when $t = T$, fitness was dependent only on energy reserves and not gut fill. I assumed that any remaining forage in the gut at the end of the time horizon did not convey a fitness benefit. A full list of parameters and variables, their description and values are given in Table 4.5. The scenarios for the form of the fitness function and the extent of the behavioural refuge are given in Table 5.5.

5.2.2 Patch configuration

I represented landscape configuration with five patches within the home range to keep the model computationally reasonable (Fig. 5.1). Landscapes were created to represent a range of aggregations while holding inter-patch distances approximately equal (within 10% of the same average distance among patches). The first landscape contained five patches arranged in two local aggregations, consisting of two and three patches, where the inter-aggregate distance was greater than the average inter-patch distance within each local aggregate (aggregated; Fig. 5.1a). The second landscape consisted of an aggregation of four patches and a single isolated patch (isolated; Fig. 5.1b). The third landscape contained five patches with equal inter-patch distances (even; Fig. 5.1c). Lastly, as a baseline, a five-patch landscape was created where the inter-patch distances were 0 (no cost; Fig. 5.1d). I varied patch context by altering the variation in quality (intake rate and predation risk) of a patch relative to its neighbours found in the same local aggregation (e.g., whether or not the safest or most productive patches are found next to one another in the same local aggregation). This context effect was simulated by systematically varying the order of the patches in the home range while maintaining configuration. The landscape scenarios for spatial configuration and spatial context are given in Table 5.5.

5.2.3 Simulations

The Monte Carlo forward iteration method was used to simulate 100 individuals at all combinations of gut fill and energy reserves from 0 to 100 (Clark & Mangel 2000). Initially, individuals were randomly assigned to patches and subsequently followed the optimal policy. An individual's behavioural decisions, state, and survival was recorded at every time step. Due to computational limitations, simulations were limited to 100 time steps for individuals using a linear fitness function and 200 time steps for individuals using a sigmoid function. An ANOVA was calculated to explore the relative importance of factors (fitness function form, spatial configuration, spatial context, and behavioural refuge effectiveness) influencing the variation in distribution of individuals within the home range (using $\eta^2 = SS_{factor}/SS_{total}$). The values for variation in patch use, calculated as the standard deviation in use among patches, were first arcsine square root transformed to increase normality as they were necessarily bound between 0 and 0.45.

5.3 Results

Variation in patch use was most influenced by two of the four factors examined, with their interactions reflecting an individual's ability to trade-off foraging opportunities and predation risk either while within a patch or through patch choice. Together, the shape of the fitness function and the extent of the behavioural refuge within a patch explained 66% of the variation in patch use (Table 5.5). Under a linear fitness function, if individuals could completely mitigate predation risk by being inactive in a patch (Fig. 5.2: grey boxes) they concentrated their use in the most profitable patches (highest intake rate) despite the high predation risk associated with these patches. The most profitable patch, regardless of where it was located, provided the fastest way to increase energy reserves, and therefore fitness. When there were no costs to moving among patches (Fig. 5.2d; grey boxes) individuals foraged exclusively in the most profitable patch and then spent their non-foraging time (i.e., resting and rumination) in the safest patch. In contrast, when the fitness function was defined with a sigmoid function and individuals were able to use inactivity to avoid predation while in the patch (Fig. 5.2: white boxes), patch use was more even and less variable across patches. In general, individuals stayed in their initial, randomly assigned patch to avoid the cost of inter-patch movements instead becoming inactive to minimize exposure to predation risk. When individuals incurred no cost for moving among patches, under the sigmoid fitness function, they could compensate for foraging costs even in the patch with the lowest level of intake that I simulated. Therefore, they spent almost all their time in the safest patch (i.e., p1; Fig. 5.2d). If the intake in this patch had been even lower (below the metabolic cost of foraging or 2 SU), it is likely that individuals would have had to use the next safest patch, offering a higher intake rate, to balance the costs of foraging and the metabolic cost of inactivity.

When animals were either less able or unable to mitigate predation risk behaviourally once in the patch, variation in patch use under the two fitness functions differed (Fig. 5.3). In the case of a sigmoid fitness function, individuals could no longer mediate predation risk through inactive behaviours and were required to use the safest patch to maximize fitness. As a result, patch use was uneven and always concentrated in the safest patch (Fig. 5.4; white boxes). In contrast, when the fitness function was linear, use was more even and less variable across patches because individuals were forced to trade-off safety and energy gain across a range of patches, being behaviourally constrained to offset predation risk with patch selection (Fig. 5.4; grey boxes). The pattern of use depended on patch configuration and the specific context of the most profitable and safest patch within the local aggregations (Fig. 5.5; grey boxes). When costs to move among patches were similar (even), individuals concentrated their use in the most profitable patches (Fig. 5.4c). However when patch configuration (isolated or aggregated) constrained the use of the most profitable patches, the resulting pattern in use was more evenly distributed among all patches (Fig. 5.4a & b).

How patch configuration influenced patch use was dependent on patch context and, as before, differed among fitness functions (Fig. 5.5). For example, the effect of the arrangement of safe and productive patches within the home range was most obvious when the safest patch (for individuals modelled with a sigmoid function) and highest intake patch (for individuals modelled with a linear fitness function) were located within the local aggregation with the fewest number of patches or a single isolated patch. In this case, some individuals were not able to afford the transit costs to the distant patch or patches; instead, they used the next best patch found in the same local aggregation. As a result, there was typically more even use of patches within the home range as individuals were required to "make do" with the next best patch located in their current local aggregation (Fig. 5.5). When the most desirable patch was located in the largest local patch aggregation within the home range, the variation in patch use increased as a reduced travel cost within the aggregation made this patch more accessible, thereby concentrating use. The influence of the spatial context of patches was a direct result of the inter-aggregation distance exceeding the inter-patch distance within the local aggregation and the resulting accessibility of the most desirable patch.

5.4 Discussion

Large-scale movements and patch use by ungulates have been attributed to the hierarchical decision making of processes that scale up from bites to landscape distribution (Senft et al. 1987, Bailey et al. 1996). Nonetheless, most studies investigating decision rules for patch residence time have typically focused on the forage resources at one spatial scale (Jiang & Hudson 1993, Laca et al. 1994, Schaefer & Messier 1995, Searle et al. 2005). However, evidence now exists that individual responses at fine spatial scales interact with the heterogeneity of foraging at larger spatial scales (Searle et al. 2006). Similar patterns may emerge for animals making trade-offs for foraging in risky habitats. Rettie & Messier (2000) hypothesized that because predation occurred across large spatial scales, it would be avoided on the largest scales, and lower scales would be dominated by the acquisition of forage or other limiting factors. Dussault et al. (2005) found evidence supporting this view: the home ranges of moose tended to avoid predation by avoiding low snowfall areas, while their selection of patches within the home range were consistent with increased foraging opportunities. Hebblewhite & Merrill (2009) found that in partially migratory elk herd trade-offs could occur at the large scale via migratory behaviour, while resident elk accessed a spatial refuge at the small scale to reduce the risk of predation.

In this chapter, I have shown that when predation risk is structured in space, herbivores have several behavioural options for avoiding predation while meeting foraging requirements: foraging in patches of low predator risk, moving quickly through areas of low forage and high risk, or employing anti-predator behaviours that reduce predation risk (Brown 1999; analogous to pre- and post-encounter behaviours in Mitchell 2009). My results show that ruminant herbivores can trade-off these behaviours in the context of patch use and that optimal trade-offs in patch use are contingent on patch configuration and animal state. When anti-predator behaviours within patches were effective (i.e., behavioural refuge), individuals were able to "pay down" the foraging costs of the patch-specific predation risk (i.e., through inactivity), except when they were constrained by their low energetic state or fitness goal, which then determined their foraging strategy. In contrast, when ruminants were unable to employ effective anti-predator behaviours or employed an energy maximizing foraging strategy, patch selection became a vital component of optimal behaviour.

The motivation of the individual either to avoid predation or acquire forage was defined by the fitness function and was constant for the entire simulation. However, in nature, individuals may have shifting fitness goals that influence the behavioural trade-offs they make. Evidence from seasonal changes in habitat selection suggest that individuals may differentially prioritize safety and the acquisition of energy at various times of the year (Main 2008, Long et al. 2009). Likewise, differing fitness goals based on sex and reproductive status may also indirectly effect the ability of individuals to trade-off predation risk and foraging opportunities either with anti-predator behaviours within a patch or with patch selection (Ruckstuhl 1998, Gustine et al. 2006, Grignolio et al. 2007, Long et al. 2009). For example, Dussault et al. (2005) noted that there was variation in patch selection between individual caribou, which they attributed to the sex and reproductive status of the individual, which represented their motivations for the trade-off between predation risk and foraging opportunities. Similarly, Gustine et al. (2006) noted that the ability of individual caribou to respond to predation risk was condition-dependent: females in poor condition took higher risks in order to access forage, as they could not afford to avoid predation. These results highlight the importance of sampling at multiple scales and the need to integrate between scales through the inclusion of behavioural motivation, which may facilitate trade-offs between predation risk and foraging opportunities (Johnson et al. 2004, Bowyer & Kie 2006)

The spatial configuration of patches within the home range provides the template on which movement occurs and patch choices are made, potentially constraining the movement of individuals through movement costs or the risk of predation during transit. While many models of ecological processes have focused on the effect of spatial configuration (Andreassen et al. 1998, McIntyre & Wiens 1999), individual behaviour may potentially mitigate the effects of spatial pattern or patterns (Roitberg & Mangel 1997, Reed & Levine 2005, Fraterrigo et al. 2009). I found that individual state-dependent behaviour minimized the difference in variation in patch use and was dependent on fitness specification, despite configuration differences. Individuals prioritizing safety used the safest patch regardless of where it was located, whereas, individuals prioritizing forage acquisition often used the next most productive patch when the patch offering the highest intake was isolated. In addition to spatial configuration, the context of patches within a "landscape of fear" may also influence their use where proximity to high forage or high risk area may increase or decrease the motivation for an individual to use a particular patch (Laundre et al. 2001, Haynes et al. 2007, Searle et al. 2008). I found that when both productive and safe patches were found within the same local aggregation, the overall use of the local aggregation tended to increase subject to its isolation. Similarly, Haynes et al. (2007) found that complementary use of patches by grasshoppers was based on surrounding patch quality. Likewise, for aquatic beetles, the spatial contagion of high fitness patches to risky areas reduced the overall use of patches (Resetarits & Binckley 2009). Shriver et al. (2004) also found that the spatial context of wetland patches, in terms of their proximity to one another, was an important determinant of salt marsh bird communities. Similar patterns have been noted in ungulates. Hins et al. (2009) showed that for caribou, the appearance of selection for cutblocks was an artifact of their close proximity to old forest stands, which the caribou require for foraging. The proximity of a refuge increased the use of otherwise risky patches in ibex (e.g. Hochman & Kotler 2007) and the presence of grassy meadows resulted in supplementary cutblock use by elk

(Weckerly 2005). O'Brien et al. (2006) found that caribou used patches more frequently when they were within the context of a cluster of high quality patches. The results from my model support the findings of these studies and highlight the need for managers to consider spatial context when planning future management actions in already fragmented landscapes. By ensuring refuge habitat or hiding cover in close proximity to foraging patches managers may be able to facilitate the anti-predator behaviours used by herbivores to minimize predation within patches. Similarly, providing safe corridors for travel between patches may facilitate trade-offs between patches.

