Small mammal foraging and population responses to northern conifer mast

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Graduate Program in Biology

A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

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SMALL MAMMAL FORAGING AND POPULATION RESPONSES TO NORTHERN CONIFER MAST

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by

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Graduate Program in Biology,
Collaborative Program in Environment & Sustainability

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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is accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy
Abstract

Conifer seeds are a component of the diet of many rodents, and post-dispersal seed predation by rodents is often implicated as a critical constraint on the regeneration of coniferous forests. However, little is known about the effects of conifer seed availability on individual rodents and their populations. The over-arching goal of this dissertation was to investigate the effects and implications of conifer seed production on the foraging and population dynamics of northern small mammals. The predominant conifer study species were white spruce (Picea glauca) and subalpine fir (Abies lasiocarpa), and the main rodents examined were the deer mouse (Peromyscus maniculatus) and southern red-backed vole (Myodes gapperi).

Nutritional analysis and laboratory experiments showed that spruce seeds are a high quality food source to rodents. Mice were able to maintain body condition on diets restricted to these seeds, and voles were able to use spruce seeds as a sole food source in the short-term. In the field, caching rates of spruce seeds varied with seed abundance, but rodents readily consumed these seeds within experimental patches regardless of abundance.

Conversely, fir seeds were avoided by rodents in experiments, as was expected based on their low nutritional value and high concentration of plant secondary compounds. Mice increased food intake and retention of digesta in the caecum to maintain body mass on diets restricted to fir seeds. However, voles did not compensate for this low quality seed-diet, and their body condition deteriorated rapidly. In the field, rodents disregarded fir seeds as a valuable resource for current or future use, even at exaggeratedly abundant seed densities.
Given these individual-level interactions, the rodent population responses to conifer mast seeding that I observed were unexpected. Summer mouse densities and breeding varied with previous fir seed production, although this may have been mediated by population responses of invertebrate post-dispersal seed predators to fir seed availability. In contrast, mouse demography was not affected by spruce mast seeding, but likely due to interspecific competition with the North American red squirrel (*Tamiasciurus hudsonicus*), a dominant pre-dispersal spruce seed predator. These results reveal direct and indirect consumer-resource pulse dynamics that require further examination.

**Keywords**

Rodent, northern coniferous forest, nutritional ecology, population dynamics, foraging behaviour, seed production, seed predation, mast seeding, resource pulses, food quality, plant secondary compounds, consumer-resource dynamics, deer mouse, southern red backed-vole, white spruce, subalpine fir, lodgepole pine, gut morphology, giving-up density, food supplementation, multi-trophic interactions.
Co-Authorship Statement

A version of Chapter 2 was published in the Canadian Journal of Zoology with Michelle Duong and John Millar as co-authors. Ms. Duong collected the field-based seed preference data under my supervision. Dr. Millar contributed to the study design, provided equipment and funding, and contributed editorial comments to the manuscript.

A version of Chapter 3 was published in Mammalian Biology with John Millar as a co-author. Dr. Millar contributed to the study design, provided equipment and funding, and contributed editorial comments to the manuscript.

A version of Chapter 4 has been submitted for publication to the Journal of Mammalogy with Derek Green and John Millar as co-authors. Mr. Green collected the subalpine fir seed data under my supervision, and contributed editorial comments on the manuscript. Dr. Millar contributed to the study design, provided equipment and funding, and contributed editorial comments to the manuscript.

A combined version of Chapters 5 and 6 has been accepted for publication in the Journal of Animal Ecology with John Millar as a co-author. Dr. Millar contributed to the study design, provided access to long-term datasets (pre-2007), provided equipment and funding, and contributed editorial comments to the manuscripts.
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# Table of Contents

CERTIFICATE OF EXAMINATION .................................................................................. ii

Abstract ........................................................................................................................... iii

Co-Authorship Statement ............................................................................................. v

Acknowledgments .......................................................................................................... vi

Table of Contents .......................................................................................................... ix

List of Tables .................................................................................................................. xv

List of Figures ................................................................................................................ xvi

List of Appendices ......................................................................................................... xxi

List of Abbreviations .................................................................................................... xxii

Chapter 1 ....................................................................................................................... 1

  1 General introduction ................................................................................................. 1
      1.1 Pre-dispersal seed predation ........................................................................... 4
      1.2 Post-dispersal seed predation ....................................................................... 5
      1.3 Differential seed predation ........................................................................... 6
      1.4 Defences against seed predation ................................................................... 7
      1.5 Combating seed defences ............................................................................. 10
      1.6 Limitations in the conifer literature ............................................................... 12
      1.7 Major study species ...................................................................................... 13
      1.8 Dissertation structure ................................................................................... 15
      1.9 References .................................................................................................... 18

Chapter 2 ..................................................................................................................... 27

  2 Conifer-seed preferences of small mammals ......................................................... 27
      2.1 Introduction .................................................................................................... 27
      2.2 Methods ......................................................................................................... 29
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.2.1</td>
<td>Laboratory seed selection trials</td>
<td>29</td>
</tr>
<tr>
<td>2.2.2</td>
<td>Field seed selection</td>
<td>31</td>
</tr>
<tr>
<td>2.2.3</td>
<td>Statistical analyses</td>
<td>32</td>
</tr>
<tr>
<td>2.3</td>
<td>Results</td>
<td>33</td>
</tr>
<tr>
<td>2.3.1</td>
<td>Laboratory seed selection trials</td>
<td>33</td>
</tr>
<tr>
<td>2.3.2</td>
<td>Field seed selection</td>
<td>42</td>
</tr>
<tr>
<td>2.4</td>
<td>Discussion</td>
<td>44</td>
</tr>
<tr>
<td>2.5</td>
<td>Acknowledgments</td>
<td>48</td>
</tr>
<tr>
<td>2.6</td>
<td>References</td>
<td>49</td>
</tr>
<tr>
<td>Chapter 3</td>
<td>The efficacy of conifer seeds as major food resources to deer mice (<em>Peromyscus maniculatus</em>) and southern red-backed voles (<em>Myodes gapperi</em>)</td>
<td>53</td>
</tr>
<tr>
<td>3.1</td>
<td>Introduction</td>
<td>53</td>
</tr>
<tr>
<td>3.2</td>
<td>Methods</td>
<td>56</td>
</tr>
<tr>
<td>3.2.1</td>
<td>Nutritional analysis of seeds</td>
<td>56</td>
</tr>
<tr>
<td>3.2.2</td>
<td>Feeding trials</td>
<td>57</td>
</tr>
<tr>
<td>3.2.3</td>
<td>Statistical analyses</td>
<td>59</td>
</tr>
<tr>
<td>3.3</td>
<td>Results</td>
<td>60</td>
</tr>
<tr>
<td>3.3.1</td>
<td>Nutritional analysis of seeds</td>
<td>60</td>
</tr>
<tr>
<td>3.3.2</td>
<td>Survival</td>
<td>62</td>
</tr>
<tr>
<td>3.3.3</td>
<td>Body mass</td>
<td>62</td>
</tr>
<tr>
<td>3.3.4</td>
<td>DM intake</td>
<td>68</td>
</tr>
<tr>
<td>3.3.5</td>
<td>Gut dimensions</td>
<td>70</td>
</tr>
<tr>
<td>3.3.6</td>
<td>Vital organs</td>
<td>71</td>
</tr>
<tr>
<td>3.3.7</td>
<td>Blood-glucose concentration</td>
<td>71</td>
</tr>
<tr>
<td>3.4</td>
<td>Discussion</td>
<td>71</td>
</tr>
</tbody>
</table>
3.5 Acknowledgments........................................................................................................... 80
3.6 References......................................................................................................................... 80

Chapter 4.................................................................................................................................. 86

4 Effects of seed quality and abundance on the foraging behaviour of northern rodents 86

4.1 Introduction....................................................................................................................... 86

4.2 Methods............................................................................................................................. 90
   4.2.1 White spruce seeds........................................................................................................ 90
   4.2.2 Subalpine fir seeds......................................................................................................... 93
   4.2.3 Statistical analysis........................................................................................................ 94

4.3 Results.................................................................................................................................. 98
   4.3.1 Assessing seed quality ............................................................................................... 98
   4.3.2 Foraging behaviours..................................................................................................... 98

4.4 Discussion............................................................................................................................ 106

4.5 Acknowledgments............................................................................................................... 112

4.6 References.......................................................................................................................... 112

Chapter 5................................................................................................................................ 117

5 Small mammal population responses to northern conifer mast ................................. 117

5.1 Introduction....................................................................................................................... 117

5.2 Methods............................................................................................................................. 122
   5.2.1 Study area and species ............................................................................................... 122
   5.2.2 Cone index ................................................................................................................ 123
   5.2.3 Seed rain..................................................................................................................... 123
   5.2.4 Small mammal trapping ........................................................................................... 124
   5.2.5 Data analysis ............................................................................................................. 125

5.3 Results.................................................................................................................................. 131
   5.3.1 Cone and seed production........................................................................................... 131
5.3.2 Population density................................................................. 131
5.3.3 Population growth and survival ............................................ 135
5.3.4 Body mass............................................................................ 139
5.3.5 Breeding................................................................................. 144
5.4 Discussion................................................................................ 144
  5.4.1 Cone and seed production.................................................... 145
  5.4.2 Population responses to white spruce seed production........... 146
  5.4.3 Population responses to subalpine fir seed production........... 149
  5.4.4 Fall population dynamics..................................................... 153
  5.4.5 Asynchronous cone production.......................................... 154
  5.4.6 Conclusion............................................................................ 155
5.5 Acknowledgments..................................................................... 155
5.6 References................................................................................ 156
Chapter 6....................................................................................... 165
6 Effects of natural food supplementation on a short-season population of deer mice 165
  6.1 Introduction............................................................................. 165
  6.2 Methods.................................................................................. 169
    6.2.1 Study area and species ..................................................... 169
    6.2.2 Deer mouse trapping.......................................................... 170
    6.2.3 Food supplementation....................................................... 171
    6.2.4 Data analysis ..................................................................... 171
  6.3 Results..................................................................................... 175
    6.3.1 Overall population density............................................... 175
    6.3.2 Overwinter population dynamics....................................... 176
    6.3.3 Summer population dynamics........................................... 180
    6.3.4 Timing of breeding ............................................................. 181
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.3.5</td>
<td>Individual breeding</td>
<td>181</td>
</tr>
<tr>
<td>6.3.6</td>
<td>Body mass</td>
<td>186</td>
</tr>
<tr>
<td>6.4</td>
<td>Discussion</td>
<td>187</td>
</tr>
<tr>
<td>6.5</td>
<td>Acknowledgments</td>
<td>193</td>
</tr>
<tr>
<td>6.6</td>
<td>References</td>
<td>194</td>
</tr>
<tr>
<td>Chapter 7</td>
<td>General discussion</td>
<td>200</td>
</tr>
<tr>
<td>7.1</td>
<td>Foraging dynamics of conifer-rodent interactions</td>
<td>201</td>
</tr>
<tr>
<td>7.1.1</td>
<td>Preferential foraging and seed quality</td>
<td>201</td>
</tr>
<tr>
<td>7.1.2</td>
<td>Effects of seed abundance on foraging behaviour</td>
<td>203</td>
</tr>
<tr>
<td>7.1.3</td>
<td>The efficacy of conifer seeds as major food resources</td>
<td>206</td>
</tr>
<tr>
<td>7.2</td>
<td>Conifer seed production and small mammal populations</td>
<td>207</td>
</tr>
<tr>
<td>7.2.1</td>
<td>Assumptions of population-level interactions</td>
<td>207</td>
</tr>
<tr>
<td>7.2.2</td>
<td>Population responses to conifer mast seeding</td>
<td>208</td>
</tr>
<tr>
<td>7.3</td>
<td>Key future research directions</td>
<td>211</td>
</tr>
<tr>
<td>7.3.1</td>
<td>Conifer recruitment and regeneration</td>
<td>211</td>
</tr>
<tr>
<td>7.3.2</td>
<td>Physiological ecology of rodent foraging dynamics</td>
<td>212</td>
</tr>
<tr>
<td>7.3.3</td>
<td>Plant secondary compounds in conifer seeds</td>
<td>213</td>
</tr>
<tr>
<td>7.3.4</td>
<td>Post-dispersal conifer seed predation by invertebrates</td>
<td>214</td>
</tr>
<tr>
<td>7.3.5</td>
<td>Multiple plant defences</td>
<td>215</td>
</tr>
<tr>
<td>7.3.6</td>
<td>Interactions between pre-dispersal seed predators and rodents</td>
<td>216</td>
</tr>
<tr>
<td>7.3.7</td>
<td>Natural food supplementation studies</td>
<td>216</td>
</tr>
<tr>
<td>7.4</td>
<td>Concluding remarks</td>
<td>217</td>
</tr>
<tr>
<td>7.5</td>
<td>References</td>
<td>218</td>
</tr>
<tr>
<td>Appendix A: Chapter 5 supplementary material</td>
<td>224</td>
<td></td>
</tr>
</tbody>
</table>
Appendix B: Chapter 6 supplementary material ......................................................... 233
Appendix C: Permission to reproduce published material .............................................. 240
Appendix D: Animal use protocol approvals .................................................................. 241
Appendix E: Research permits ....................................................................................... 246
Curriculum Vitae ............................................................................................................ 256
List of Tables