Patch depletion with increasing residency times has been assumed to reduce the motivation of a forager to remain in the patch, necessitating movement between patches (i.e., the marginal value theorem; Charnov 1976, Nonacs 2001). However, measurement of patch residency times from the field often do not match model predictions and individuals tend to forage for longer than expected (Stephens & Krebs 1986, Searle et al. 2005). Searle et al. (2005) suggest that the shortcomings of the marginal value theorem, when applied at larger spatial scale is due to its restrictive assumptions including a depleting environment, decelerating gain functions and numerous randomly arranged patches. Mitchell & Lima (2002) noted that movement occurred between patches to reduce the risk of predation even when depletion was not considered (Mitchell 2009). Similar shifts in patch use may occur due to state-dependent changes in motivation, such as having achieved a fitness goal, or the presence of conspecifics, or result from dietary or digestive constraints (McNamara & Houston 1990, Searle et al. 2005). I observed individuals leaving patches due to changing prioritization of forage acquisition or the avoidance of predation that arose from changes in the individuals state-dependent motivation. The cost of movement also influenced the ability of an individual to trade-off predation risk and forage acquisition by moving between patches. Including depletion into the model would result in reduced motivation to remain in a patch. However, individuals employing a time minimizing foraging strategy may remain in a depleted patch, as long as foraging there covers their metabolic costs and if it is relatively safe from predators. Conversely, individuals maximizing energy gain would shift patches as foraging gains decrease. As the entire landscape becomes depleted, the relative ranking of patches in terms of predation risk and foraging opportunities will determine the selection of patches, dependent on foraging strategy and state, resulting in a similar pattern of patch use to what I have described. That is, energy maximizing individuals will always select patches purely based on foraging opportunities and time minimizing individuals will prioritize use of safe patches regardless of the dynamics of forage abundance.

The application of a multi-scale approach to trade-offs between foraging and predation risk is sure to increase our understanding of the distribution of individuals in heterogeneous landscapes (Rettie & Messier 2000, Bowyer & Kie 2006, Searle et al. 2008). However, researchers must be sure to account for individual behaviour and motivation in these trade-offs as they may potentially structure patterns of patch use. I found that the inclusion of state-based behaviour into models of patch use and within patch behaviour suggests that individuals are able to behavioural mediate the effect of spatial configuration through anti-predator behaviour. However, this ability was contingent on the state-dependent motivation of the individual. In particular, it was dependent on the formulation of the fitness function, which specified the foraging strategy of the individuals, and the effectiveness of anti-predator behaviours during inactivity. Individuals that were able to become behaviourally unavailable for predation (as a result of their energetic state, foraging strategy, or the effectiveness of anti-predator behaviours) were able to mitigate the potential travel cost associated with the spatial configuration of patches. However, when this was not possible, patch choice became an effective way of minimizing the risk of predation. The simulations presented here are a first step in explicitly incorporating behavioural decision making into models of foraging at multiple scales in fragmented landscapes. Dynamic state variable models provide a rich theoretical context for understanding patch selection and behaviour at two scales for free ranging individuals, thus helping to bridge the gap between animal behaviour and landscape ecology (Lima & Zollner 1996).

5.5 Tables

Patch	Condition	Predation risk	Intake rate
p1	Safest	0.002	2
p2	-	0.004	4
p3	-	0.006	6
p4	-	0.008	8
p5	Most Productive	0.01	10

Table 5.1: Conditions of the five patches located within the home range, representing the trade-off between the risk of predation and intake. Thus, the safest patch has the lowest intake and the lowest predation rate while the most productive patch has both the highest intake rate and predation risk. Predation risk is given as the patch-specific probability of death during each time step spent foraging, while intake rate is measured as the state unit increase in gut fill with each time step spent foraging. Rumination rate was held constant across all patches.

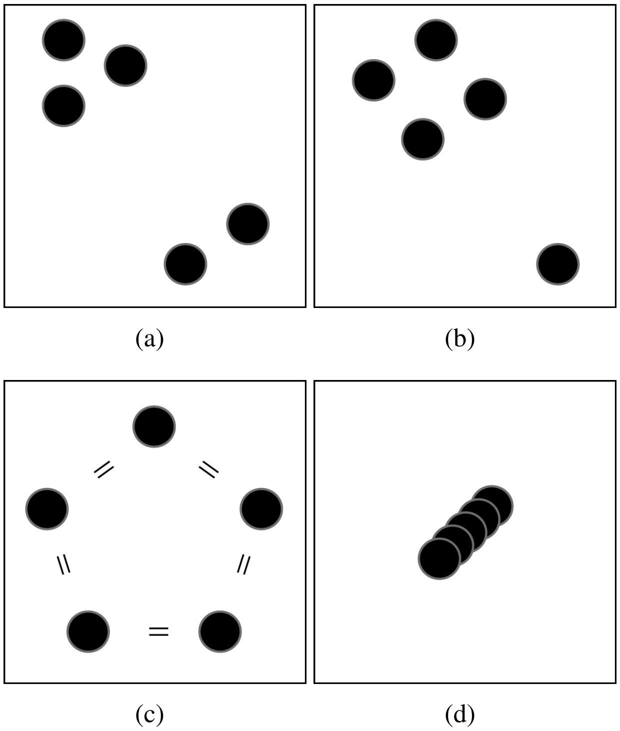
Scenario	Simulated Conditions or Values
Spatial configuration	isolated, aggregated, uniform, no cost
Patch context	5 rotations of conditions
Fitness function	linear, sigmoid
Extent of behavioural refuge	complete, incomplete, ineffective

Table 5.2: Simulated scenarios and conditions used to investigate the effect of spatial configuration, patch context, the shape of the fitness function, and the effectiveness of the behavioural refuge on the variation in patch use across the home range. Spatial configuration represents the distribution of patches within the home range (see Fig. 1). Patch context refers to the relative position of the patches to one another. In the case of uniform and no cost spatial configurations, varying the context has no effect so only a single simulation for each of the other scenarios was conducted. The shape of the fitness function was compared for fitness modelled as either a linear function or a sigmoid function of increasing energy reserves. In general linear fitness prioritized the acquisition of energy while sigmoid fitness prioritized safety (chapter 3). The extent of the behavioural refuge relates to the degree of predation experienced by the simulated individual while undertaking inactive (resting and ruminating) behaviours relative to active foraging. This is analogous to the effectiveness of anti-predator behaviours (such as vigilance), ranging from perfectly effective (complete refuge), partly effective (incomplete refuge), and ineffective (resulting in the same predation rate as foraging).

Source	DF	Sum of Squares	η^2
Context	4	249.4	0.019
Configuration	3	488.0	0.037
Fitness function	1	889.3	0.067
Extent of behavioural refuge	3	2673.5	0.202
Fitness x Refuge	2	5226.3	0.394

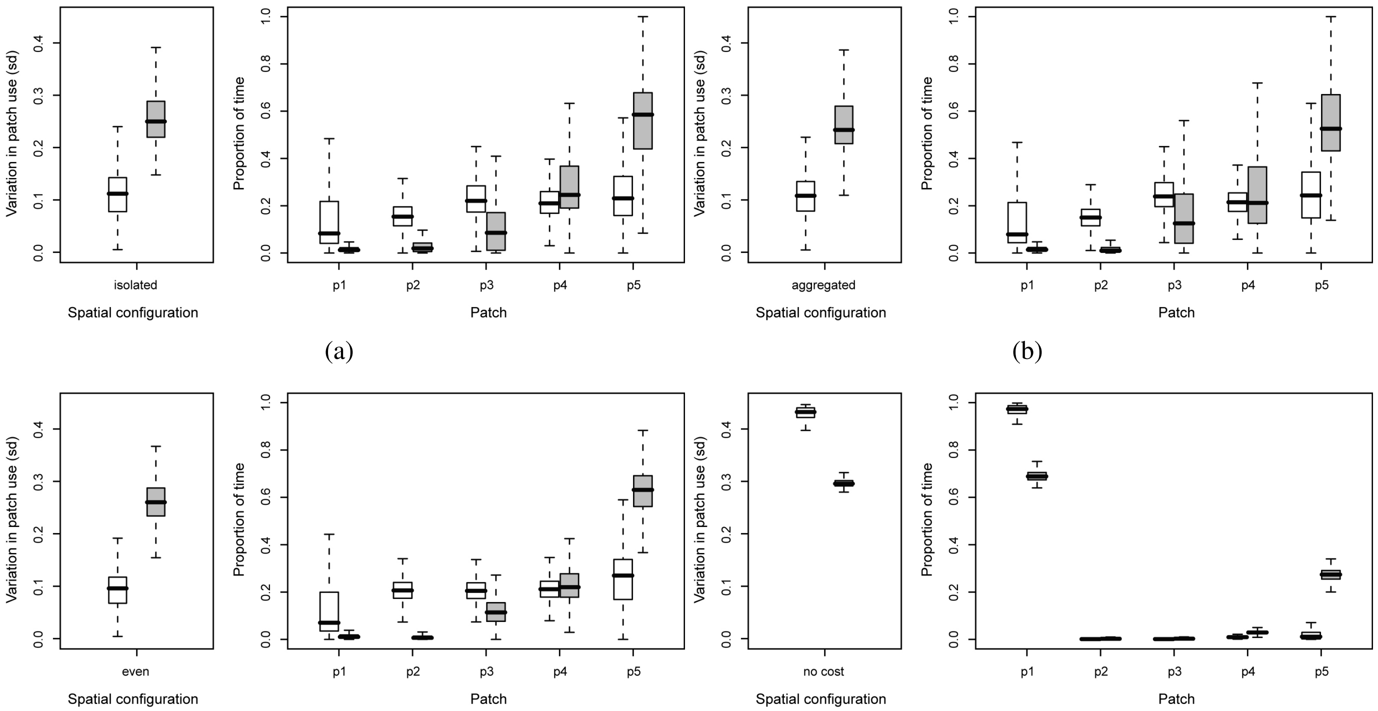
Table 5.3: Factors influencing the variance in patch use (sd). The relative influence of the (categorical) factors was compared as η^2, calculated as the SS_{factor}/SS_{total} in an ANOVA framework. Only interactions explaining greater than 5% of the variation in the variance in patch use are included. For the ANOVA the standard deviation in patch use was arcsine square root transformed. p values are not given due to the effect of the large number of simulations on significance.

5.6 Figures



(a) (b) (c) (d)

Figure 5.1: Representative landscapes containing five patches within a simulated individual's home range. Patches were located to represent a gradient of configuration from (a) isolated, (b) aggregated, (c) even (uniform), and (d) zero inter-patch distance (where movement between patches comes at no cost or risk).



(a) (b)

(c) (d)

Figure 5.2: Proportional patch use and variation in patch use when the behavioural refuge is complete (predation risk while inactive = 0) and the patches are configured to form (a) an isolated landscape, (b) an aggregated landscape, (c) an even landscape, (d) a no cost landscape. The white boxes refer to the distribution of individuals simulated with a sigmoid fitness function while the grey boxes represent the distribution of individuals simulated with a linear fitness function. These are a summary of all context scenarios, where pX (X=1, 2, 3, 4, 5) refers to the patch on the landscape.