Table 2.1. Results of discriminant function analysis of consumption of lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds by deer mice (Peromyscus maniculatus), southern red-backed voles (Myodes gapperi), heather voles (Phenacomys intermedius), long-tailed voles (Microtus longicaudus), and meadow voles (Microtus pennsylvanicus) in laboratory cafeteria-style feeding experiments. .......................... 37

Table 2.2. Classification of deer mice (Peromyscus maniculatus), southern red-backed voles (Myodes gapperi), heather voles (Phenacomys intermedius), long-tailed voles (Microtus longicaudus), and meadow voles (Microtus pennsylvanicus) based on discriminant function analysis of their consumption of lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds in laboratory cafeteria-style feeding experiments. .................................................................................................................................................................................. 41

Table 3.1. Results of nutritional analysis of control food (LabDiet 5001 Rodent Diet), and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds. .......................................................................................................................................................................................................................... 61

Table 3.2. Mean daily change (%) in body mass (compared to initial mass) of deer mice (Peromyscus maniculatus) fed control food and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds over a 14-day period. ..... 65

Table 3.3. Mean daily change (%) in body mass (compared to initial mass) of red-backed voles (Myodes gapperi) fed control food and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds over a 14-day period. .................. 66

Table 3.4. Results of ANOVAs comparing daily body mass changes of red-backed voles (Myodes gapperi) fed control food and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds over a 14-day period. ......................... 67

Table 4.1. Description of foraging behavioural scoring of each rodent visit to seed patches. .................................................................................................................................................................................................................................................. 96
Table 5.1. Evaluation of the parsimony of linear models examining the annual variation in average deer mouse density, population growth, and overwinter survival relative to previous population density and white spruce, subalpine fir, and total cone indices. .......................... 136

Table 5.2. Evaluation of the parsimony of Cormack-Jolly-Seber models examining the relationship between summer survival of overwintered deer mice and the previous fall’s white spruce, subalpine fir, and total cone indices. ........................................................................ 140

Table 5.3. Results of linear regression models testing for the effects of the previous fall’s white spruce, subalpine fir, and total cone production on various deer mouse body mass and breeding parameters. .................................................................................................................. 141

Table 6.1. The most parsimonious Cormack-Jolly-Seber models for the analysis of summer survival of overwintered deer mice at the control and treatment grids from 2004-2011. .... 183
List of Figures

Figure 2.1. Discriminant function scores derived from consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds in laboratory cafeteria-style feeding experiments differentiating deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), heather voles (*Phenacomys intermedius*), long-tailed voles (*Microtus longicaudus*), and meadow voles (*Microtus pennsylvanicus*). ..................................................................................................................................... 36

Figure 2.2. Total daily seed consumption by deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), heather voles (*Phenacomys intermedius*), long-tailed voles (*Microtus longicaudus*), and meadow voles (*Microtus pennsylvanicus*) in laboratory cafeteria-style feeding experiments. ..................................................................................................................................... 38

Figure 2.3. Consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds by deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), heather voles (*Phenacomys intermedius*), long-tailed voles (*Microtus longicaudus*), and meadow voles (*Microtus pennsylvanicus*) in laboratory cafeteria-style feeding experiments. ..................................................................................................................................... 39

Figure 2.4. Difference between masses of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) seeds consumed by deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), heather voles (*Phenacomys intermedius*), long-tailed voles (*Microtus longicaudus*), and meadow voles (*Microtus pennsylvanicus*) in laboratory cafeteria-style feeding experiments. ..................................................................................................................................... 40

Figure 2.5. Consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds by deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*) in the field. ..................................................................................................................................... 43

Figure 3.1. Body mass of (a) deer mice (*Peromyscus maniculatus*) and (b) red-backed voles (*Myodes gapperi*) fed control food and lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds over a 14-day period. ..................................................................................................................................... 64
**Figure 3.2.** Dry matter intake of (a) deer mice (Peromyscus maniculatus) and (b) red-backed voles (Myodes gapperi) fed control food and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds over a 14-day period. .......................... 69

**Figure 3.3.** Gut dimensions of deer mice (Peromyscus maniculatus) fed control food and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds over a 14-day period. (a) Lengths of the total gut and individual components. (b) Masses of the total gut and individual components. ........................................ 72

**Figure 3.4.** Gut dimensions of red-backed voles (Myodes gapperi) fed control food and lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds over a 14-day period. (a) Lengths of the total gut and individual components. (b) Masses of the total gut and individual components. ........................................ 73

**Figure 4.1.** Examples of foraging behaviours of deer mice (Peromyscus maniculatus) observed visiting seed containers. Red-backed voles (Myodes gapperi) exhibit identical behaviours. ........................................................................................................................................ 97

**Figure 4.2.** Absolute giving-up densities of rodents visiting white spruce seed and subalpine fir seed patches. .................................................................................................................................................. 101

**Figure 4.3.** Final proportions of seeds consumed and/or removed by rodents visiting white spruce seed and subalpine fir seed patches. ............................................................................................................ 102

**Figure 4.4.** Proportions of deer mouse visits to white spruce seed and subalpine fir seed patches that contained feeding, removal, and no feeding or removal behaviours .................. 103

**Figure 4.5.** Proportions of red-backed vole visits to white spruce seed and subalpine fir seed patches that contained feeding, removal, and no feeding or removal behaviours ............ 104

**Figure 4.6.** Proportions of deer mouse visits to high-abundance and low-abundance white spruce seed patches that contained feeding, removal, and no feeding or removal behaviours .............................................................................................................................. 105

**Figure 5.1.** White spruce and subalpine fir cone production in the Kananaskis Valley, Alberta from 2001-2011. ............................................................................................................................................... 132
Figure 5.2. White spruce and subalpine fir seed rain densities in the Kananaskis Valley, Alberta from 2006-2010. ................................................................. 133

Figure 5.3. Long-term white spruce and subalpine fir cone production, and deer mouse population densities in the Kananaskis Valley, Alberta. ................................................... 134

Figure 5.4. Average summer deer mouse population densities for the (a) full, (b) overwintered, and (c) young-of-the-year populations in relation to the previous fall’s subalpine fir cone production, the best predictor in models examining annual variation in average summer population densities between 2002-2011. ................................................... 137

Figure 5.5. Deer mouse summer population growth (intrinsic rate of increase week$^{-1}$) in relation to the preceding spring mouse population density, the best predictor in models examining annual variation in summer population growth rates between 2002-2011. ............ 138

Figure 5.6. Average summer mass of overwintered male deer mice in relation to the previous fall’s subalpine fir cone production, the best predictor in models examining annual variation in average summer body masses between 2002-2011. ................................................... 142

Figure 5.7. The proportion of pregnant resident overwintered female deer mice in relation to the previous fall’s (a) subalpine fir and (b) white spruce cone production. ......................... 143

Figure 6.1. Mean ± SE deer mouse population densities on the control and treatment grids in the spring, summer, and early fall of 2004-2011. ................................................................. 177

Figure 6.2. Winter deer mouse population growth (intrinsic rate of increase week$^{-1}$) on the control and treatment grids from 2004-2011. ................................................................. 178

Figure 6.3. Overwinter survival of deer mice on the control and treatment grids from 2004-2011................................................................. 179

Figure 6.4. Summer deer mouse population growth (intrinsic rate of increase week$^{-1}$) of (a) the full population, (b) overwintered adults only, and (c) young-of-the-year only, on the control and treatment grids from 2004-2011. ................................................................. 182
Figure 6.5. Ratio of the average summer and fall young-of-the-year population densities of deer mice on the treatment grid to those on the control grid.
List of Appendices

Appendix A: Chapter 5 supplementary material .......................................................... 224
Appendix B: Chapter 6 supplementary material .......................................................... 233
Appendix C: Permission to reproduce published material .............................................. 240
Appendix D: Animal use protocol approvals ............................................................... 241
Appendix E: Research permits .................................................................................... 246
List of Abbreviations

ADF: Acid Detergent Fibre

AIC\textsubscript{c}: Akaike’s Information Criterion, corrected for small sample sizes

CJS: Cormack-Jolly-Seber

CV: Coefficient of Variation

DFA: Discriminant Function Analysis

DM: Dry Matter

GUD: Giving-Up Density

NDF: Neutral Detergent Fibre

OW: Overwintered

PSC: Plant Secondary Compound

YY: Young-of-the-Year
Chapter 1

1 General introduction

Coniferous forests are the predominant forest type in Canada, comprising 68% of all forested land (Canadian Forest Service 2006). The majority of the boreal forest, as well as many subalpine regions, are made up of mixed conifer stands composed of different species of spruce (Picea), pine (Pinus), and fir (Abies; Canadian Forest Service 2006). These trees have significant ecosystem (Maguire et al. 2005) and economic (Persson 2005) value, and their lifecycle (Powell 2009), physiology (Smith and Hinckley 1995), diseases and pests (Schowalter and Filip 1993), and regeneration patterns (Greene 2002; Mallik 2003) have been extensively studied.

One of the key regulative processes in coniferous forests is the production and recruitment of seeds (Radwan 1970). In northern areas, seeds of many species mature in cones over the summer and are released in the fall; the number of cones produced each year can be highly variable (e.g. Alexander et al. 1990; Nienstaedt and Zasada 1990; Wendel and Smith 1990). Conversely, some species (e.g. Picea mariana, Pinus contorta) produce predominantly serotinous cones in consistent numbers each year, and seeds that matured in previous seasons are dispersed in small amounts throughout the year or in an accelerated manner after a fire (Lotan and Critchfield 1990; Viereck and Johnston 1990). Plant-mediated and abiotic factors such as competition, allelopathy, temperature, and soil structure and nutrition can limit the recruitment success of conifer seeds (see reviews in Mallik 2003; Gartner et al. 2011). However, seed predation is often implicated as a
critical constraint on the regeneration and community dynamics of coniferous forests (Smith and Aldous 1947; Abbott 1961; Pank 1974).

Several species of vertebrates and invertebrates consume conifer seeds, with predation occurring either before or after seed dispersal. While other seed predators are briefly discussed in this and other chapters, the main focus of the experimental and observational studies in my dissertation is post-dispersal conifer seed predation by small mammals. Conifer seeds are a component of the diet of many rodents (Jameson 1952; Drożdż 1966; Abbott and Quink 1970; Merritt and Merritt 1978), and rodents have repeatedly been implicated as major post-dispersal seed predators in coniferous forests (e.g. Abbott 1961; Radvanyi 1971; Pank 1974; Sullivan and Sullivan 1982). However, it is largely unknown how the seeds of several conifer species are, and to what extent they can be, utilized by northern rodents. Conducting comprehensive diet and foraging studies of small nocturnal mammals can be challenging, especially in relation to this inconspicuous, but potentially important, food resource. A number of studies (described in more detail below and in the relevant chapters of this dissertation) have approached the conifer-rodent interaction by focusing on the effects of rodents on the fate of conifer seeds. This has been done mainly through quantification of the rates of seed predation by rodents, as well as their impact on seed recruitment and forest regeneration. However, little is known about the effects of conifer seed availability on individual rodents and their populations.

The over-arching goal of my dissertation is to investigate the patterns and implications of conifer seed production on the foraging and population dynamics of northern small mammals. I have approached this objective as a predator-prey interaction at both the individual- and population-levels, examining the foraging dynamics of individual rodents
in relation to varying abundance and quality of conifer seeds, and how these elements contribute to population-level trends. When investigating large-scale bottom-up relationships between food abundance and populations, there are often several critical assumptions about the behaviour of individuals that are overlooked (e.g. Shimada and Saitoh 2006). Examples of these include the overall and relative palatability of different foods, the efficacy of abundant lower-quality foods as a major resource to individuals, the conditions required to facilitate food storage and consumption, and the effects of food availability on specific demographic parameters. By providing insights at multiple scales and testing these key assumptions in the laboratory and in the field, I have attempted to present a comprehensive picture of the major trends and specific underlying mechanisms involved in bottom-up interactions between conifer seeds and rodents.

In this chapter, I present a summary of the identities and impacts of various major conifer seed predators. I also review the defensive strategies utilized by conifers, both at the individual-seed and plant-population levels, to limit seed predation, and how individual predators and their populations are affected by these defences. I then discuss the mechanisms that predators can use to overcome these plant- and seed-defences. These sections primarily focus on conifers and small mammals, but literature on other types of seeds and seed predators are included when relevant. Finally, I provide a summary of the limitations of the current conifer-rodent literature, and describe the major study species and objectives of the five data chapters of this dissertation.
1.1 Pre-dispersal seed predation

Pre-dispersal seed predation takes place when cones are removed and/or seeds are consumed from the parent plant prior to cone opening. Pre-dispersal seed predators are typically specialists, since seed production is generally clustered and predictably distributed spatially and temporally (Hulme and Benkman 2002). The majority of pre-dispersal conifer seed predators are invertebrates, particularly of the orders Coleoptera, Diptera, and Lepidoptera. Their lifecycles are timed to coincide with cone production by one or a few conifer species, with larvae typically feeding on developing cones and seeds (see reviews in Hedlin et al. 1980; Turgeon et al. 1994). Seed losses to invertebrate predation can be severe, but are generally highly variable. For example, Sweeney and Quiring (1998) reported that the spruce cone maggot (*Strobilomyia neanthracina*) destroyed 90% of white spruce (*Picea glauca*) seeds during a low cone crop, but less than 5% of seeds when cone production was high.

Vertebrates such as North American red squirrels (*Tamiasciurus hudsonicus*) and Clark’s nutcrackers (*Nucifraga columbiana*) are also important pre-dispersal seed predators, and evidence suggests that their behaviours have significantly influenced the evolution of cone morphology and seed defences in some conifers (e.g. *Pinus flexilis*, *P. glauca*; Smith 1970; Samano and Tomback 2003; Sipielski and Benkman 2008a; Fletcher et al. 2010; Archibald et al. 2012). Cone harvesting by squirrels can be particularly extensive, typically with up to 95% of available cones on an individual’s territory removed and cached (Smith 1968; Peters et al. 2003; Samano and Tomback 2003; Fletcher et al. 2010). This has major consequences for recruitment success; Sipielski and Benkman (2008b)
showed that the presence of squirrels reduced stand densities of limber pines (*P. flexilis*) and whitebark pines (*Pinus albicaulis*) by half.

### 1.2 Post-dispersal seed predation

Post-dispersal seed predators are typically generalists, as dispersed seeds are often scattered widely, and the amount and quality of seeds available after pre-dispersal predation can be highly variable (Hulme and Benkman 2002). Small mammals are the predominant post-dispersal conifer seed predators. Seeds are an integral component of the diet of many forest rodents, and a critical food source in the fall and winter, when other plant matter and invertebrates are scarce (Jameson 1952; Drożdż 1966; Abbott and Quink 1970; Whitaker 1966). Several species of mice (e.g. *Peromyscus maniculatus*, *Peromyscus leucopus*) and voles (e.g. *Myodes gapperi*) have been commonly observed destroying up to 95% of naturally- and experimentally-available seeds, including those of white pine (*P. strobus*; Abbott 1961; Abbott and Quink 1970), white spruce (Radvanyi 1970), lodgepole pine (*P. contorta*; Radvanyi 1971; Sullivan and Sullivan 1982), Douglas fir (*Pseudotsuga menziesii*; Gashwiler 1967; Sullivan 1978), and black spruce (*P. mariana*; Côté et al. 2003). The severity of seed predation by rodents in turn significantly limits the regeneration and succession of several conifer species (Radwan 1970; Pank 1974; Lindsey 1975; Duchesne et al. 2000; Côté et al. 2003). For example, Peters et al. (2004) used experimental exclosures to demonstrate that small mammals were responsible for reducing white spruce recruitment rates by 79%. Small mammals are also mainly responsible for large seed losses, and subsequent limited success, in regeneration projects involving direct seeding (Graber 1969; Radwan 1970; Radvanyi 1973; Pank 1974). Invertebrates such as ants (order Hymenoptera) and carabid beetles (order...
Coleoptera) may also be important post-dispersal seed predators in some systems, but their interactions with, and impacts on, conifers are largely unknown compared to other temperate and tropical seeds (Radwan 1970; Nystrand and Granström 2000; Ordóñez and Retana 2004; Lundgren 2009).

1.3 Differential seed predation

It is not surprising that seeds are a valuable food source to so many species, as they contain relatively large reserves of fat, protein, and carbohydrates, especially compared to other plant tissues (Marquis and Batzli 1989; Crawley 2000). However, all seeds are not of equivalent nutritional quality, and preferential consumption of higher quality seeds can have important implications for both the plant and predator populations. First, selection of specific species of seeds over common associates can dramatically alter plant community dynamics (Davidson 1993). Abbott (1962) suggested that the low palatability of fir seeds to small mammals appears to significantly influence the high ratio of fir to spruce seedlings observed in mixed coniferous forests. Similarly, experimental supplementation has shown that the presence of highly-preferred sunflower seeds can dramatically reduce predation of Douglas fir (Sullivan 1978) and lodgepole pine (Sullivan and Sullivan 1982) seeds by rodents. Second, seed production patterns of preferred seeds can regulate the habitat use and population dynamics of major seed predators (e.g. Halvorson 1982; Pucek et al. 1993; Wolff 1996; Di Pierro et al. 2011), which in turn can affect seed survival and competitive interactions among both plant and predator species (Schnurr et al. 2002). However, preferences and relative palatability among commonly-associated conifer seeds are largely unknown for many northern rodent species. Furthermore, most studies of preferential seed predation in coniferous forests
only examine one or two of the several predator species present (e.g. Abbott 1962), and none have considered interactions among both pre- and post-dispersal seed predators, thereby limiting our overall understanding of resource partitioning in this consumer-resource system.

### 1.4 Defences against seed predation

Given their high nutritional value, seeds typically receive greater investment in defences than other plant tissues (Janzen 1971). Small mammals typically select experimental foods with high energy and intermediate protein contents in preference trials in the laboratory and in the field (Vickery et al. 1994; Lewis et al. 2001), but other factors, including various defensive strategies, influence foraging on natural foods such as seeds (Grodziński and Sawicka-Kapusta 1970; Janzen 1971; Kerley and Erasmus 1991).

Conifers utilize several mechanisms to limit predation of seeds after dispersal. First, some seeds, such as those of several fir species, contain high concentrations of plant secondary compounds (PSCs) that act as a significant feeding deterrent (Abbott 1962; Drożdż 1966, Smith 1970; Rubino et al. 2012; Lobo unpublished data). Tannins are mainly responsible for feeding deterrence in acorns (Quercus spp.; Smallwood et al. 2001; Shimada and Saitoh 2003), while monoterpenes may be most important in conifer seeds (Rubino et al. 2012; Lobo unpublished data). However, the PSC profiles of conifer seeds are largely unknown, especially compared to acorns and other deciduous seeds. Both pre- and post-dispersal predators typically avoid consuming conifer seeds containing high concentrations of PSCs if other food options are available (Abbott 1962; Di Pierro et al. 2011). Even small amounts of PSCs can reduce protein digestibility, cause weight loss,
inhibit growth, damage the liver, kidneys and gastrointestinal system, and shorten life span (Freeland and Janzen 1974; Freeland et al. 1984; Lindroth and Batzli 1984; Dietz et al. 1994; Shimada and Saitoh 2003). While rodents preferentially cache some PSC-rich acorns for winter use (Shimada 2001; Smallwood et al. 2001; Xiao et al. 2008), this does not occur with all types of seeds (Hadj-Chikh et al. 1996; Xiao et al. 2006). Similarly, Di Pierro et al. (2011) showed that European red squirrels (Sciurus vulgaris) alter their habitat use with the availability of highly-palatable Norway spruce (Picea abies) seeds, but ignore the production of silver fir (Abies alba) seeds, which contain high amounts of monoterpenes (Rubino et al. 2012).

Second, physical characteristics of seeds can affect their risk of predation. Seed size generally acts as a proxy for nutrient content, and larger seeds tend to be preferentially consumed and/or cached by rodents (Hulme 1998; Wang and Chen 2009; Vander Wall 2010). However, the increased handling time associated with large seeds can be a deterrent to small mammals (Kerley and Erasmus 1991), and the relative importance of seed size and internal seed chemistry in influencing conifer seed predation by rodents is unknown. The significance of indigestible fibres in deciduous seeds as an anti-feedant has recently received some attention in the literature (e.g. Chen et al. 2012), but this requires further examination in conifer seeds, which can also markedly differ in fibre content (Lobo and Millar 2011/Chapter 3).

Finally, high interannual variability in the amount of seeds produced plays an important role in regulating losses to predators. Many deciduous (e.g. Quercus spp., Fagus spp.), tropical (e.g. Dipterocarpaceae), and coniferous (e.g. P. glauca, Abies lasiocarpa) species utilize mast seeding, defined as the intermittent, synchronous production of large seed
crops by most reproductive adults in a plant population (Silvertown 1980; Kelly 1994; Ostfeld and Keesing 2000). The periodic production of large seed crops satiates predators and allows a greater proportion of seeds to escape consumption, thereby enhancing the reproductive success of individual plants (Janzen 1971; Silvertown 1980; Kelly 1994; Kelly and Sork 2002; Fletcher et al. 2010).