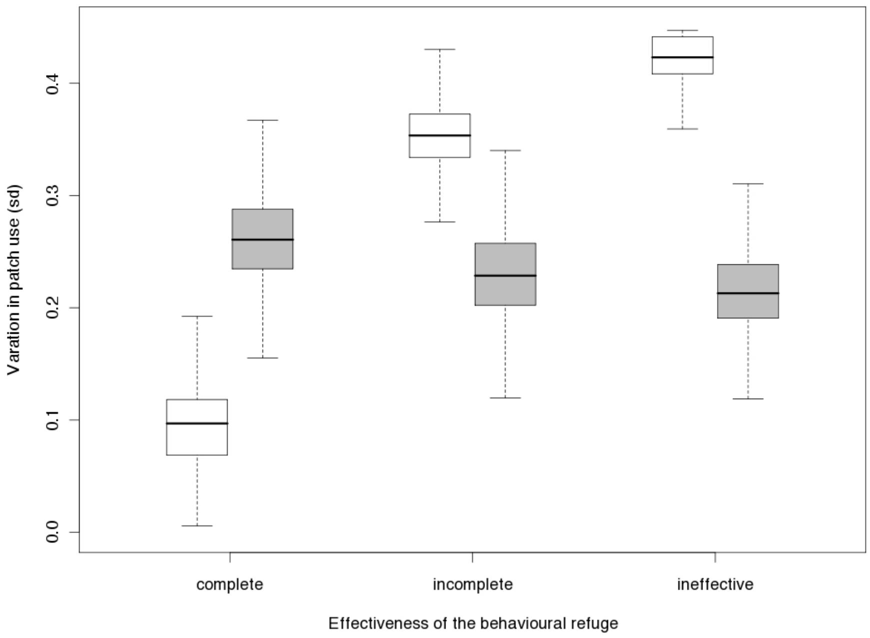
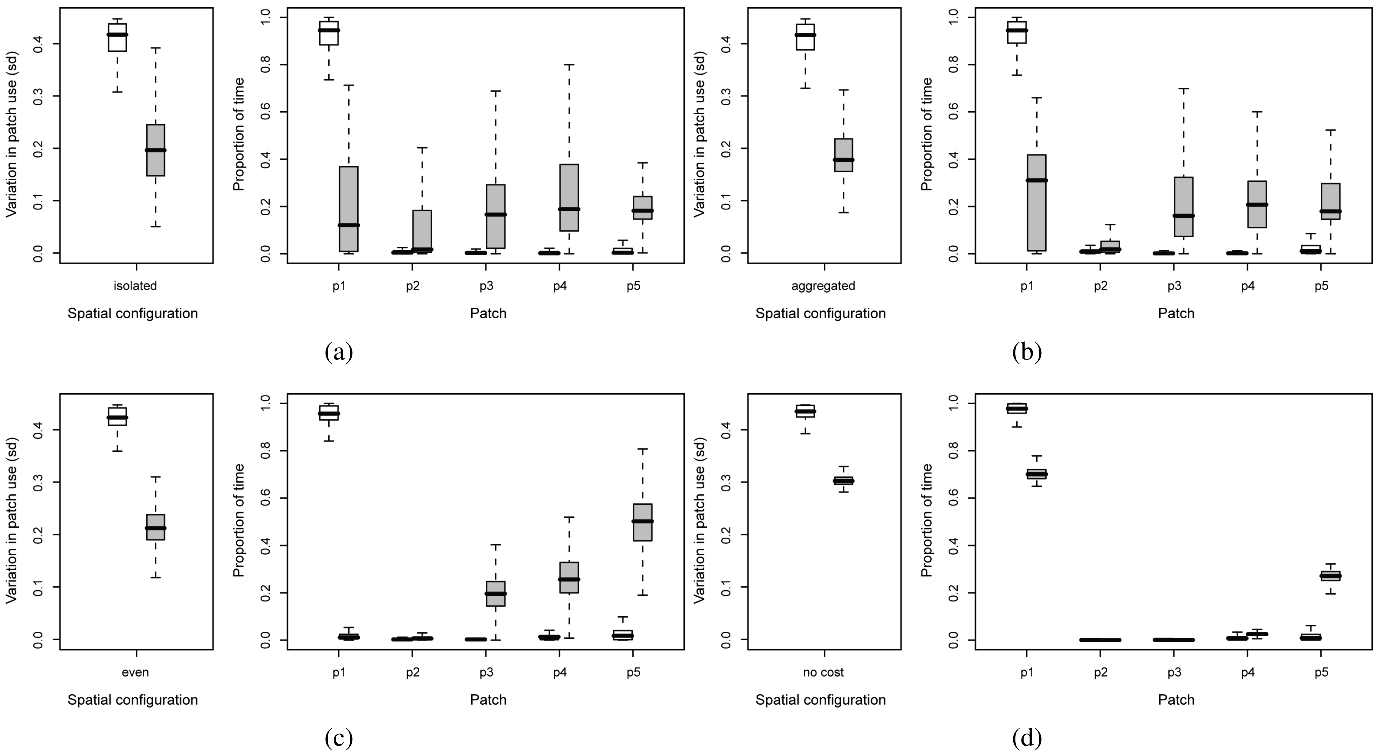


Figure 5.3: The influence of the effectiveness of anti-predator activity on the variation in patch use within the home range for the landscape where patches were evenly spaced. The effectiveness of anti-predator behaviour formed a complete refuge, incomplete refuge (predation risk = foraging - 0.002), and ineffective refuge (predation risk = foraging) during inactivity. This same pattern was evident in all scenarios. The white boxes refer to the distribution of individuals simulated with a sigmoid fitness function while the grey boxes represent the distribution of individuals simulated with a linear fitness function.



(a) (b)

(c) (d)

Figure 5.4: Proportional patch use and variation in patch use when the behavioural refuge is completely ineffective (predation risk while inactive = foraging) and the patches are configured to form (a) an isolated landscape, (b) an aggregated landscape, (c) an even landscape, (d) a no cost landscape. The white boxes refer to the distribution of individuals simulated with a sigmoid fitness function while the grey boxes represent the distribution of individuals simulated with a linear fitness function. These are a summary of all context scenarios, where pX (X=1, 2, 3, 4, 5) refers to the patch on the landscape.

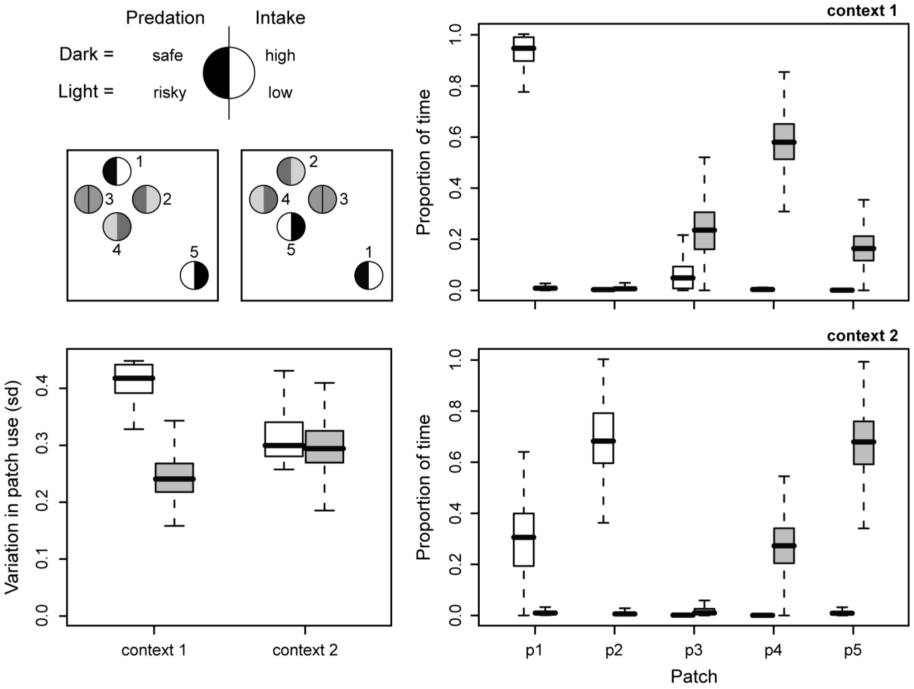


Figure 5.5: Example of the effect of patch context on patch use (right panels) and variation in patch use (lower left panel) in an isolated landscape. Two different context scenarios are given where the shading of the representative "map" of the patches (upper left panel) indicates the degree of risk on the left side of the patch (darker = safer) and rate of intake on the right hand side of the patch (darker = higher intake). The white boxes refer to the distribution of individuals simulated with a sigmoid fitness function while the grey boxes represent the distribution of individuals simulated with a linear fitness function. pX (X=1, 2, 3, 4, 5) refers to the patch on the landscape indicated by the number next to the patch on the "map".

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Foraging strategies and variation in patch use by elk in west central Alberta

6.1 Introduction

Elk face the same ubiquitous problem that confronts all foragers, namely, how to effectively trade-off foraging opportunities with the potential risk of predation (Lima & Dill 1990). In forested landscapes of west central Alberta, elk are increasingly faced with anthropogenic disturbances that alter the spatial and temporal structure of forage and predation risk across the landscape. One such anthropogenic feature is cutblocks (Timoney & Lee 2001). Elk are commonly found in cutblocks in Alberta because they have increased forage relative to the surrounding conifer forests (Visscher & Merrill 2009). The abundance of forage in cutblocks, both herbaceous and browse, also changes as a function of time since felling (Jenkins & Starkey 1993, 1996, Cook et al. 1998, Visscher & Merrill 2009), which creates spatial variability in foraging opportunities across the landscape. Predation risk in cutblocks can also be higher than surrounding forests because prey are easily detected and roads associated with cutblocks facilitate travel (Gehring 1995, Kuzyk et al. 2004, Bergman et al. 2006, Frair et al. 2008). Cutblocks provide a unique opportunity to study the patch-use behaviour of elk in the context of trade-offs in predation risk and foraging opportunities because they are *a priori* defined patches, discernible to both the animals and researcher alike. As cutblocks increase across the landscape, a better understanding of the role they play in structuring foraging opportunities and predation risk will also help to inform ecologically sound management plans in forest dominated landscapes (Kuzyk et al. 2004, Frair et al. *in preparation*).

Elk possess a rich repertoire of behaviours that can be used to reduce the risk of predation while acquiring energy. In my previous chapters, I have shown how the availability of behavioural refuges within patches and costs of transit among patches influences an animals fitness. Within patches I allowed inactivity to form a behavioural refuge, but modification of group size and vigilance may also reduce risk within patches (Wolff & Van Horn 2003, Creel & Winnie 2005, Creel et al. 2005, Winnie & Creel 2007, Liley & Creel 2008). I found that the flexibility to use a within-patch behavioural refuge depended on the ability of the individual to afford “spare time” when animals were in a high energetic state; otherwise these activities came at a fitness cost - the so called non-consumptive effect of predation (Fortin et al. 2004, Trussell et al. 2008). Relocation to adjacent patches (chapter 4) and variability in multi-patch use (chapter 5) also depended on the effectiveness of within-patch anti-predator behaviours. In all cases, the other primary determinant of the optimal set of behaviours depended on the state of the animal and whether or not individuals prioritized safety (sigmoid fitness curve) or forage intake (linear fitness curve) as a foraging strategy. Schoener (1971) defined the ends of the foraging strategy continuum as representing “time minimizing” and “energy maximizing”. In previous studies these foraging strategies have been show to differ seasonally and among the sexes (Barboza & Bowyer 2001, Ruckstuhl & Neuhaus 2002, Bonenfant et al. 2004, Main 2008). Time minimizers, by virtue of high energetic states, high rates of intake, or reduced requirements, can afford the foraging costs of anti-predator behaviours (Clark 1994, Illius & Fitzgibbon 1994, chapter 3), while foragers in a lower energetic state or in environments where intake is inefficient may follow an energy maximization strategy and are not expected to be able to afford anti-predator behaviour without a fitness cost (chapter 3 & 5). Therefore, by ignoring the within patch behaviours, researchers may underestimate the ability of an individual to cope with predation and miss a key process that contributes to the distribution of individuals in the landscape (chapter 5).