Large fluctuations in seed production can also affect populations of post-dispersal seed predators such as small mammals. Spring and summer densities of several species of mice and voles peak following fall masting in deciduous forests, while low food supply during the interval between mast years results in low rodent density during the next masting event, allowing greater escape from seed predation (Jensen 1982; Pucek et al. 1993; Kelly 1994; Wolff 1996; Ostfeld and Keesing 2000; Falls et al. 2007). However, the effects of conifer mast seeding on rodent populations are more complex, and largely inconsistent. Gashwiler (1979) found that conifer masting resulted in a delayed increase in rodent populations, but other studies have observed inconsistent population peaks (Jameson 1953; Elias et al. 2006), population declines (Stickel and Warbach 1960), or no population response (McCracken et al. 1999; Schnurr et al. 2002; Boonstra and Krebs 2006) in relation to heavy seed crops. Given the importance of rodents as conifer seed predators and the significance of their population fluctuations for structuring bird and insect community dynamics (Elkinton et al. 1996; McShea 2000; Ostfeld and Keesing 2000), long-term datasets on annual conifer seed production and intensive rodent trapping can provide valuable insights into the patterns and mechanisms of this important interaction in forest ecosystems.
Mast seeding may also facilitate seed caching by rodents (e.g. Jansen et al. 2004), which can ultimately reduce predation rates and enhance the recruitment of conifer seeds (Vander Wall 1992). However, Abbott and Quink (1970) found that the majority of white pine seeds in caches are typically harvested by rodents prior to germination, although they speculated that seed caches in a mast year may exceed energy requirements, leaving a surplus that enhances forest regeneration.

1.5 Combating seed defences

Just as plants have evolved defences to limit seed predation, seed predators employ numerous behavioural, morphological, biochemical, and population-level adaptations to combat plant defences. These mechanisms are well-studied in herbivores (see reviews in Freeland and Janzen 1974; Dearing et al. 2005), and have received some attention in granivores in deciduous forests (e.g. Shimada and Saitoh 2003), but have been poorly studied in conifer seed predators. Seeds containing high fibre and PSC contents are of relatively low nutritional value; however, highly granivorous small mammals may still be able to use them as a major food source by increasing their seed intake and the size of their gut and vital organs in order to compensate for the low quality diet and facilitate efficient degradation and assimilation (Green and Millar 1987; Harju and Tahvanainen 1994; del Valle et al. 2006). Reducing the meal size and increasing the interval between meals may also be a useful strategy for rodents consuming these seeds as a supplemental part of their diet when other food resources are scarce (Shimada and Saitoh 2003; Torregrossa et al. 2011). However, these mechanisms require experimental testing in conifer-rodent interactions. Furthermore, research on the use of PSC-rich plants by the
generalist herbivore *Neotoma albigula* indicates that water consumption may also be key to mitigate the negative effects of PSCs on body condition (Torregrossa et al. 2011).

Physiological and biochemical detoxification mechanisms are prevalent in small mammals, and likely play a major role in their foraging interactions with conifer seeds. The induction of salivary proline-rich proteins and tannase-producing bacteria permit Japanese wood mice (*Apodemus speciosus*) to consume acorns containing high PSC concentrations (Shimada and Saitoh 2003; Shimada et al. 2006). Similar mechanisms may exist in deer mice (*P. maniculatus*) and white-footed mice (*P. leucopus*) feeding on northern conifer seeds. Similarly, digestive and detoxification enzymes in the small intestine, caecum, and liver may help combat the physical and chemical defences of conifer seeds (Freeland and Janzen 1974; Harju and Tahvanainen 1994; del Valle et al. 2006), but these processes require further testing in this system.

On a population-scale, the function of masting as a swamp-and-starve adaptation against seed predation has been circumvented by several pre-dispersal seed predators. There are reports of numerous insects using environmental cues allowing them to emerge in synchrony with *Chionochola* masting events (McKone et al. 2001). Similarly, prolonged diapause of acorn-feeding weevils (*Curcuilo* spp.) can reduce the efficacy of predator satiation by synchronizing their life-cycle with periodic mast seeding by oaks (Maeto and Ozaki 2003). In coniferous forests, North American and European red squirrels are able to anticipate heavy spruce cone crops and increase breeding before a masting event, thereby increasing the number of juveniles and overall population size to coincide with high cone production (Boutin et al. 2006).
Among vertebrate post-dispersal seed predators in deciduous forests, deer mice (Falls et al. 2007) and eastern chipmunks (Tamias striatus; Bergeron et al. 2011) in southeastern Canada increase reproductive activity and juvenile production in anticipation of masting by sugar maple (Acer saccharum) and American beech (F. grandifolia) trees, respectively. Similarly, edible dormice (Glis glis) use an unknown cue to breed only in the spring prior to European beech (F. sylvatica) mast seeding (Ruf et al. 2006). However, these are the only examples of anticipatory responses by rodents to deciduous mast seeding, while there are numerous examples of the traditional lagged population response to this resource pulse described earlier (e.g. Jensen 1982; Pucek et al. 1993; Kelly 1994; Wolff 1996; Ostfeld and Keesing 2000; Falls et al. 2007). There is also no evidence that vertebrate post-dispersal seed predators are able to anticipate and adapt to future seed availability in coniferous forests. However, an increased number of conifer seeds would likely be cached during mast years, potentially providing a fall and winter food supply sufficient to exceed the energy requirements of small mammals (Abbott and Quink 1970)

1.6 Limitations in the conifer literature

The sections above demonstrate that there is a considerable body of literature regarding plant defences and seed predation by small mammals. However, with relatively few exceptions, most previous research has focused on herbivores and granivores in tropical and deciduous forests. As previously mentioned, most studies on conifer-rodent interactions have examined the effects of rodents on the survival and recruitment of conifer seeds; little is known about the effects of seed production by various conifer species on foraging by individual rodents, as well as their populations. The effect of
conifer mast seeding on the pre-dispersal foraging and population ecology of red squirrels have recently been well-documented (Boutin et al. 2006; Fletcher et al. 2010; Archibald et al. 2012), but small mammals have received considerably less attention. Given the importance of both conifers and small mammals in forest ecosystems, it is important to have a comprehensive understanding of this complex interaction.

Although there is little published research on the effects of conifer seed abundance and quality on northern rodents, the wealth of relevant literature on the foraging and population dynamics of herbivorous and granivorous rodents in other ecosystems provided a sound foundation for making predictions in my experimental and observational studies. The continuing themes in my approach to addressing the key questions in my dissertation were to utilize the relevant literature on small mammals in tropical and deciduous forests, and to design laboratory and field experiments that would elucidate the underlying mechanisms of large-scale observations.

1.7 Major study species

All data collection for my dissertation was conducted in the Kananaskis Valley in southwestern Alberta, Canada. The Kananaskis Valley is a 4200-km² montane/subalpine multi-use recreation area located in the front ranges of the Canadian Rocky Mountains. The main tree species are white spruce, subalpine fir, and lodgepole pine. Small mammal interactions with white spruce seeds are examined in each data chapter (Chapters 2-6) of this dissertation, while interactions with subalpine fir and lodgepole pine seeds are also examined in Chapters 2-5 and Chapters 2-3, respectively. White spruce and subalpine fir are masting species (Alexander et al. 1990; Nienstaedt and Zasada 1990), while
lodgepole pine produces consistent annual seed crops, but in predominately serotinous cones (Lotan and Critchfield 1990). Spruce and fir seeds mature in late-summer, and are released when cones open in the fall (Alexander et al. 1990; Nienstaedt and Zasada 1990). Fir seeds also contain very high concentrations of PSCs, while pine and spruce invest few resources into chemical defences in seeds (Rubino et al. 2012; Lobo unpublished data).

The most abundant rodent species in the study area is the deer mouse, but southern red-backed voles (*M. gapperi*) are also common in densely-forested areas (Millar et al. 1985); the interactions of these species with conifer seeds are the main foci of this dissertation. Chapters 2-4 investigate the foraging dynamics of deer mice and red-backed voles, while Chapters 5-6 examine the population fluctuations of deer mice exclusively. Deer mice are omnivorous, and seeds are a significant component of their diet during most of the year (Jameson 1952; Martell and Macaulay 1981). On the other hand, the diet of red-backed voles consists mainly of lichens, fungi, and non-seed plant matter, and they are only partially granivorous (Maser et al. 1978; Martell 1981). Deer mouse populations in the Kananaskis Valley show annual cycles, where densities increase over the summer breeding season, and decline through the fall and winter (Millar and McAdam 2001). Breeding is highly seasonal and constrained, and generation time and longevity are enhanced compared to populations in more temperate environments (Millar and McAdam 2001). Less is known about the population dynamics of red-backed voles in our study area, but low densities, a constrained breeding season, and poor overwinter survival are characteristic of North American populations (Boonstra and Krebs 2012).
Additional specific details on conifer seed production and nutritional characteristics, as well as rodent food habits and population demography are provided in the relevant chapters of this dissertation.

### 1.8 Dissertation structure

The five data chapters in my dissertation were conceived and prepared as separate research projects, each intended for independent publication and united by the common theme of investigating the interactions between conifer seeds and the nutritional and population ecology of small mammals. As such, there is some degree of repetition in parts of the introduction and methods sections. These have been kept to a minimum, but have been retained in order to allow each chapter to stand as an independent manuscript. Chapters 2 and 3 have been published, Chapter 4 is currently under review for publication, and a combined version of Chapters 5 and 6 is *in press*.

In Chapter 2, I investigated the preferences of five species of small mammals (the deer mouse, red-backed vole, heather vole (*Phenacomys intermedius*), long-tailed vole (*Microtus longicaudus*), and meadow vole (*Microtus pennsylvanicus*) for white spruce, subalpine fir, and lodgepole pine seeds. Previous research has examined the diets of these rodents to varying degrees, but little is known about their granivorous food habits in relation to conifer seeds. Given that these conifers are common associates in western Canada, and that small mammals are major post-dispersal seed predators, determining their seed preferences has important implications for understanding how they partition resources in nature, as well as how differential seed predation may influence plant
regeneration and community dynamics. This study was conducted using cafeteria-style feeding experiments, both in the laboratory and in the field.

In Chapter 3, I examined the efficacy of white spruce, subalpine fir, and lodgepole pine seeds as major food resources to deer mice and red-backed voles. While it has been shown that conifer seeds are a component of the diet of many rodents, it is not known whether these seeds can be used as a major food source, depending on their nutritional value and PSC contents. Investigating this is critical to understanding whether, and how, different rodents can utilize large quantities of specific conifer seeds; this is one of the key mechanisms underlying their population interactions with seed production by coniferous trees. I examined the nutritional quality of these seeds, as well as the effects of restricted seed-diets on the survival, body condition, food consumption patterns, and gut morphology of rodents in the laboratory.

In Chapter 4, I investigated the effects of conifer seed quality and abundance on the foraging behaviour of deer mice and red-backed voles. The decision to consume or cache seeds when they are encountered can be influenced by numerous factors such as their abundance, nutritional value, and PSC contents. While low quality conifer seeds are avoided by rodents in the laboratory when other food options are available, they may be preferentially cached in the field when abundant for future use during unpredictable times. I used artificial food patches in the field to experimentally examine the foraging behaviours of rodents in response to varying abundances of white spruce and subalpine fir seeds. I also used a standardized variant of giving-up densities to assess rodents’ perception of the quality of seeds in patches, as well as the lower threshold density at which they cease active foraging for each seed species. Further, these measures allowed
me to examine two key assumptions underlying the hypothesis that rodent populations respond to fall mast seeding by conifer trees: (1) the seeds are cached for use in the fall and winter; and (2) a sufficient quantity of seeds are released during a masting event to effectively enhance the food supply to the population.

In Chapter 5, I investigated the effects of variable conifer seed production on deer mouse populations. While the relationship between rodent populations and mast seeding is clear and well-documented in deciduous forests, there is little evidence in the literature of consistent effects of fall conifer masting on rodent populations. Based on my knowledge of interactions between conifer seeds and individual mice from Chapter 2-4, I hypothesized that there would be a positive relationship between mouse populations and white spruce seed production, but no effect of subalpine fir masting. I tested this hypothesis by examining the population, breeding, and body mass dynamics of a deer mouse population in relation to white spruce and subalpine fir seed production over a 10-year period.

Finally, in Chapter 6, I investigated the effects of natural food supplementation on deer mouse demography. Based on my knowledge of interactions between conifer seeds and deer mice, both at an individual- and population-level, from Chapters 2-5, I supplemented a long-term deer mouse population monitoring grid with an excess of white spruce seeds in order to test the hypothesis that increased seed availability to mice during the fall would lead to enhanced survival and breeding. This population was compared to a control population from a nearby long-term monitoring grid for several years prior to, and one year after, supplementation in order to determine the effect of increased fall spruce seed availability on the population, breeding, and body mass dynamics of deer mice.
1.9 References


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Chapter 2

2 Conifer-seed preferences of small mammals

2.1 Introduction

Seed predation by small mammals destroys a significant proportion of the annual seed crop of forest trees, and has substantial negative effects on the regeneration of coniferous forests (Abbott 1961; Abbott and Quink 1970; Pank 1974; Sullivan and Sullivan 1982; Gurnell 1993; Côté et al. 2003). In a study on white spruce (Picea glauca) regeneration in Alberta, Radvanyi (1970) found that small mammals consumed 20%-50% of randomly distributed seeds. Peters et al. (2004), using experimental exclosures, demonstrated that small mammals were mainly responsible for reducing white spruce recruitment rates by 79% between the seed rain period in the fall and the following summer. Similarly, the consumption of lodgepole pine (Pinus contorta) seeds by rodents can affect the regeneration of the species (Lindsey 1975); Radvanyi (1971) found small mammals to be responsible for the removal of 21%-33% of lodgepole pine seeds over one summer, and Sullivan and Sullivan (1982) reported that small mammals harvest greater than 85% of lodgepole pine seeds in less than 3 weeks. Abbott (1961) also found that small mammals consumed large amounts of white pine (Pinus strobus) seeds. Seed predation by small

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1 A version of this chapter has been published and is presented here with permission from NRC Research Press.

mammals is believed to be a critical factor in white pine succession in mixed forests (Duchesne et al. 2000).

Preferential consumption of seeds by rodents can dramatically alter overall plant-community structure (Abbott 1962; Davidson 1993). Field and laboratory studies have shown that deer mice (*Peromyscus maniculatus*) consume 10 times more white pine seeds than balsam fir (*Abies balsamea*), and show a strong preference for seeds of white pine over black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Martell 1979; Duchesne et al. 2000). Similarly, white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*) prefer white pine and red pine (*Pinus resinosa*) seeds over white spruce and balsam fir seeds (Abbott 1962). Southern red-backed voles (*Myodes gapperi*) consumed more red spruce (*Picea rubens*) seeds than white pine and balsam fir seeds in laboratory trials (Abbott 1962), and more white pine than black spruce and jack pine seeds (Martell 1979). Differences in seed preference can cause differential effects of species-specific seed production on the abundance of various small mammal populations, which in turn affects seed survival and competitive interactions among species (Schnurr et al. 2002). Determining which seeds rodents prefer is a necessary first step to understanding how rodents partition resources in nature, because many species can occupy similar habitats (see Millar et al. 1985).

The objective of this study was to examine conifer-seed selection by small mammals in the Kananaskis Valley, Alberta (the deer mouse, southern red-backed vole, heather vole (*Phenacomys intermedius*), long-tailed vole (*Microtus longicaudus*), and meadow vole) using cafeteria-style feeding experiments in the laboratory, as well as seed selection by deer mice and red-backed voles in the field. We expected to see distinct preferences
among different types of seeds within each species. The use of captive-animal studies is ideal for quantifying food preferences because natural constraints, such as competition and food availability, abundance, and distribution, are avoided (Molloy and Hart 2002). There have been very few cafeteria-style feeding experiments, which control the abundance and availability of different types of foods, to test conifer seed preferences of small mammals (see Abbott 1962; Martell 1979). Foods eaten by *P. maniculatus* (Jameson 1952; Martell and Macaulay 1981; Gagné et al. 1999), *M. gapperi* (Merritt and Merritt 1978; Martell 1981; Norrie and Millar 1990; Gagné et al. 1999; Kasparian and Millar 2004), and *M. pennsylvanicus* (Thompson 1965; Lindroth and Batzli 1984; Norrie and Millar 1990) have been well documented, and the food habits of *P. intermedius* (Nagorsen 1987; Côté et al. 2003) and *M. longicaudus* (Van Horne 1982; Norrie and Millar 1990) have received some attention, but conifer-seed preferences among these small mammal species are relatively unknown. Preferences among lodgepole pine, white spruce, and subalpine fir (*Abies lasiocarpa*) seeds were examined in this study because they are the dominant conifer species in the study area.

## 2.2 Methods

### 2.2.1 Laboratory seed selection trials

Animals were live-trapped in the Kananaskis Valley (51°02′N, 115°03′W), Alberta, from May to September of 2006 and 2007. At capture, individuals were weighed (±0.5 g) using a 60 g Pesola spring balance, age was determined based on size and dorsal pelage colour, and breeding condition was recorded. Males were classified as scrotal (testes descended) or non-scrotal, and females as non-perforate, perforate, pregnant (as determined by body mass and swelling of the abdomen), and/or lactating (nipples
enlarged and prominent). Juveniles and pregnant and lactating females were not used for this study, and released upon capture. All other individuals (P. maniculatus, n = 10; M. gapperi, n = 10; P. intermedius, n = 8; M. longicaudus, n = 6; M. pennsylvanicus, n = 13) were transported to the laboratory at the Biogeoscience Institute of the Canadian Rockies and Foothills (University of Calgary) and held in plastic cages (0.29 m × 0.18 m × 0.12 m) containing cotton bedding, aspen chips, plastic tubing, and provided with sunflower seeds, oats, rodent chow (LabDiet 5001 Rodent Diet; PMI Nutrition International, St. Louis, Missouri), and water ad libitum. They were also provided twice daily with natural forage found at trapping sites known to be palatable to voles (Norrie and Millar 1990), including grass, dandelion (Taraxacum officinale), and willow (genus Salix). The daily photoperiod in the laboratory was 16 h light : 8 h dark, and temperature was maintained at 20 °C.

Animals were acclimated in the laboratory for three or more days before being transferred to indoor Plexiglas® experimental enclosures (0.8 m × 0.4 m × 0.6 m) containing cotton bedding, aspen chips, plastic tubing, and a 600 mL food-storage container (12 cm × 12 cm) containing a thin layer of white horticultural sand. Food-storage containers were modified by cutting large holes in two opposing sides, allowing animals to enter and exit freely. Rodent chow and water were provided ad libitum and fresh natural forage was provided twice daily. Individuals were acclimated to their enclosures for two days and weighed (±0.01 g) using an electronic balance at the beginning and end of the acclimation period.

Food selection trials were conducted for three days using lodgepole pine, white spruce, and subalpine fir seeds acquired from the Alberta Tree Improvement and Seed Centre.
(Smoky Lake, Alberta) and the British Columbia Ministry of Forests and Range Tree Seed Centre (Surrey, British Columbia). On the first day of trials, 2.25 g of each species of seed (2.25 g of seed was established as 20% excess of what is normally consumed in a 24 h period in preliminary trials) were weighed (±0.01 g) on an electronic balance, mixed with white horticultural sand, and placed in a modified food-storage container. This replaced the food-storage container holding plain sand in the enclosure during acclimation. Rodents dig up seeds when foraging, so sand was used to simulate natural foraging conditions. At 24 h intervals, all seeds were removed from the enclosure (including husks and seeds in the bedding) and each food-storage container was replaced with one containing new seeds. Sand, husks, and other waste materials were separated from the remaining intact seeds, which were then dried, separated by species, and weighed. The mass of consumed seeds was determined by subtraction of the remaining intact seed mass from the initial mass provided. Individuals were weighed at the end of the third day of feeding trials and were released at their original capture site.

2.2.2 Field seed selection
Seed preferences of *P. maniculatus* (*n* = 15) and *M. gapperi* (*n* = 13) were tested in the field from June to August of 2008. Longworth live traps were cleaned, supplied with fresh bedding, and baited with 2.25 ± 0.01 g each of lodgepole pine, white spruce, and subalpine fir seeds. Traps were set at 18:00 and checked the following morning at 07:00. Seeds from traps containing animals were removed, dried, and weighed, and consumption of each species of seed was calculated. Animals were marked with ear tags, weighed, and breeding condition was assessed prior to their release at the site of capture. Seed consumption was averaged for individuals caught more than once.
Rodent capture and handling protocols followed guidelines of the Canadian Council on Animal Care (1993) and the Alberta Wildlife Animal Care Committee Class Protocol No. 007 (Small Mammal Handling and Trapping), and were approved by the University of Western Ontario Animal Use Subcommittee.

2.2.3 Statistical analyses

Prior to analysis, all body mass and seed consumption data were screened for errors, missing values, and outliers, with none found. Checks were also made for normality and multivariate outliers, with none being found. All analyses were performed using SPSS version 16.0 (SPSS Inc. 2007). Differences among groups were considered statistically significant at \( p \leq 0.05 \). Data are presented as means ± SE.

2.2.3.1 Laboratory seed selection trials

We tested each small mammal species for changes in body mass over the acclimation and trial periods using ANOVAs. Each small mammal species was individually tested for differences in seed consumption (total daily mass of seeds consumed and masses of each species of seed consumed) among trial days using MANOVAs, followed by ANOVAs and Tukey’s HSD tests, where appropriate. Recorded body masses and masses of seeds consumed during each of the three trial days were averaged for each individual, and these mean values were used in subsequent statistical tests. Pearson’s correlation coefficients were used to examine the relationship between body mass and seed consumption (total daily mass of seeds consumed, and masses of each species of seed consumed) for each small mammal species.
We used direct discriminant function analysis (DFA) to test for differences in seed consumption among the small mammal species, and whether there was a preference among lodgepole pine, white spruce, and subalpine fir seeds within each small mammal species. We included all predictor variables in our interpretation of each discriminant function, and subsequently analyzed predictors using ANOVAs and Tukey’s HSD tests, where appropriate, to further identify differences among groups.

2.2.3.2 **Field food selection**

Pearson’s correlation coefficients were used to examine the relationship between body mass and seed consumption (total daily mass of seeds consumed, and masses of each species of seed consumed). We tested each species for differences in consumption of types of seeds using ANOVAs and Tukey’s HSD tests, where appropriate. Differences in seed consumption between laboratory and field experiments were tested using MANOVAs for each small mammal species.

2.3 **Results**

2.3.1 **Laboratory seed selection trials**

There were no significant changes in body mass over the acclimation and trial periods in any of the species (all $p > 0.60$). For all species, total mass of seeds consumed (-0.53 < $r$ < 0.71, all $p > 0.11$) and masses of lodgepole pine (-0.47 < $r$ < 0.68, all $p > 0.13$), white spruce (-0.51 < $r$ < 0.76, all $p > 0.08$), and subalpine fir (-0.61 < $r$ < 0.63, all $p > 0.06$) seeds consumed were not significantly correlated with body mass. *Myodes gapperi* showed a difference in seed consumption among trial days (Wilks’ $\lambda = 0.56$, $F_{6,50} = 2.85$, $p = 0.02$), specifically the amount of subalpine fir seeds consumed ($F_{2,27} = 7.16$, $p =$...
0.003); more subalpine fir seeds were consumed on the first trial day (0.10 ± 0.03 g) than the second (0.02 ± 0.01 g; \( p = 0.01 \)) and third (0.02 ± 0.01 g; \( p = 0.01 \)) days. All other species showed no difference in seed consumption among trial days (all \( p > 0.15 \)). No species of seed was consumed solely on any day and no diet was completely depleted over the course of the trials. *Microtus longicaudus* and *P. intermedius* consumed whole seeds during trials, while *P. maniculatus*, *M. gapperi*, and *M. pennsylvanicus*, chewed apart the seed coat and only consumed the endosperm and embryo (also see Radvanyi 1971).