I use a dynamic state variable model to generate expectations for patch use and activity patterns using a time minimizing (sigmoid fitness) and energy maximizing (linear fitness) foraging strategy of an average female elk located in the montane regions of the central east slopes of the Rocky Mountains of Alberta during summer. From chapters 3 and 5, I expected that if elk followed a time-minimizing strategy there would be a negative relationship between their cutblock use and predation risk and that within risky cutblocks they would be less active, even if inactivity only partially reduces predation risk. Conversely, if they use an energy maximizing strategy there would be a positive relationship between cutblock use and forage abundance, and within risky cutblocks they would tend to be more active. Additionally, if cutblock configuration limits movement among cutblocks, then variation in cutblock use within a home range would decrease as cutblocks were less aggregated. In this chapter, I test these expectations, based on a model parameterized for elk and qualitatively compared to free-ranging elk. Finally, I discuss the ramifications of the foraging strategy used by elk for their ability to trade-off foraging opportunities and predation risk at multiple scales and the potential role that cutblock management plays in this process.

6.2 Methods

6.2.1 Dynamic state variable model

The general model of state-dependent behaviour was based on an elk with 3 states: energy reserves, gut fill, and a location (i.e., patch). At each 2 hr time step, an individual had the option to engage in foraging, ruminating, or resting while in a patch. The decision to forage resulted in intake and increased gut fill at a metabolic cost to energy reserves, while ruminating and resting incurred a lower metabolic cost relative to foraging. Ruminating converted gut contents into energy reserves. Details of model structure and accompanying equations are given in chapter 4. Stochastic dynamic programming was used to calculate the optimal policy and Monte Carlo simulations were conducted using the optimal policy to simulate the variation in patch use within the home range for an average female elk in summer, using both a linear and sigmoid fitness function (Mangel & Clark 2000).

6.2.2 Elk parameters

I parameterized the model for an average female elk (210 kg; Cook et al. 2001) during the summer season (15 June - 15 September). All parameters are given energy (kJ) but are ultimately expressed as “state units” (SU; see below). The maximum energy reserves were calculated from a fat reserve constituting 24% of a 210-kg elk body mass (Cook et al. 2001), where fat has an energy content of 8703 kJ/kg (Hudson et al. 2002). The energy threshold for reproduction was assumed to be 5% body fat (10.5 kg fat, or 91,382 kJ,

Table 1), below which reproductive failure occurred (Cook et al. 2001). The energetic costs of foraging and inactive behaviours (Table 6.1) were derived from daily energy requirements of free-ranging elk, weighted by their daily activity patterns (Hudson et al. 2002). I calculated the movement cost of an elk across the landscape based on walking speeds on flat terrain (550 kJ/km for movement cost plus 7300 kJ/time step for activity cost; Parker et al. 1984).

Dry matter intake rates (in kJ per time step) were calculated from a statistical relationship between available biomass and intake (Wickstrom et al. 1984: Fig. 1). Maximum wet weight gut fill was 24 kg (Cook 2002, Weckerly et al. 2003), which was converted to dry weight using a wet to dry weight conversion for forage of 2.7 (P. DeWitt, *unpublished data*) and to gross food energy, assuming 18,500 kJ/kg dry weight forage. I used an average digestibility coefficient of 0.7 and average metabolizable energy coefficient of 0.82. Lastly, a rough estimate of rumination rate (defined here as the conversion of gut contents to energy stores) was estimated based on literature values, which suggested an emptying of 10% of total gut fill at each time step (McCorquodale 1991, Spalinger et al. 1992, Robbins 1993).

To reduce the number of possible total energetic states (i.e., up to 94,391 for gut fill and 438,631 for energy reserves), I divided all values by the parameter with the lowest energetic value, which was the metabolic cost of resting or ruminating (3400 kJ) to arrive at a more computationally feasible maximum of 29 and 129 state units (SU) for gut fill and energy reserves, respectively. All other energetic values were similarly converted to SU and rounding was used to achieve integer values as required (Mangel & Clark 2000). While I recognize the simplification of many biological processes into the values used here, I suggest that the overall dynamics of an elk's energy balance is maintained in a useful way. Parameter values and their respective state units are listed in Table 6.1, while a schematic representation of the model elk and the flow of energy is given in Figure 6.1.

6.2.3 Model simulations

I used the model to investigate variations in cutblock use within a home range. For computational reasons, the number of patches within the simulated elks home range was limited to five. Patch-specific intake rates were assigned based on the assumption that they co-varied with predation risk (e.g., the patch with the highest intake also had the highest predation risk). I modelled two sets of landscapes. In the first case, the five patches were located in two local aggregations, such that the inter-aggregate distance exceeded the inter-patch distance within the aggregate (referred to as aggregated). In the second case, a single patch was isolated from a local aggregation of four patches (referred to as isolated; see chapter 5 for full details of landscapes). These scenarios were used to describe the general patterns of cutblock use that may be expected for real elk, in particular, the proportion of time spent in high risk / intake patches versus low risk / intake patches constrained by configuration. Individuals were randomly assigned to a starting patch to begin the simulation. For full details of this model and a complete exploration of the factors influencing the variation in patch use with a home range, please see chapter 5. All simulation scenarios were conducted with both linear and sigmoid fitness functions, representative of an energy maximizing and time minimizing foraging strategies, respectively.

6.2.4 Elk, cutblocks, and home range data

Thirty two adult, female elk in west central Alberta were captured during winter (2000-2004) using a net gun from a helicopter. Each animal was fitted with a Lotek GPS2200 collar (Lotek Wireless, Ontario, Canada) that collected locations every 2 hours (for a full description of the collaring procedure and collar protocol please see Frair 2005). For the present analysis, I used data for locations that were collected only during summer (15 June - 15 September). GPS locations during this period were used to construct a 95% minimum convex polygon (MCP) summer home range for each collared elk. The MCP represents and contains a large extent of the landscape that the individual may potentially use, or is exposed to, and as such is suitable for delineating the home range for this analysis (Van Moorter et al. 2009).

Within this summer home range I identified all cutblocks within the MCP. For each of the cutblocks I derived the cutblock age from forest harvest records acquired from forestry companies active in the study area. Cutblock ages were then used to estimate the average abundance of herbaceous biomass in each cutblock using equations presented in Visscher & Merrill (2009). The predation risk of a cutblock was derived as the average relative probability of selection of a wolf calculated with a resource selection function (RSF; Johnson et al. 2006), calculated based on GPS location of wolves from 4 packs in the study area (see Frair et al. 2007 and Webb 2009). I tested whether predation and forage abundance were correlated in order to determine if elk were required to make a trade-off between foraging opportunities and predation risk. To quantify the configuration of cutblocks within each elks home range, I used a patch index program, FRAGSTATS (McGarigal & Marks 1994), to determine cutblock density, the number of cutblocks, patch cohesion, and the proportion of the home range that were cutblocks within the summer MCP of each elk. Other measures of configuration were investigated, but all tended to provide the same information as patch cohesion, which was used for all subsequent analyses.

6.2.5 Elk use and relationships to forage and predation risk

From the 2 hr GPS locations of each elk, I calculated the proportional use of a cutblock based on the frequency of GPS points relative to all other GPS location in all other cutblocks. I divided the proportional use by the area of the cutblock to account for differences in cutblock size. I regressed the area adjusted proportional use of a cutblock against the forage abundance and predation risk of the cutblocks to determine if an elk's use was most consistent with a time minimizing or energy maximizing foraging strategy. To determine if elk were behaving consistently with a time minimizing or energy maximizing strategy within cutblocks, I also measured step length as a proxy to activity within a cutblock. I ranked 6570 step lengths for all elk in cutblocks based on their risk of predation. I then took the highest and lowest ranked 15% of the sample ($\approx$1000 in each group) and compared their distributions of move lengths using a Kolmogorov-Smirnov test for goodness of fit. From the proportional use of each cutblock, I also calculated the variation in cutblock use within the home range. I used the coefficient of variation for each elks MCP as a simple measure of variation in patch use that was related to measures of cutblock configuration within the home range and the variability in predation risk and forage abundance using regression analysis and model selection (Burnham & Anderson 2002).

6.3 Results

6.3.1 Model expectations

As shown in chapter 5, the formulation of the fitness function had a large effect on the distribution of individuals within their home range. Individuals modelled with a sigmoid fitness function (i.e., using a time minimizing foraging strategy) focused their time on the safest patches, regardless of home range configuration (Fig. 6.2; white boxes). Individuals modelled with a linear fitness function (i.e., using an energy maximizing foraging strategy) displayed a much more even patch use, but tended to use the most productive patches relative to time minimizing individuals (Fig. 6.2; grey boxes). This pattern depended on the spatial arrangement of patches within the home range. When the home range consisted of patches that were clustered into two local patch aggregations (containing 2 and 3 patches), individuals used the 3 most productive patches in proportion to their forage abundance, as well as using the safest patch. In home ranges where patches were distributed such that there was a single, isolated patch and a local cluster of 4 patches, proportional patch use was related to the abundance of forage within patches, although patches were generally used evenly. Therefore, model outputs parameterized for elk were consistent with my expectation that time minimizers use the safest patch, while energy maximizers typically use patches based on their relative forage abundance.

6.3.2 Foraging strategies in free-ranging elk

Elk used cutblocks within their home ranges that had higher forage abundance (t_{647}=-2.23, p=0.03) and were less risky (t_{654}=-2.28, p=0.02) relative to those cutblocks within the home range they do not use (Table 6.3). Of the cutblocks that were used by elk within their home ranges, I found that their proportional use was a significantly decreasing function of predation risk ($F_{2,735}$=3.56, r^2=0.01, p=0.03; Table 6.2). However, the relationship with forage was not as expected (negative), but rather had a nonsignificant positive slope (Table 6.2). This may have occurred because of the weak, but significant correlation between predation risk and forage availability (r=0.08, p=0.02; Fig. 6.3), which necessitated a trade-off.

Additionally, the within cutblock behaviour of elk (i.e., inactivity) was also consistent with a time minimizing strategy. The step lengths in the 15% of the safest and riskiest moves were located in approximately the same number of cutblocks ($\approx$75); however, their distribution of step length were significantly different (D=0.078, p=0.004; Fig. 6.4). Individuals tended to take longer step lengths in low risk cutblocks compared to high risk cutblocks and this effect was not due to differences in cutblock sizes in the two groups (t_{84}=-1.29, p=0.20).