Differences in seed consumption by the small mammal species were detected by the DFA (\( \chi^2_{12} = 36.93, p < 0.001 \); Figure 2.1). After removal of the first function, association using the second function was also significant (\( \chi^2_{6} = 13.24, p = 0.04 \)). The first and second discriminant functions accounted for 68% and 27% of the variation in discriminating among groups, respectively. Association using the third function was not significant (\( \chi^2_{2} = 2.10, p = 0.35 \)), and was not included in the final analysis.

The first discriminant function (root 1) separated small mammal species by total daily mass of seeds consumed (\( F_{4,42} = 7.69, p < 0.001 \); Figure 2.1), driven by deviances from *P. intermedius*, and reflected the relative avoidance of subalpine fir seeds (Table 2.1). Total daily seed consumption of *P. intermedius* was less than *P. maniculatus* (\( p < 0.001 \)), *M. gapperi* (\( p = 0.02 \)), and *M. pennsylvanicus* (\( p = 0.001 \)), but did not significantly differ from *M. longicaudus* (\( p = 0.20 \); Figure 2.2). Differences in total daily seed consumption among the other species were not significant (all \( p > 0.09 \)). All species other than *P. intermedius* (\( F_{2,21} = 1.61, p = 0.22 \); Figure 2.3) also showed differences in consumption of the different species of seeds (all \( p < 0.01 \); Figure 2.3). *Peromyscus maniculatus* (all \( p \)
< 0.001) and *M. pennsylvanicus* (all *p* < 0.04) preferred lodgepole pine and white spruce seeds over subalpine fir seeds, while *M. gapperi* and *M. longicaudus* showed a preference for lodgepole pine seeds over subalpine fir seeds (both *p* ≤ 0.01), but no difference between white spruce and subalpine fir seed consumption (both *p* ≥ 0.27).

The second discriminant function (root 2) showed that lodgepole pine seeds were preferred over white spruce seeds (Table 2.1), and separated small mammal species by their relative preference for lodgepole pine seeds compared to white spruce seeds (*F*<sub>4,42</sub> = 2.99, *p* = 0.03; Figure 2.1). *Peromyscus maniculatus, M. gapperi,* and *M. pennsylvanicus* consumed more lodgepole pine seeds than white spruce seeds (all *p* ≤ 0.003), while *M. longicaudus* showed no significant difference between consumption of lodgepole pine and white spruce seeds (*p* = 0.06; Figure 2.3). *Myodes gapperi* and *M. pennsylvanicus* also showed a greater difference between masses of lodgepole pine and white spruce seeds consumed (mass of lodgepole pine seeds consumed – mass of white spruce seeds consumed) than *P. intermedius* (both *p* ≤ 0.05; Figure 2.4). There was no difference in the relative consumption of lodgepole pine and white spruce seeds among the other species (all *p* > 0.10). There was also no difference in the mass of subalpine fir seeds consumed among the species (*F*<sub>4,42</sub> = 1.54, *p* = 0.21).

The DFA correctly classified 60% of *P. maniculatus*, 40% of *M. gapperi*, 88% of *P. intermedius*, 33% of *M. longicaudus*, and 15% of *M. pennsylvanicus* based on the seed consumption of individuals of each species. For detailed predicted classifications of each species see Table 2.2.
Figure 2.1. Discriminant function scores derived from consumption of lodgepole pine (Pinus contorta), white spruce (Picea glauca), and subalpine fir (Abies lasiocarpa) seeds in laboratory cafeteria-style feeding experiments differentiating deer mice (Peromyscus maniculatus; open circles), southern red-backed voles (Myodes gapperi; shaded circles), heather voles (Phenacomys intermedius; open diamonds), long-tailed voles (Microtus longicaudus; shaded diamonds), and meadow voles (Microtus pennsylvanicus; open triangles). Small symbols represent individual scores and large symbols indicate centroids.
Table 2.1. Results of discriminant function analysis of consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds by deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), heather voles (*Phenacomys intermedius*), long-tailed voles (*Microtus longicaudus*), and meadow voles (*Microtus pennsylvanicus*) in laboratory cafeteria-style feeding experiments, showing pooled within-group correlations of canonical roots, standardized canonical discriminant function coefficients, and significance level of variables contributing to the discriminant function.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Correlation of predictor variables with discriminant functions</th>
<th>Standardized canonical discriminant function coefficients</th>
<th>$F_{4,42}$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass of lodgepole pine seeds consumed</td>
<td>0.88 0.43</td>
<td>0.53 1.04</td>
<td>6.78</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Mass of white spruce seeds consumed</td>
<td>0.86 -0.23</td>
<td>0.73 -1.46</td>
<td>6.12</td>
<td>0.001</td>
</tr>
<tr>
<td>Mass of subalpine fir seeds consumed</td>
<td>0.34 0.23</td>
<td>-0.25 0.97</td>
<td>1.54</td>
<td>0.21</td>
</tr>
</tbody>
</table>
**Figure 2.2.** Total daily seed consumption by deer mice (*Peromyscus maniculatus* (Pm); *n* = 10), southern red-backed voles (*Myodes gapperi* (Mg); *n* = 10), heather voles (*Phenacomys intermedius* (Pi); *n* = 8), long-tailed voles (*Microtus longicaudus* (Ml); *n* = 6), and meadow voles (*Microtus pennsylvanicus* (Mp); *n* = 13) in laboratory cafeteria-style feeding experiments. Groups with different letters were significantly different from one another based on Tukey’s HSD test (*p* < 0.05). Bars represent means ± SE.
Figure 2.3. Consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds by deer mice (*Peromyscus maniculatus* (Pm); *n* = 10), southern red-backed voles (*Myodes gapperi* (Mg); *n* = 10), heather voles (*Phenacomys intermedius* (Pi); *n* = 8), long-tailed voles (*Microtus longicaudus* (Ml); *n* = 6), and meadow voles (*Microtus pennsylvanicus* (Mp); *n* = 13) in laboratory cafeteria-style feeding experiments. Within each species, groups with different letters were significantly different from one another based on Tukey’s HSD test (*p* < 0.05). Bars represent means ± SE.
Figure 2.4. Difference between masses of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) seeds consumed by deer mice (*Peromyscus maniculatus* (Pm); \( n = 10 \)), southern red-backed voles (*Myodes gapperi* (Mg); \( n = 10 \)), heather voles (*Phenacomys intermedius* (Pi); \( n = 8 \)), long-tailed voles (*Microtus longicaudus* (Ml); \( n = 6 \)), and meadow voles (*Microtus pennsylvanicus* (Mp); \( n = 13 \)) in laboratory cafeteria-style feeding experiments. Groups with different letters were significantly different from one another based on Tukey’s HSD test \( (p < 0.05) \). Bars represent means ± SE.
Table 2.2. Classification of deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), heather voles (*Phenacomys intermedius*), long-tailed voles (*Microtus longicaudus*), and meadow voles (*Microtus pennsylvaniaicus*) based on discriminant function analysis of their consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds in laboratory cafeteria-style feeding experiments.

<table>
<thead>
<tr>
<th>Actual Species</th>
<th>Predicted Group Membership (%)</th>
<th>Peromyscus maniculatus</th>
<th>Myodes gapperi</th>
<th>Phenacomys intermedius</th>
<th>Microtus longicaudus</th>
<th>Microtus pennsylvaniaicus</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Peromyscus maniculatus</em></td>
<td>60</td>
<td>20</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td><em>Myodes gapperi</em></td>
<td>10</td>
<td>40</td>
<td>30</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td><em>Phenacomys intermedius</em></td>
<td>0</td>
<td>0</td>
<td>88</td>
<td>12</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Microtus longicaudus</em></td>
<td>0</td>
<td>0</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td><em>Microtus pennsylvaniaicus</em></td>
<td>39</td>
<td>8</td>
<td>15</td>
<td>23</td>
<td>15</td>
<td></td>
</tr>
</tbody>
</table>
2.3.2 Field seed selection

Both *P. maniculatus* \((F_{2,42} = 94.62, p < 0.001)\) and *M. gapperi* \((F_{2,36} = 17.81, p < 0.001)\) showed preferences among conifer seeds in the field (Figure 2.5); both species showed the greatest preference for lodgepole pine seeds (*P. maniculatus*, all \(p < 0.001\); *M. gapperi*, all \(p < 0.02\)), and consumed more white spruce seeds than subalpine fir seeds (*P. maniculatus*, \(p < 0.001\); *M. gapperi*, \(p = 0.01\)). One *P. maniculatus* individual was trapped four times and two individuals were trapped twice during the study; all other *P. maniculatus* individuals and all *M. gapperi* individuals were only trapped once during the study. Total mass of seeds consumed (*P. maniculatus*: \(r = 0.04, p = 0.88\); *M. gapperi*: \(r = 0.42, p = 0.16\)) and masses of lodgepole pine (*P. maniculatus*: \(r = -0.25, p = 0.36\); *M. gapperi*: \(r = 0.48, p = 0.09\)), white spruce (*P. maniculatus*: \(r = 0.27, p = 0.32\); *M. gapperi*: \(r = 0.20, p = 0.52\)), and subalpine fir (*P. maniculatus*: \(r = -0.22, p = 0.44\); *M. gapperi*: \(r = -0.03, p = 0.93\)) seeds consumed were not significantly correlated with body mass. There was no difference between laboratory and field trials in total daily seed consumption (*P. maniculatus*: \(F_{1,23} = 0.59, p = 0.45\); *M. gapperi*: \(F_{1,21} = 0.22, p = 0.64\)), or masses of lodgepole pine, white spruce, and subalpine fir seeds consumed (*P. maniculatus*: Wilks’ \(\lambda = 0.83, F_{3,21} = 1.39, p = 0.27\); *M. gapperi*: Wilks’ \(\lambda = 0.81, F_{3,19} = 1.45, p = 0.26\)).
Figure 2.5. Consumption of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds by deer mice (*Peromyscus maniculatus* (Pm); *n* = 15) and southern red-backed voles (*Myodes gapperi* (Mg); *n* = 13) in the field. Within each species, groups with different letters were significantly different from one another based on Tukey’s HSD test (*p* < 0.05). Bars represent means ± SE.
2.4 Discussion

There were similar patterns of seed preference in most of the small mammal species in this study. Most species showed a distinct preference for lodgepole pine seeds, intermediate consumption of white spruce seeds, and avoidance of subalpine fir seeds. Many individuals did not consume even a single subalpine fir seed during trials. Most small mammal species also consumed the different species of seeds in relatively similar proportions. *Phenacomys intermedius* behaved very differently in that it consumed very few seeds in total. Most *P. intermedius* individuals were correctly classified by the DFA, demonstrating the disparity in their seed consumption behaviour from the other small mammal species. The inaccurate classification of a large percentage of *P. maniculatus*, *M. gapperi*, *M. longicaudus*, and *M. pennsylvanicus* individuals is based on low discrimination of their seed consumption patterns, and further demonstrates the high degree of similarity in their seed consumption behaviour.

The excess amounts of seeds provided, the availability of other palatable food sources and the maintenance of body mass by all species indicated that individuals were not forced to consume seeds in the laboratory trials, but were instead selecting them. Seed selection was partial rather than absolute, which is consistent with previous studies testing all-or-nothing optimal diet strategies (Vickery 1984; Krebs and Kacelnik 1991). This sampling behaviour is believed to benefit rodents, especially with novel foods, by allowing them to assess the nutritional value of each food-type available to them (Vickery 1984). While most species did not differentially consume seeds over the three
trial days, *M. gapperi* sampled the subalpine fir seeds on the first trial day, and subsequently avoided them for the remainder of the study.