6.3.3 Factors influencing the variation in cutblock use within an elk's home range

The coefficient of variation in cutblock use within the home range was related to the number and configuration of cutblocks within the home range, and to a lesser extent with the variation in forage and predation risk observed in the home range (Table 6.4). The variables retained in the top model selected by AIC included patch cohesion (pc), the total number of cutblocks ($ncut$) found within the elks home range, and the variation in predation risk (cv_p) among cutblocks within the home range (Table 6.5). This model explained approximately half of the variation in the data ($F_{3,30}$=9.76, p=0.0001, r^2=0.49). Variation in cutblock use within the home range was related to the number of cutblocks found within the home range, such that elk used cutblocks more variably when there were more cutblocks to choose from. Likewise, with increasing patch cohesion within the home range, the coefficient of variation in patch use increased. Variation in forage abundance and predation risk were retained, either individually or together, in all three of the top models. However, in all of these cases the confidence intervals around the parameter estimates of the coefficient of variation in forage abundance and predation risk contained zero, suggesting they added very little biologically to the model and may have been included due to the propensity of AIC to over-fit models (Bozdogan 1987).

6.4 Discussion

Elk clearly make trade-offs between the risk of predation and foraging opportunities, and the effects of these trade-offs may be far reaching (Ripple et al. 2001, Fortin et al. 2005, Creel et al. 2005, Winnie & Creel 2007). Trade-offs occur in habitat selection and differential patch use (Creel et al. 2005) as well as behaviours (e.g., vigilance) that can occur within patches (Winnie & Creel 2007). Typically, researchers have investigated these foraging strategies based on the selected diet of herbivores during a single season (Belovsky 1978, Owen-Smith 1993, Forchhammer & Boomsma 1995, Bergmen et al. 2001) and have not arrived at a consensus regarding whether or not an ungulate should be an energy maximizer or time minimizer. Forchhammer & Boomsma (1995) found evidence for an energy maximizing foraging strategy in muskoxen. However, the extreme conditions of muskoxen habitat may require an energy maximizing foraging strategy in order to obtain sufficient energy for thermoregulation and coupled with a relative lack of predation risk may reduce their need to engage in anti-predator behaviours. Conversely, Bergman et al. (2001) found that during summer, bison clearly selected a diet that resulted in a time minimizing foraging strategy. They attribute this strategy to the bison's attempt to avoid insect harassment, engage in social activities, and reduce the risk of predation through anti-predator behaviours (Bergman et al. 2001). From their investigation of female mule deer time budgets, Kie et al. (1991) also concluded, that mule deer employed a time minimizing foraging strategy when foraging conditions are good, but shifted to an energy-maximizing foraging strategy when forage conditions were poor. They attribute the time minimizing strategy to the need for individuals to trade-off foraging opportunities and the risk of predation (Kie et al. 1991). Similarly, I provide evidence that in west central Alberta, where wolves are at densities ranging up to 12/1000 km^2 (Webb 2009), adult female elk used a time minimizing foraging strategy that is evident in their patch choice and behaviour within patches.

The flexibility in time allocation that is available to an individual employing a time minimizing foraging strategy may help them cope with increased predation risk, while still meeting energetic or fitness goals - a luxury that may not be possible with an energy maximizing strategy. Indeed, this is the basis behind the indirect effects or non-consumptive effects of predation: individuals forced to interrupt foraging for the sake of avoiding predation may suffer reduced growth and / or reproductive rates (Werner & Anholt 1993, Werner & Peacor 2003). The strength of the non-consumptive effects of predation may be such that they outweigh the direct effect of predation (i.e., direct removal of an organism by a predatory event) and have the potential to structure ecosystems through cascading behavioural effects (Schmitz et al. 1997, Schmitz et al. 2004). In Yellowstone National Park the reintroduction of wolves caused substantial changes to the habitat selection and behaviour of elk, which in turn has had important implications for the landscape (Laundre et al. 2001, Ripple et al. 2001, Fortin et al. 2005, Mao et al. 2005). Mao et al. (2005) found that shifts in habitat use by elk may have facilitated the use of anti-predator behaviour (specifically grouping) when they were unable to spatially segregate from wolves in winter. Similarly, Winnie & Creel (2007) and Liley & Creel (2008) noted that elk increased their vigilant behaviour, in exchange for foraging, in the presence of wolves. They suggest that while females were able to "pay down" the foraging cost of vigilance, males were unable to reduce foraging efforts in an attempt to remain safe, due to poor body condition and subsequently suffered a higher risk of predation from wolves (Winnie & Creel 2007). Understanding how individuals change their behaviours, both in terms of patch choice and anti-predator behaviours within patches, when under the risk of predation threat may shed light on their ability to "pay down" the fitness consequences of predation by matching their behaviour to both the temporal and spatial variation in predation risk (Lima & Bednekoff 1999, Ferrari & Chivers 2009, chapter 4).

While individual behaviour and foraging strategies may be key determinants in the trade-off between predation risk and forage acquisition, it is important to remember that these ecological processes occur on the template provided by landscape pattern. I found that elk tended to use safer cutblocks and reduced their activity in risky situations, but used only a subset of cutblocks available within their home range. The cutblocks they did use were, on average safer and had more forage than those they did not use. The variable nature of cutblock use within the home range suggests that the relative context and makeup of local cutblock aggregations has just as much to do with their use as the absolute values of forage and predation risk for a given cutblock. There was little evidence that the spatial variation in forage and predation risk modified the spatial variation in cutblock use by elk. This may not be surprising given the focus on cutblocks in the analysis. In reality these patches exist in a greater habitat matrix or spatial context, which may influence their use (Weckerly 2005). Landscape heterogeneity influences that ability of elk to avoid encounters and the potential to be killed by wolves (Hebblewhite et al. 2005, Kauffman et al. 2007). Hebblewhite et al. (2005) attributed this, in part, to the ability of elk to use behaviours such as vigilance, grouping, and evasion to avoid predation. Similarly, Kauffman et al. (2007) showed that the locations of elk killed by wolves in Yellowstone National Park in winter was determined by landscape characteristics that influence the detection of predators and the ability of wolves to capture elk. They suggest that landscape heterogeneity provides the opportunity for prey to use movement and habitat selection to avoid predation (Kauffman et al. 2007). Habitat selection studies of elk under the threat of predation seem to corroborate the results of these predation studies. Anderson et al. (2005) found that the composition and size of elk home ranges in Wisconsin was dependent on foraging potential, cover, habitat type, and the potential risk of predation. Similarly, Frair et al. (2005) found that the movement patterns of elk were indicative of a trade-off between foraging and potential risk and that landscapes constrained elk habitat use due to inherent risk of wolves or humans. Landscapes may also facilitate the trade-off between risk and reward. In a partially migratory elk herd, Hebblewhite & Merrill (2009) found that some elk reduced their exposure to risk by migrating, while those that did not migrate used a spatial refuge from wolves, provided by proximity to human activity. The predation refuge use of elk in this study allowed them to access forage in an otherwise apparently risky landscape. Habitat selection and behaviour within patches represent complex trade-offs that occur between competing needs, including avoiding predation and accessing forage, and must be investigated as a whole (or in a hierarchical fashion) rather than simply investigating cutblock use in isolation (Rettie & Messier 2000, Dussault et al. 2205).

In managed landscapes like those in west central Alberta, managers may be able to facilitate the trade-off between predation risk and forage acquisition at multiple scales by reducing the inter-patch distance between cutblocks and by creating retention patches of intact forest within the boundaries of a cutblock (Sullivan et al. 2008). However, managers may not be able to encourage more even use of cutblocks just by providing more foraging patches. The variation in cutblock use within a home range by elk was most influenced by the number and spatial arrangement of cutblocks it was exposed to. With an increasing number of cutblocks within the home range, elk use becomes more variable, highlighting the importance of the spatial context within which cutblocks are embedded. Weckerly (2005) found that cutblocks were used when they were associated with grassy meadows and the meadows did not provide sufficient forage due to cutblocks containing a relatively low abundance of grass. In west central Alberta, elk also selected for natural openings and cutblocks due to their high forage abundance, relative to the conifer forests that cover most of the study area (Frair et al. *in preparation*). However, this preference for cutblocks may be reduced with increased creation of cutblocks and the road infrastructure associated with them (Frair et al. 2008, Godvik et al. 2009, Frair et al. *in preparation*). Therefore, managers must find a balance between the creation of new cutblock and providing sufficient cover habitat (Visscher & Merrill 2009), which may be used by elk as a way of minimizing predation spatially in addition to using behaviour within a cutblock.

Elk appear to use a time minimizing foraging strategy, potentially resulting in "spare time", to engage in anti-predator behaviours. They may be able to trade-off predation risk with little movement cost as well as in-transit predation risk by taking advantage of structural and behavioural refuges. This study represents an initial investigation into the foraging strategies of elk at multiple scales. Although initial results contain a lot of variation, this work highlights important consideration for trade-offs between foraging opportunities and predation risk that occur in a heterogeneous landscape. By constraining investigations to a single scale we may miss the trade-offs occuring at other scales that produce the foraging strategies observed. Managers may be able to facilitate trade-offs at both scales by reducing the costs and risk of inter-patch movement through the careful placement of new cutblock and deactivation of unused road networks and by increasing the effectiveness of within patch anti-predator behaviours by maintaining hiding cover within the boundaries of a cutblock.

6.5 Tables

Parameter	Description	Units	Value	State units	References
$\mathbf{x_g}_{crit}$	critical values for gut fill	kJ	0	0	-
$\mathbf{x_e}_{crit}$	critical values for energy reserves	kJ	0	0	-
$\mathbf{x_g}_{max}$	maximum values for gut fill	kJ	94,391	29	Weckerly et al. 2003[a]
$\mathbf{x_e}_{max}$	maximum values for energy reserves	kJ	438,631	129	Cook et al. 2001[b]
m_f	metabolic cost of active foraging	kJ/TS	6800	2	Jiang & Hudson 1992[c]
$m_{r/z}$	metabolic cost of ruminating and resting	kJ/TS	3400	1	Jiang & Hudson 1992[c]
rep	reproductive threshold	kJ	91,382	27	Cook et al. 2001[d]
u_{ij}	predation rate in transit from patch i to j	-	0.001	-	-
c_{ij}	cost of transit from patch i to j	-	1	-	-
T	Final time horizon	time steps	100	-	-
Variable	Description	Units	Value	State units	References
β	intake rate	kJ/TS	13,805	4	Wickstrom et al. 1984[e]
α	rumination rate	kJ/TS	10,200	3	Spalinger et al. 1992[f]
p_i	patch specific probability of predation	-	0.005	-	-

Table 6.1: Parameterized initial conditions and variables of the stochastic dynamic program used to simulate a female elk in summer. All calculations are based on an average elk weight of 210 kg (Cook et al. 2001) and the time step is taken to be 2 hours. Fat energy is calculated as 8703 kJ/kg (thus rep = 5% × 210 kg × 8703 kJ/kg). Forage energy is calculated based on the conversion from kg to kJ as: kg of food × 18,500 (gross energy per kg of forage) × 0.70 (average forage digestibility in summer) × 0.82 (metabolizable energy of digestible energy); thus intake and gut contents can be expressed in kJ. A wet to dry conversion factor of 2.7 was used to estimate gut contents (Phil Dewitt, *unpublished data.* State units refer to the simplification of the system for computational purposes. This was achieved by dividing all values by the lowest common multiple of energy (metabolic cost of rumination). Times steps (TS) are in 2 hour intervals

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[a] also Cook 2002; gut estimates to hold 24 kg of forage then converting to kJ based on the equation for forage energy content

[b] based on fat comprising 24% of body mass (ranging from 20-26%) and having an energetic content of 8703 kJ/kg

[c] based on daily energy requirements weighted by daily activity patterns

[d] based on reproductive failure at a body composition below 5% fat by weight at an energetic content of 8703 kJ/kg

[e] also Collins et al. 1978; estimated from graphs based on the availability of biomass in a cutblock (200 g/m^2) and the conversion of forage mass to forage energy

[f] also Robbins 1993; McCorquodale 1991; estimated as 9-10% of total fill per time step

Variable	Estimate	Lower CI	Upper CI	p value
intercept	0.017	0.011	0.023	<0.0001
forage	0.00002	-0.00002	0.00006	0.36
predation	-0.016	-0.004	-0.028	0.01

Table 6.2: Parameter estimates, confidence intervals, and significance for variables related to the proportional use of a cutblock in summer by elk range ($F_{2,735}$=3.56, p=0.03, r^2=0.01). Forage is the average available forage (g/m^2) and predation is the relative probability of occurrence of a wolf from a RSF.

Variable	Used cutblocks	Unused cutblocks
forage	105.9 (31.2)	100.8 (33.8)
predation	0.38 (0.10)	0.40 (0.11)

Table 6.3: Forage availability (g/m^2; mean(sd)) and predation risk (relative probability of occurrence from a wolf resource selection function; mean(sd)) in used and unused cutblocks. There was a significant difference in forage (t_{647}=-2.23, p=0.03) and predation risk (t_{654}=-2.28, p=0.02) and elk appear to use the more productive and safer cutblocks from those available to them.

Variables	AIC	ΔAIC	w_i
$pc, ncut, cv_p$	366.06	0	0.41
$pc, ncut, cv_p, cv_f$	367.67	1.61	0.19
$pc, ncut, cv_f$	367.78	1.72	0.18
pc, agg	368.74	2.68	0.11
$pc, ncut$	368.76	2.7	0.11
$pc, pcut$	373.80	7.74	<0.01

Table 6.4: AIC table for factors influencing the variance in patch use. pc is a measure of patch cohesion and agg is an aggregation index, both measured using FRAGSTATS. $ncut$ is the total number of cutblocks within the home range, $pcut$ is the proportion of the home range contained in cutblocks, cv_f is the coefficient of variation of average forage among cutblocks in the home range, and cv_p is the coefficient of variation of average predation (from a wolf RSF) among cutblocks in the home range. The index of patch cohesion ranges from 0 to 100 and as values approach 0 the proportion of the landscape comprised of cutblocks decreases and becomes increasingly subdivided and loses connectivity.

Variable	Estimate	Lower CI	Upper CI
intercept	-204.19	-433.92	25.53
pc	3.64	1.30	5.98
$ncut$	0.80	0.34	1.26
cv_p	1.68	-0.42	3.78

Table 6.5: Parameter estimates and confidence intervals for the top model from the AIC selection process. The model was significant in explaining the variation in patch use within an elk's home range ($F_{3,30}$=9.76, p=0.0001, r^2=0.49). pc is a patch cohesion index measured with FRAGSTATS, $ncut$ is the total number of cutblock within the home range and cv_p is the coefficient of variation of average predation (from a wolf RSF) among cutblocks in the home range.

6.6 Figures

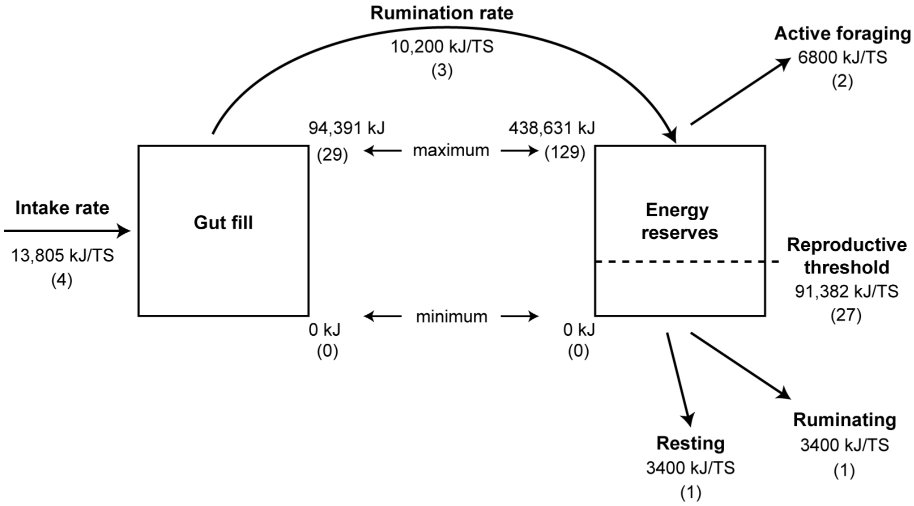
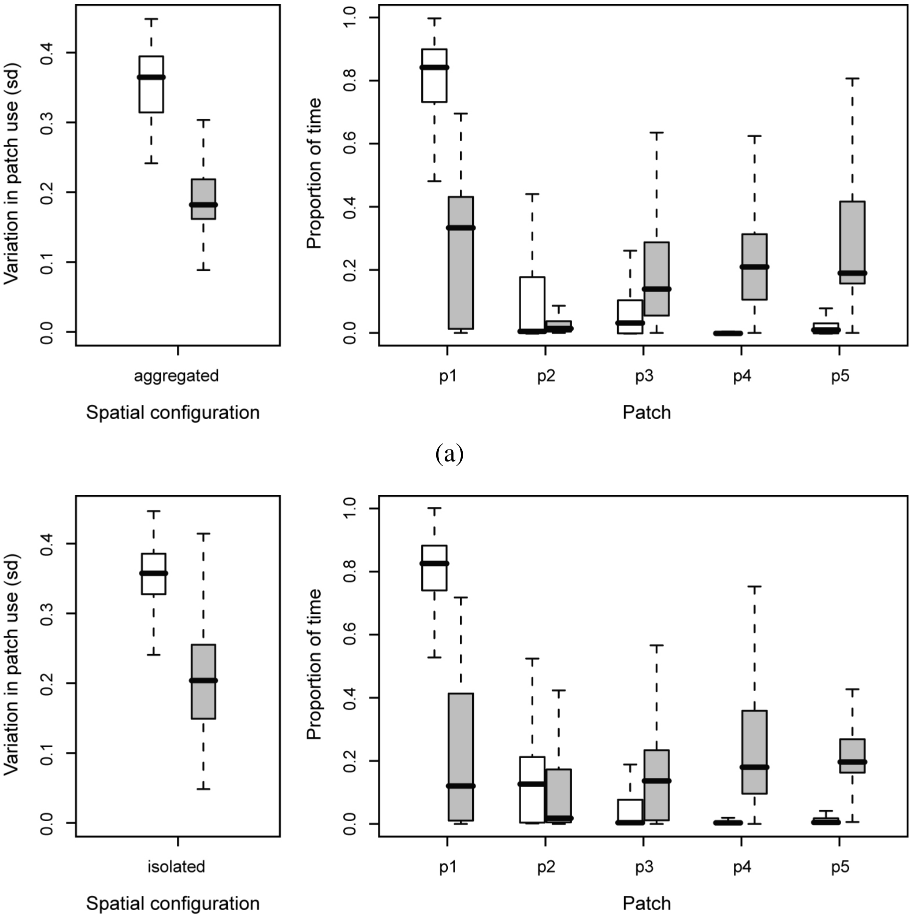


Figure 6.1: Schematic figure of the states and state dynamics used to model behavioural decisions by elk. States (gut fill and energy reserves) are impacted by the dynamics of intake into the gut and rumination/conversion of gut contents to energy stores (assumed to be exclusively fat stores). Values in kJ and kJ per time step (TS) are given. Values in parenthesis are the state unit conversions for computational simplicity. State unit values are reached by dividing the kJ values by the lowest common multiple (in this case ruminating cost) thus 1 state unit (SU) = 3400 kJ. Note that these are the baseline values, while intake and rumination rates are patch-specific.



(a)

(b)

Figure 6.2: Patch use and variation in patch use within a home range when anti-predator behaviours are partly effective and the landscape was either (a) aggregated (represented with two local aggregation of patches containing 2 and 3 patches, respectively) or (b) isolated (represented with a single isolated patch and a local cluster of 4 patches). White boxes represent individuals modelled with a sigmoid fitness function while grey boxes represent individuals modelled with a linear fitness function.

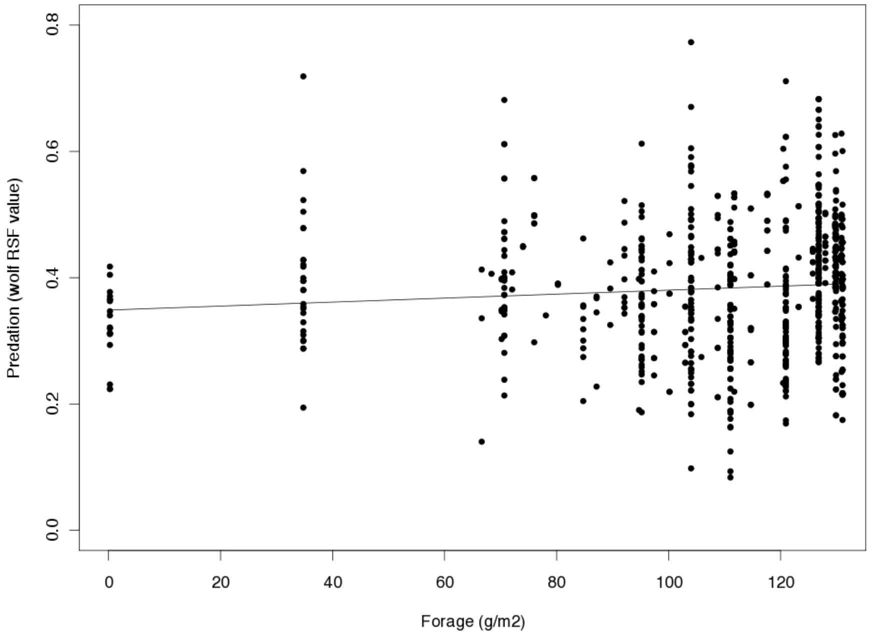


Figure 6.3: Correlation between the predation risk of a cutblock, based on a wolf RSF, and forage availability (n=738, r=0.08, p=0.02). The line simply illustrates the general trend of the correlation and is not meant to be indicative of a causal relationship.