Côté et al. (2003) showed that the main food items of *P. intermedius* are berries and leaves from vascular plants, and that *P. intermedius* consume a very small percentage of seeds available to them. Although the difference in total daily seed consumption between *P. intermedius* and *M. longicaudus* was not statistically significant, *M. longicaudus* consumed over 6.5 times more seeds than *P. intermedius*; we believe this marked difference is biologically relevant. *Microtus longicaudus* are not very abundant in the Kananaskis Valley (Millar et al. 1985) and are rarely found in dense populations (Van Horne 1982), making them difficult to trap. A larger sample size of *M. longicaudus* could further discriminate seed-consumption patterns in this species. Low overall seed consumption also explains why *P. intermedius* did not show a preference among seed species, as they prefer alternative food options. A study providing seeds as the only food available would further elucidate their seed preference. Furthermore, *P. intermedius* and *M. longicaudus* show very high niche overlap and low microhabitat segregation in the Kananaskis Valley, and their primarily herbivorous food habits are also similar (Millar et al. 1985). It is possible that their co-existence is partially explained by differential seed consumption.

*Myodes gapperi* and *M. pennsylvanicus* showed a greater relative preference for lodgepole pine seeds over white spruce seeds than *P. intermedius*. However, because *P. intermedius* did not show an overall preference among seed species, this result is very misleading. There was no disparity in the degree to which lodgepole pine seeds were preferred over white spruce seeds among *P. maniculatus*, *M. gapperi*, *M. longicaudus*,
and *M. pennsylvanicus*, all of whom showed similar overall preferences in seed consumption.

Findings from the field seed selection trials were consistent with laboratory results. *Peromyscus maniculatus* and *M. gapperi* showed very similar patterns of total daily seed consumption and consumption of each species of seed, as well as preference among the different species of seeds in the laboratory and the field. This is in agreement with Drożdż (1966), who used field food selection experiments and stomach-content analysis to show that cafeteria-style feeding experiments accurately represent the actual food habits of small mammals. Field seed selection trials were not conducted on *P. intermedius*, *M. longicaudus*, and *M. pennsylvanicus* because of their relatively low abundance in the Kananaskis Valley (Millar et al. 1985), which made trapping difficult. However, our results suggest that seed consumption by these species in the laboratory would be similar in the field.

The basis for seed selection by animals has been shown to involve characteristics such as size, seed coat, digestibility, palatability, nutritional content, and secondary compounds (Janzen 1971; Kerley and Erasmus 1991; Vickery et al. 1994; Ramos 1996; Lewis et al. 2001). Lodgepole pine seeds contain high-energy storage tissues (Despain 2001). The size of lodgepole pine and white spruce seeds are relatively similar and are both smaller than subalpine fir seeds. Larger seeds are generally favoured by rodents (Price 1983; Hulme 1998). However, the increase in handling time associated with larger seeds is a possible deterrent (Kerley and Erasmus 1991). Fir seeds are also thought to possess a natural repellence to small mammals (Abbott 1962), likely because of the presence of secondary compounds, and individuals often ignore these seeds if other species are
available (Abbott 1962; Drożdż 1966; Schreiner et al. 2000). The relative importance of these factors is not known for the selection of lodgepole pine, white spruce, and subalpine fir seeds and should be the focus of future studies.

The results of our study predict that post-dispersal seed predation by small mammals would not be a major problem in the regeneration of subalpine fir stands through either natural or artificial (e.g., direct seeding) processes. Subalpine fir should also be successful in recruitment and colonization of new sites in forests. Conversely, the white spruce consumption patterns reiterate findings by Peters et al. (2004), who showed that post-dispersal seed predation by small mammals negatively affects recruitment success. Abbott (1962) suggests that avoidance of fir seeds by predators may contribute to the high ratio of fir to spruce seedlings in mixed forests.

The distinct preference for lodgepole pine seeds by small mammals should severely decrease its regeneration and recruitment success, especially in mixed forests. Direct seeding coupled with diversionary foods has been shown to be an effective strategy to curtail seed predation by rodents; Sullivan and Sullivan (1982) dramatically reduced the loss of lodgepole pine seeds to rodents using a ratio of two sunflower seeds to one pine seed. Lodgepole pine (subspecies latifolia) trees in the Kananaskis Valley produce predominantly serotinous cones (remain closed at maturity until they have been subjected to temperatures in excess of 50 °C), which has been suspected to be a natural defence against post-dispersal seed destruction by small mammals (Despain 2001; Sjöberg and Danell 2001). Crown fires cause the release of seeds stored in cones, which flood newly available sites and overwhelm most coniferous competitors (Despain 2001). Herbaceous vegetation and small mammal populations are also reduced long enough to allow the
successful establishment of seedlings (Despain 2001). Other forms of disturbance (e.g.,
clearccuting) are also beneficial to lodgepole pine; small mammal populations often
respond in a similar way as they would to a fire (Simon et al. 2002), and a fast growth
rate and the ability to tolerate dry, low nutrient soil allow seeds released by the non-
serotinous cones to be more successful (Despain 2001).

The overall effect of seed predation may not be very important when other stages of
recruitment are limiting (Hulme 1998), especially when seed production and dispersal
varies in competing species. While the knowledge of seed preference allows us to make
predictions of how successful certain conifer species will be over others in mixed forests
and new areas, further studies are required to evaluate the direct effects of species-
specific differences in seed predation by small mammals on recruitment and natural and
artificial regeneration.

2.5 Acknowledgments

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Research Council of Canada.
2.6 References


SPSS Inc. 2007. SPSS 16.0 for Windows. SPSS Inc., Chicago.


Chapter 3

3 The efficacy of conifer seeds as major food resources to deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*)

3.1 Introduction

Tree seeds are an integral component of the diet of many forest rodents (Drożdż 1966; Abbott and Quink 1970; Everett et al. 1978). In coniferous forests, rodents have been shown to both consume (Radvanyi 1970; Radvanyi 1971; Despain 2001) and cache (Shaw 1954; Abbott 1961; Abbot and Quink 1970) significant proportions of seeds available to them. Seed consumption is believed to be critical to the survival of rodents in the fall and winter when other food sources are limited (Jameson 1952; Fitch 1954; Williams 1959; Drożdż 1966; Whitaker 1966).

Rodents are also known to prefer some species of conifer seeds over others (Abbott 1961; Martell 1979; Duchesne et al. 2000; Lobo et al. 2009/Chapter 2). Internal seed chemistry greatly influences seed selection, largely through the presence of plant secondary compounds (PSCs) that act as a deterrent (Freeland and Janzen 1974; Marquis and Batzli 1989). Even small amounts of PSCs, such as flavonoids, tannins, and phenolic acids, reduce protein digestibility, cause weight loss, inhibit growth, damage the liver, kidneys,

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and gastrointestinal system, and shorten life span (Freeland and Janzen 1974; Freeland et al. 1985; Lindroth and Batzli 1984; Hagerman and Klucher 1986; Dietz et al. 1994; Shimada and Saitoh 2003). Nutrition plays an important role in food preference as well (Schlesinger 1975), and rodents appear to select foods that have high energy and intermediate protein content (Vickery et al. 1994; Lewis et al. 2001).

Lobo et al. (2009/Chapter 2) found that deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), long-tailed voles (*Microtus longicaudus*) and meadow voles (*Microtus pennsylvanicus*) all showed a distinct preference for lodgepole pine (*Pinus contorta*) seeds and consumed intermediate quantities of white spruce (*Picea glauca*) seeds, but almost completely avoided subalpine fir (*Abies lasiocarpa*) seeds. Since seed availability and abundance were kept constant, foraging theory dictates that the mice and voles were selecting “higher quality” foods (lodgepole pine and white spruce seeds) over “lower quality” (subalpine fir seeds) foods (Ellis et al. 1976; Belovsky 1984; Vickery 1984; Bozinovic et al. 1997). Fir seeds are thought to possess a natural repellence to rodents, which is likely due to a high concentration of PSCs (Abbott 1962; Drożdż 1966; Schreiner et al. 2000). Selective feeding of seeds and other plant matter by rodents is the initial response against PSCs and lower quality foods (Bozinovic et al. 1997).

Although rodents may select higher quality seeds under optimal conditions, large amounts of low quality seeds may be consumed even when more preferred seeds are available if the low quality seeds are very abundant (Drożdż 1966; Ellis et al. 1976). Subalpine fir is a masting species, so seed predators are periodically exposed to large quantities of their seeds (Alexander et al. 1990). However, it is unknown whether rodents
will consume subalpine fir seeds if they are the major/only food source available, or if these seeds can be digested effectively. Little is known about the biological interactions between conifer seeds and rodents, and the effects of conifer seed production on the population ecology of rodents. Consequently, investigating this question is important for understanding this resource-consumer interaction in coniferous forests. The predator satiation hypothesis, the main hypothesis for the ultimate function of masting, suggests that masting causes an increase in the populations of seed predators (Silvertown 1980; Kelly 1994) because it assumes that the seeds produced are a nutrient resource for the predators (Shimada and Saitoh 2003; Shimada and Saitoh 2006). The efficacy of this hypothesis to conifer-rodent interactions should be reviewed if rodents will not consume or cannot process the seeds effectively (Shimada and Saitoh 2003).

The main objective of this study was to examine the effect of subalpine fir seed-diets on the body condition, behavioural and morphological responses of rodents. The effects of lodgepole pine and white spruce seed-diets on rodents were also examined for purposes of comparison, since rodents prefer these over subalpine fir seeds (Lobo et al. 2009/Chapter 2), and all three tree species are common associates (Alexander et al. 1990). Deer mice and southern red-backed voles were used in this study, since they are the dominant rodent species in the study area (Millar et al. 1985) and are very common across North America. We hypothesized that subalpine fir seed-diets would have substantial negative effects on rodents, while no detrimental effects would occur in animals fed lodgepole pine and white spruce seeds. Specifically, we predicted that mice and voles fed subalpine fir seeds would exhibit decreased survival and body mass compared to the other seed diets, and increased blood-glucose concentrations in response
to prolonged stress (Boonstra et al. 1998). Animals fed subalpine fir seeds should also increase their food intake and decrease throughput time in order to compensate for the low quality diet (Green and Millar 1987; Derting and Bogue 1993; Harju and Tahvanainen 1994; Bozinovic 1995; Bozinovic et al. 1997). Furthermore, the gut and vital organs (liver, kidneys, spleen) of mice and voles on subalpine seed-diets should be larger than those feeding on other seeds, in order to more efficiently process food that is low in quality and likely contains PSCs (Sibly 1981; Lindroth and Batzli 1984; Green and Millar 1987; Penry and Jumars 1987; Harju and Tahvanainen 1994; Lee and Houston 1995; Koteja 1996; del Valle et al. 2006).

We also examined the relative nutritional quality of lodgepole pine, white spruce, and subalpine fir seeds by determining their crude protein, acid detergent fibre (ADF), and neutral detergent fibre (NDF) content. These measures are key indicators of diet quality (Bergeron and Jodoin 1987; Green and Millar 1987; Norrie and Millar 1990).

3.2 Methods

3.2.1 Nutritional analysis of seeds

Lodgepole pine, white spruce, and subalpine fir seeds used in this study were acquired from the Alberta Tree Improvement and Seed Centre (Smoky Lake, Alberta) and the British Columbia Ministry of Forests and Range Tree Seed Centre (Surrey, British Columbia). The nutritional analysis of seeds was performed by A&L Canada Laboratories Inc. (London, Ontario). 200 g of each seed was submitted for testing. Whole seeds were dried overnight (105 °C), and subsequently ground for testing. The percentage of dry matter and moisture in the seeds were determined. Total nitrogen content was
determined (combustion method, Leco FP-428; Leco Corporation, St. Joseph, Michigan), and multiplied by a protein conversion factor of 6.25 to calculate the crude protein content (Association of Official Analytical Chemists 1990; Undersander et al. 1993). ADF and NDF contents were also determined (filter bag technique, Ankom® Fibre Analyzer; Ankom Technology, Macedon, New York). The crude protein, ADF, and NDF contents of rodent chow (LabDiet 5001 Rodent Diet; PMI Nutrition International, St. Louis, Missouri) were obtained from the manufacturer.