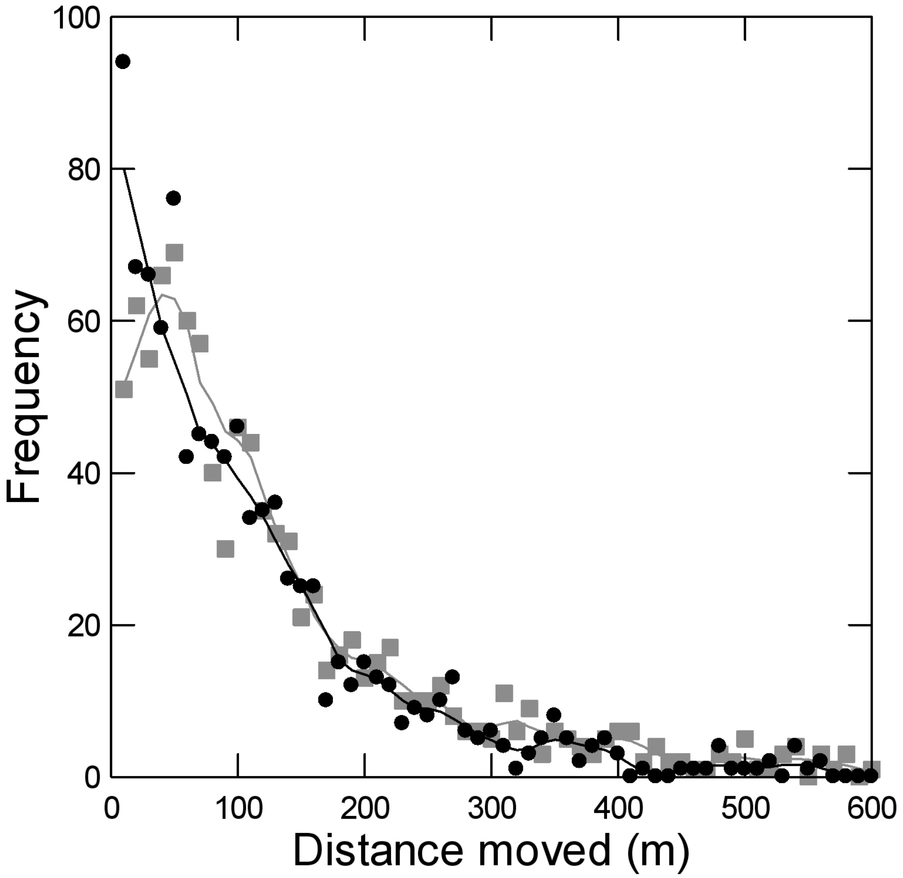


Figure 6.4: Frequency of step lengths in high (black circles and line) and low (grey squares and line) predation risk cutblocks. There are 1000 steps from 77 cutblocks represented in the low risk data and 974 step lengths and 75 cutblocks represented in the high risk cutblocks. Lines are LOWESS smoothed lines (to aid in visualizing the trends) and data are counts of step lengths in 10 metre bins. The distributions are statistically different using the bootstrap version of the Kolmogorov-Smirnov test (D=0.078, p=0.004).

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Synthesis

Ungulates, like elk, face the task of any forager, namely, to maintain adequate energy reserves via the acquisition of forage while simultaneously avoiding being predated upon. However, they are increasingly forced to accomplish this task in anthropogenically modified and fragmented landscapes. The rate at which cutblocks are being created within the study area of the research presented in this thesis is increasing. Therefore, understanding and managing how elk may use these foraging patches may be key for the continued persistence of elk in this ever changing landscape. What follows is an overview of the key findings from this thesis and their implications for elk management in an increasingly human-modified landscape. Additionally, I assess the inevitable shortcomings of the models presented and provide some insights for potential future exploration.

7.1 Inactivity: The ability to "pay down" predation effects

Increasingly, evidence has been presented showing how the fear of predation may be a more important determinant of individual behaviour, population dynamics, and ecosystem function, than the direct removal of individuals from the population. In my first application of dynamic state variable models I investigated patterns of optimal activity and the potential for non-consumptive effects of predation. In addition, I examined how optimal activity was influenced by predation risk, the ratio of intake to rumination rate, and the form of the fitness function in a state-dependent fashion. I found that depending on the form of the fitness function, which specified the prioritization of safety or forage acquisition, individuals were able to mediate the non-consumptive effects of predation without a loss of fitness. This potential was due to periods of inactivity, which provided time for anti-predator behaviours (Caro 2005). In particular, individuals that were modelled with a sigmoid fitness function employed inactivity as a means to reduce predation risk through anti-predator behaviours (e.g., vigilance). Conversely, individuals modelled with a linear fitness function suffered increased predation rates as they did not incorporate resting behaviours. The use of inactivity in free-ranging organisms has been noted when predators are present, suggesting that in fact it does facilitate a reduction in predation risk via reduced detectability, increased vigilance or the potential to form larger groups (Anholt & Werner 1995, 1998, Anholt et al. 2000, Wolff & van Horn 2003, Biro et al. 2004, Winnie & Creel 2007).

The ratio of intake to rumination rate, which may be indicative of foraging conditions, limited the ability of individuals to pay down the cost of predation, potentially exposing them to the non-consumptive effects (NCE) of predation. When intake rate was slower than rumination, individuals were required to forage more often to meet fitness goals, thus exposing them to predation. Indeed, under conditions of low intake and high predation risk, some surviving individuals were unable to meet their fitness goals or had a reduced final energy state. In contrast, when intake was rapid (relative to rumination rate), individuals benefited from a reduced influence of predation due to the anti-predator behaviours they could employ while inactive. Trussell et al. (2008) noted the effect of the particular forage resource (mussels or barnacles) in their study of NCE of predation in a tri-trophic experimental ecosystem; however, they attributed this to the refuge effect for snails foraging in mussel beds. Future work to uncover the influence of forage quality (via intake rates) on the potential of predation to structure trophic cascades may be fruitful in understanding how organisms are limited by digestion processes or gut constraints when additional time can be allotted to anti-predator behaviours without a loss in overall foraging.

The inability to employ inactive behaviours appears to predispose individuals to the consequences of the NCE of predation and may arise from a reduced energetic state, a high reproductive threshold, low forage availability, or the individual's prioritization of safety. The need for rumination may provide individuals with "free time" during which to engage in anti-predator behaviours. This result is analogous to the findings of Fortin et al. (2004) that during handling, limited foraging ungulates are able to exploit vigilant behaviour with no foraging cost by matching their periods of vigilance to chewing.

Further investigations, both in terms of models and measurement in the field, should explore the ability of ungulates to modify the extent to which they fill their rumens as a way of making more spare time available during periods of increased predation risk. This potential exists since rumen fill is typically incomplete in wild ungulates (Owen-Smith 1994). Evidence from dairy cows suggests that when cows are aware of a reduced potential to forage (i.e., the onset of night) they fill their rumens more than during mid-day foraging bouts (Taweel et al. 2004). Therefore, the potential ability to match periods of inactivity to temporal variation in predation risk provides ungulates with an important tool to reduce the indirect costs of predation.

7.2 Connectivity: Motivation to travel to "greener pastures"

The increasing awareness of the role that behaviour plays in unifying ecological processes and landscape patterns is exemplified in the idea of functional connectivity of landscapes or how connectivity is maintained between patches beyond structural or physical connectedness (Taylor et al. 1983, Ricketts 2001, Revilla et al. 2004, Belisle 2005, Rizkalla & Swihart 2007). I modelled connectivity by explicitly incorporating the behavioural decision making process of an individual in a state-dependent fashion. Simulations contained a pair of patches separated by some distance and I presented individuals with patch based motivation to move over inter-patch distances in the form of increased intake and rumination rate and decreased predation risk. As a measure of connectivity, I calculated the proportion of time spent in the distant patch relative to the individual's starting location. I found that increased intake rates maintain connectivity over the largest inter-patch distances. I also incorporated the behavioural decision that may arise during transit between patches and allowed individuals to minimize either the energetic cost of movement or the predation risk during transit. As expected, individuals that were able to minimize the biggest "threat" during transit (energetic cost or predation) maintained connectivity over and above the connectivity that arose from increased patch-based motivations. Connectivity appears to be based on individual behaviour and is influenced by state-dependence and ability to meet some fitness goal, as specified by the fitness function. I further used the dynamic state variable model structure to titrate the marginal rate of substitution of energy acquisition for increasing patch isolation, similar to a giving-up density experiment (Brown 1988). This provided a measure of the additional motivation (e.g., increased intake) that was required for individuals to use a previously unused and isolated patch. This form of the model could potentially be used as a tool to determine the effectiveness of management or conservation efforts for maintaining connectivity, or to rank potential management scenarios based on the level of connectivity they maintain. Dynamic state variable models have similarly been used to prioritize conservation actions and the allocation of conservation funds (Westphal et al. 2003, Wilson et al. 2006, McDonald-Madden et al. 2008).

To the best of my knowledge, this study is the first application of dynamic state variable models to address the explicit problem of landscape connectivity. While the addition of movement behaviour to such studies is required (Belisle 2005), I acknowledge that by nature dynamic state variable models are aspatial. This would seem to be a fairly large hurdle in their application to landscape level processes. In fact, many early models (McNamara & Houston 1990) did not consider the effect of movement and assumed that the foraging patch and a refuge were immediately adjacent and required essentially no travel. This is obviously not the case for large herbivores occupying a heterogeneous landscape. Travel costs are well known to influence the foraging decisions of animals (Charnov 1976) and were incorporated by including the *effect* of spatial distance, in terms of energy costs and predation risks as a function of inter-patch distance (Nonacs 2001, Van Gils et al. 2006). Similarly, in my model, I included the time to move between spatial location as cost of movement assuming that faster travel incurred a higher energetic cost (but potentially lower predation risk). Incorporating time constraints into the model by requiring animals to travel for a certain number of time steps may limit their time to forage and meet energy goals if the total number of time steps of the simulation is small. However, functionally this may be similar to penalizing individuals by reducing their reserves and forcing them to make up this energetic loss.

Typically, studies of connectivity rely on proximate measures based on landscape characteristics or empirical observation of the movement on individuals. Often, measures of connectivity are based on minimal assumptions about an animal's ability to move in a structural landscape (i.e., least cost path; Tischendorf & Fahrig 2001), however, it is clear that individual behaviour shapes the decision-making process of individuals (Ricketts 2001, Revilla et al. 2004, Rizkalla & Swihart 2007, Pinto & Keitt 2009). Indeed the same path through a landscape could be used in different ways by different individuals, resulting in different trade-offs. While the inclusion of behaviour into connectivity measures may not be feasible for rapid assessment of landscape level connectivity in heterogeneous landscapes, it is important that practitioners understand the consequences of ignoring or failing to account for individual behaviour. Misestimating connectivity as being either to high or too low may have important ramifications for conservation. If individuals maintain connectivity above what is estimated, valuable conservation dollars and effort may be poorly directed (Westphal et al. 2003, Williams & Snyder 2005, Windle et al. 2009). Conversely, overestimating connectivity may lead the fragmentation of a local population with dire consequences (Heinz et al. 2005, Fahrig 2007, Fischer & Lindenmayer 2007).

7.3 Hierarchical trade-offs between risk and reward: Constraints at two scales

Brown (1999) suggested that individuals trade-off risk and reward at two scales: behaviourally within patches, and between patch via patch choice. Mitchell (2009) quantifies these trade-offs as pre- and post-encounter behaviours, used by individuals to reduce the risk of predation. The goal of pre-encounter behaviours is to reduce the encounter rate with predators (i.e., predator-prey games in space) while post-encounter behaviours aim to influence the outcome of an encounter (i.e., games of vigilance; Mitchell 2009). Rarely do studies look at both scales simultaneously (but see Mitchell & Lima 2002 and Mitchell 2009). I presented a model explicitly incorporating individual behaviour at both scales and investigated the constraints facing individuals as a result of trade-offs unique to each scale. In general, individuals were constrained by the specification of the fitness function as it prioritized either safety or the acquisition of energy, providing “free time” for anti-predator behaviours, the cost of moving between patches (which was a function of landscape configuration) and the effectiveness of anti-predator behaviour during inactivity.

Individuals were constrained to use patch selection to trade-off risk and reward when anti-predator behaviours were completely ineffective and exposed them to the same risk during either inactivity or foraging. This situation encouraged individuals to move to safer patches and make-do with the reduced intake levels. This was particularly important for individuals modelled with a sigmoid fitness function, which resulted in a time minimizing strategy as they spent much of their time employing inactive behaviours. Conversely, when the distribution of patches made moving to the safest patch costly and individuals were able to become behaviourally unavailable to predation via inactivity, individuals remained in the patch within which they started the simulation. Similarly, when Alonzo et al. (2002) employed a game theoretic predator-prey model (using dynamic state variable models), they found that the foraging strategy (i.e., time minimizing vs rate maximizing) had a large effect on the outcome of their model and was a major determinant of the distribution on foragers (penguins) and prey (krill).

I found some evidence that the spatial context of the patch (i.e., the conditions of the patches found in the same local aggregation) influenced the variability in patch use within the home range. This effect has been noted in a number of other studies. Hochman & Kotler (2007) found that ibex preferentially foraged in patches close to refuge cover (cliffs). Likewise, the spatial proximity of high fitness patches to risky areas reduced the overall use of these patches in aquatic beetles (Resetarits & Binckley 2009). Conversely, local aggregations of relatively rich patches increased use by both grizzly bears and mule deer in an experimental study by Searle et al. (2006). Perhaps most applicable to this present study are the findings of Weckerly (2005), where it was shown that elk use of cutblocks was supplementary to their use of neighbouring meadows and meadow use was higher when they were in closer proximity to other meadows. By increasing the number of patches in my simulations, I expect that the relative context of patches in local aggregations will result in a skewed overall patch use, as individuals use only a few patches (the most productive or safest ones depending on foraging strategy) within local aggregation and rarely move between the aggregations.

A hierarchical approach to foraging theory has been beneficial in advancing our understanding of animal distributions; however, hierarchy theory has not been extensively applied to trade-offs between foraging and predation risk outside of habitat modelling (Senft et al. 1987, Bailey et al. 1996, Rettie & Messier 2000, Searle et al. 2008, Mayor et al. 2009). While hierarchical habitat selection studies have been conducted to investigate the factors influencing or potentially constraining the distribution of individuals at multiple scales, they remain a static representation of the outcome of many trade-offs (Rettie & Messier 2000, Dussault et al. 2005, Mayor et al. 2009). It is difficult to incorporate behaviour into habitat selection studies as such studies are not mechanistic and behaviours must be assumed by the researcher according to perceived relationships with landscape variables or movement parameters (Morales et al. 2004, Frair et al. 2005, Van Moorter et al. 2010). Dynamic state variable models, in the context I have presented, have the potential to provide a better behavioural understanding of the hierarchical nature of trade-offs and predict under what conditions one scale may become more important for the fitness of an individual. Dynamic state variable models will remain strategic in nature, potentially providing general rules that may aid managers, but they will never be fully tactical in the sense that they will not describe a specific animal-habitat relationship and cannot provide specific management recommendations.

7.4 Model assumptions and simplifications

While dynamic state variable models are ideally suited for incorporating an individual's decision-making process into models of foraging, and have successfully been used in this manner (Houston & McNamara 1999 and references therein), they have a number of limitations. One limitation of dynamic state variable models is that they require relatively simple systems of limited states or decision variables. Incorporating many states and processes quickly results in the "curse of dimensionality" and computational limitations. In general, these constraints require that the model builder maintain biologically reality while making necessary simplifying assumptions. Some of the simplifications I have made to reduce the “curse of dimensionality” involved the obvious simplification of an ungulate to describe it as a gut and energy reserve. Such simplifications require some assumptions about ungulate foraging and physiology, and are described in the following paragraphs.

The inclusion of ruminating behaviour in this investigation (of behaviour and patch selection) is a relatively unique addition to dynamic state variable models (but see Newman et al. 1995). Rumination provided a constraint to an individual’s foraging behaviour, however individuals were not constrained by the amount of forage that could be stored in the gut (Bednekoff & Houston 1994). Rather, their behaviour was constrained by the need to maintain some forage in the gut at all time and the requirement to convert forage into energy for a gain in fitness. The avoidance of the critical lower gut fill level shapes the individual’s need to forage (if resting behaviour is not used), however the value of the critical value of gut fill does not change the dynamics of the models, only the average gut fill of the individual (D. Visscher *unpublished data*). In nature, the rumen of a ungulate tends not to be filled to capacity (Hofmann 1973, Owen-Smith 1994) and consistency in fill and forage improves rumen functioning as gastrointestinal microbes become adapted for a particular diet (Spalinger et al. 1993, Gross et al. 1996, Owens et al. 1998, Gordon et al. 2002). Mechanistic models of digestion in ruminants and rumen dynamics are complex, given both passage and retention/digestion dynamics of varying particle sizes (Spalinger & Robbins 1992, Seo et al. 2009). Newman et al. (1995) modelled a more complex version of rumination in an ungulate with a dynamic state variable model, relative to what I have presented. However, their focus was on optimal diet selection and the two potential forages competed for digestion in space and time. I was less concerned with the overall physiology of the individual and focused instead on the behavioural opportunities that rumination provided. By including a background level of rumination, as done in Newman et al. (2005), I would have been adding a constant to energy reserves at each time step, as rumination rate did not vary in a forage- or patch-specific fashion.

In all versions of the model, I assumed that an individual’s behaviour was unaffected by conspecifics and that it did not interact with predators. There is theoretical and empirical evidence that this is not the case (Alonzo 2002, Mitchell & Lima 2002, Richards 2002, Childress & Lung 2003, Rands et al. 2003, Noonburg et al. 2007), however, the influence of conspecifics was ignored for the sake of computational simplicity and tractability (E. Noonburg *personal communication*). Indeed, McNamara & Houston (1990) found that state-dependent ideal free distributions did not result in a static distribution of individuals, but that changes in state due to foraging resulted in a “re-shuffling” of individuals at each time step. The presence of conspecific may present a forager with a double-edge sword. On one hand, competition for food within a patch may reduce an individual’s potential intake and increased group size may influence the detectability of the group to a predator (Fretwell & Lucas 1970, Hebblewhite & Pletscher 2002). On the other hand, the presence of conspecifics may present an anti-predator advantage through the dilution and the “many eyes” effect (Hamilton 1971, Lima 1995). This is clearly an area of potentially fruitful research and incorporating conspecific effects may lend new insights into the already complex trade-offs that animals make to reduce predation and acquire forage in natural systems (Noonburg et al. 2007, Mitchell 2009).

7.5 Management implications for elk

In this thesis, I found that cutblocks provide considerably more herbaceous forage relative to the surrounding conifer forests (Jenkins & Starkey 1993, 1996). However, they produce slightly less browse potentially effecting their seasonal importance as foraging patches. Approximately a decade following felling cutblocks provided the most forage in terms of absolute abundance. Therefore, managers using the succession sequence of cutblock regeneration, through carefully implemented harvesting regimes (spatially and temporally), have the potential to increase the forage base for elk across the landscape. However, while increased cutblocks may be advantageous for elk, many other species may not share the same tolerance for increased forest harvesting and human activity. Likewise, increased harvesting in areas already predominated by cutblocks may result in the loss of other key habitat features including security cover. Security cover is of particular importance given the enhanced human access and hunting pressure that may result from the increased need for a road network to extract timber (Hershey & Leege 1976, Lyon &

Jensen 1980, Farmer et al. 2006, Frair et al. 2008). The challenge for managers is to strike a balance between forage availability and forest cover to ensure elk remain a viable member of the large herbivore community.

From GPS telemetry of free-ranging elk, I found that the space use of elk and their behaviour within cutblocks appears to be most consistent with a time minimizing foraging strategy. This trend appeared at both the scale of patch choice as well as within cutblocks. Within their summer home ranges, elk generally used cutblocks that were safer and had higher forage abundance than those they did not use. Of the cutblocks they did use, they tended to use safer cutblocks and within risky cutblocks their movement patterns reflect increased inactivity. This suggests that elk hierarchically order their use of cutblocks to avoid predation while still acquiring adequate forage. However, the spatial configuration of cutblocks may still constrain their use within the home range.

Despite being highly mobile and having the ability to behaviourally compensate for patch isolation and predation risk, elk may display thresholds in patch use, albeit at relatively large inter-patch distances. To mitigate this potential, when planning the development of cutblocks into previously uncut forest, managers should try to maintain patches at relatively close inter-patch distances to facilitate movement. Seeding herbaceous vegetation into cutblocks may reduce seedling survival (Powell et al. 1994), but it may be an attractive means for enhancing the foraging opportunities of resident elk. Providing within cutblock retention (uncut patches of mature trees) may also encourage use by providing additional hiding cover that may be used by elk to mitigate predation risk with little associated travel costs (Potvin & Bertrand 2004, Sullivan et al. 2008). Likewise, by reducing the “harshness” of the inter-cutblock matrix, managers will reduce the cost associated with transit by individuals. Practically this could be done a number of ways. In west central Alberta a major determinant of elk survival (and therefore movement behaviour) is the presence of linear features and roads, which attract wolves and human hunters, respectively (Frair et al. 2005, 2007, 2008). Restricting the creation of and deactivating these features will reduce the predation risk individuals are exposed to while in transit.

By creating landscape conditions that facilitate movement through patch enhancement and matrix modification, managers may be able to encourage expansion of use into previously unused areas. Cutblocks may act as “stepping stones” of increased patch quality that promote use into unused areas (Uezu et al. 2008). While elk are fairly flexible in their ability to adapt to landscape fragmentation (Frair et al. *in preparation*), care must be taken when applying these ideas to other species that may be adapted to different levels of landscape fragmentation and will show very different patterns of use in increasingly fragmented landscapes (Fahrig 2007). Indeed, it is important to note that despite a tolerance for fragmentation, all individuals display a critical threshold inter-patch distance beyond which patch use is minimal (With & Crist 1995).

Providing elk with cutblocks of varying ages may be the best opportunity for managers to present elk with relatively safe older cutblocks which provide increasing hiding cover with age but low forage and relatively high forage availability young cutblocks but lacking hiding cover, in order to allow them to behavioural mediate the trade-off between foraging and predation risk (Visscher & Merrill 2009). The two-pass harvest system currently used in west central Alberta is ideally suited to creating and maintaining this heterogeneity on the landscape. By staggering cutting times in a local area by about the time it takes a cutblock to reach peak biomass (approximately a decade following felling) managers may ensure a shifting mosaic of foraging opportunities and cover as cutblocks age (Boston & Sessions 2006). Similarly, by allowing retention patches of intact forest to remain within a cutblock, managers may be able to allow elk to mitigate this trade-off with little movement cost and in-transit predation risk. (Potvin & Bertrand 2004, Sullivan et al. 2008). This management action has been increasingly incorporated into forest management in west central Alberta (L. Morgantini *personal communication*).

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