### 3.2.2 Feeding trials

Animals were live-trapped throughout the Kananaskis Valley (51°01’N, 115°03’W), Alberta, Canada, from May to August of 2008. At capture, individuals were weighed (±0.5 g) using a 60 g Pesola spring balance, age was determined based on size and dorsal pelage colour, and breeding condition was recorded. Juveniles and pregnant and lactating females were released upon capture and not used in the study. All other individuals were transported to the laboratory at the Biogeoscience Institute of the Canadian Rockies and Foothills (University of Calgary) and held individually in Plexiglas® cages (0.40 m × 0.20 m × 0.20 m) containing cotton bedding, aspen chips, plastic tubing, and provided with rodent chow and water ad libitum. The daily photoperiod in the laboratory was 16 h light : 8 h dark, and temperature was maintained at 20 °C.

After acclimation to the laboratory for two or more days, rodent chow was provided to animals inside a 600 mL food-storage container (12 cm × 12 cm) placed inside each cage. Food-storage containers were modified by cutting large holes in two opposing sides, allowing animals to enter and exit freely. Individuals were acclimated to the container for
two days, and weighed (±0.01 g) using an electronic balance at the beginning and end of the acclimation period.

Feeding trials were conducted for up to 14 days using lodgepole pine (deer mice: \( n = 5 \); red-backed voles: \( n = 5 \)), white spruce (deer mice: \( n = 5 \); red-backed voles: \( n = 4 \)), and subalpine fir seeds (deer mice: \( n = 5 \); red-backed voles: \( n = 5 \)). Control trials were also conducted using rodent chow (deer mice: \( n = 5 \); red-backed voles: \( n = 4 \)). On the first day of trials, 7.00 ± 0.01 g of a specific species of seed (established as excess of what was consumed in a 24 h period in preliminary trials) was weighed on an electronic balance and placed in a modified food-storage container. This replaced the previous food-storage container in the cage. At 24 h intervals, all seeds were removed from the cage (including discarded seed coats), and each food-storage container was replaced with one containing new seeds of the same species. Discarded seed coats were separated from the remaining intact seeds; intact seeds were then left out to dry overnight, and weighed the following morning. The masses of offered and remaining seeds were corrected for percentage of dry matter (DM), so all food intake data are recorded on a DM basis. The mass of consumed seeds (DM intake) was determined by subtracting the remaining intact seed mass (DM) from the initial mass (DM) provided. The mass of consumed control food (DM intake) was similarly determined in order to observe whether food consumption and nutritional requirements changed with time in the laboratory; however, these data are not comparable to seed consumption data because the control food did not contain any husks or waste materials, and was consumed whole. Individuals were also weighed daily between 10:30 and 12:00 during trials. Trials were terminated prior to 14 days if an individual lost 25% of its initial body mass.
At the end of trials, animals were euthanized within 3 min of handling by carbon dioxide asphyxiation, and blood samples were obtained by suborbital bleeding. Blood collection always took place between 10:30 and 12:00 to avoid time-of-day effects. Glucose levels were measured using a glucose dehydrogenase reaction (Therasense Freestyle glucose monitor; Abbott Laboratories, Abbott Park, Illinois). Animals were weighed and dissected, and the following were recorded: (1) wet mass of the liver; (2) wet mass of the spleen; (3) wet mass of the kidneys; (4) length of the stomach; (5) wet mass of the stomach (including contents); (6) length of the small intestine; (7) wet mass of the small intestine (including contents); (8) length of the caecum; (9) wet mass of the caecum (including contents); (10) length of the colon; and (11) wet mass of the colon (including contents).

### 3.2.3 Statistical analyses

Logarithmic transformations of body mass, DM intake, blood-glucose concentration, and organ length and mass data best satisfied the assumptions of normality. All analyses were performed using SPSS version 16.0 (SPSS Inc. 2007). Differences among groups were considered statistically significant at \( p \leq 0.05 \), unless otherwise stated. Data are presented as means ± SE.

We tested for differences in blood-glucose concentrations and initial and final body masses of animals among the groups using ANOVAs, and differences between the initial and final body masses of animals within each group using repeated-measures ANOVAs. Daily body mass changes were calculated as daily body mass change = \( \frac{BM_t - BM_0}{BM_0} \), where \( BM_t \) represents the body mass on day \( t \) (Shimada and Saitoh 2003).
Differences in daily body mass changes among the groups were tested using ANOVAs and Tukey’s HSD tests, where appropriate.

We used repeated-measures ANOVAs to test for differences in control DM intake by animals among experimental days. ANOVAs and Tukey’s HSD tests, where appropriate, were used to test for differences among the groups in daily seed DM intake and average seed DM intake over the experimental period.

ANCOVAs and Tukey’s pair-wise LSD tests ($\alpha = 0.05/6 = 0.008$), where appropriate, were used to test for differences among groups in the masses of vital organs, and masses and lengths of the total gut and its individual components. Corrected body masses (total body mass – mass of the organ/total gut/gut component) were used as the covariate.

3.3 Results

3.3.1 Nutritional analysis of seeds

Subalpine fir seeds ranked lowest in crude protein content (DM) and highest in ADF and NDF contents (DM) relative to lodgepole pine and white spruce seeds (Table 3.1). Lodgepole pine seeds contained the highest crude protein content (DM), but white spruce seeds possessed lowest ADF content (DM; Table 3.1). The crude protein content (DM) of control food closely resembled that of white spruce seeds, but contained much lower ADF and NDF contents (DM; Table 3.1).
Table 3.1. Results of nutritional analysis of control food (LabDiet 5001 Rodent Diet), and lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds. Values reported are for dry matter (DM).

<table>
<thead>
<tr>
<th></th>
<th>Crude protein (% DM)</th>
<th>Acid Detergent Fibre (% DM)</th>
<th>Neutral Detergent Fibre (% DM)</th>
</tr>
</thead>
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<tr>
<td>Control food</td>
<td>23.9</td>
<td>6.7</td>
<td>15.6</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>33.0</td>
<td>22.1</td>
<td>30.0</td>
</tr>
<tr>
<td>White spruce</td>
<td>25.1</td>
<td>19.8</td>
<td>30.6</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>11.4</td>
<td>46.1</td>
<td>47.2</td>
</tr>
</tbody>
</table>
3.3.2 Survival

All mice survived the full 14 days of trials in each group. Three (60%) voles were euthanized in the subalpine fir group after losing greater than 25% of their initial body masses. One vole each was euthanized on days four (-30.6% of initial mass), six (-31.0% of initial mass), and seven (-29.7% of initial mass) of the experiment. We also observed these voles to suffer extreme lethargy, blindness, and loss of fur. All voles survived to the end of the experiment in the lodgepole pine, white spruce, and control groups.

3.3.3 Body mass

Initial ($F_{3,16} = 0.69, p = 0.57$) and final ($F_{3,16} = 0.82, p = 0.51$) body masses of mice did not differ among the groups (Figure 3.1a). There was also no change between the initial and final body masses of mice within each group (control: $F_{1,4} = 0.38, p = 0.57$; lodgepole pine: $F_{1,4} = 0.71, p = 0.45$; white spruce: $F_{1,4} = 0.16, p = 0.71$; subalpine fir: $F_{1,4} = 0.46, p = 0.53$; Figure 3.1a).

Daily body mass changes of mice in the control group were consistently positive, but mostly negative in the other groups (Table 3.2). Body mass changes differed only on days one ($F_{3,16} = 3.81, p = 0.03$) and two ($F_{3,16} = 4.22, p = 0.02$) of the experiment; these differences were between mice eating control food and subalpine fir seeds (both $p = 0.03$; Table 3.2).

Initial ($F_{3,14} = 0.21, p = 0.89$) and final ($F_{3,14} = 1.78, p = 0.20$) body masses of voles also did not differ among the groups (Figure 3.1b). Final body mass was lower than the initial mass in the white spruce (-11.3%; $F_{1,3} = 23.74, p = 0.02$) and subalpine fir (-20.1%; $F_{1,4}$
= 8.03, \( p = 0.05 \) groups, but did not differ in the control \( (F_{1,3} = 2.81, p = 0.19) \) and lodgepole pine \( (F_{1,4} = 2.55, p = 0.19) \) groups (Figure 3.1b).

Daily body mass changes of voles in the control group were consistently positive, but consistently negative in the seed groups (Table 3.3). Results of ANOVAs comparing daily body mass changes of the different groups are presented in Table 3.4. The decrease in body mass of voles fed white spruce seeds was less than that of voles fed subalpine fir seeds on day one \( (p = 0.02; \text{ Table 3.3}) \). However, there were no other differences in daily body mass changes among the lodgepole pine, white spruce, and subalpine fir groups for the remainder of the experimental period (all \( p > 0.05; \text{ Table 3.3} \)). Body mass changes of voles in the control and white spruce groups differed only from the middle of the experiment and onwards, on days seven \( (p = 0.05) \), eight \( (p = 0.05) \), nine \( (p = 0.03) \), ten \( (p = 0.05) \), twelve \( (p = 0.05) \), thirteen \( (p = 0.04) \), and fourteen \( (p = 0.04; \text{ Table 3.3}) \).

Conversely, body mass changes of voles fed control food and subalpine fir seeds differed early in the experiment, on days one \( (p < 0.001) \), two \( (p = 0.02) \), three \( (p = 0.04) \), five \( (p = 0.01) \), and six \( (p = 0.05) \), and on day nine \( (p = 0.04; \text{ Table 3.3}) \). The final changes in body mass were also different between the control and subalpine fir groups \( (p = 0.04; \text{ Table 3}) \). Body mass changes between the control and lodgepole pine groups differed only on days one \( (p = 0.03) \) and nine \( (p = 0.04; \text{ Table 3.3}) \).
Figure 3.1. Body mass of (a) deer mice (*Peromyscus maniculatus*) and (b) red-backed voles (*Myodes gapperi*) fed control food ((C); mice, *n* = 5; voles, *n* = 4) and lodgepole pine (*Pinus contorta* (LP); mice and voles, *n* = 5 each), white spruce (*Picea glauca* (WS); mice, *n* = 5; voles, *n* = 4), and subalpine fir (*Abies lasiocarpa* (SF); mice and voles, *n* = 5 each) seeds over a 14-day period. In (b), SF final mass differs from day 14 mass due to mortality of voles in this group during the experimental period; hence final mass is displayed separately. Data are means ± SE. Within each group, * denotes significant differences from the initial mass based on repeated-measures ANOVAs (*p* < 0.05).
Table 3.2. Mean daily change (%) in body mass (compared to initial mass) of deer mice (*Peromyscus maniculatus*) fed control food (C) and lodgepole pine (*Pinus contorta* (LP)), white spruce (*Picea glauca* (WS)), and subalpine fir (*Abies lasiocarpa* (SF)) seeds over a 14-day period. Within each day, different superscripts denote significant differences among groups based on Tukey’s HSD test (*p* < 0.05). Values in parentheses denote sample sizes.

<table>
<thead>
<tr>
<th>Days</th>
<th>C</th>
<th>LP</th>
<th>WS</th>
<th>SF</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.3 (5)</td>
<td>-4.0 (5)</td>
<td>-2.5 (5)</td>
<td>-4.7 (5)</td>
</tr>
<tr>
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<td>2.7 (5)</td>
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<tr>
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<tr>
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<td>4.8 (5)</td>
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<tr>
<td>6</td>
<td>7.4 (5)</td>
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<td>-4.3 (5)</td>
<td>-2.8 (5)</td>
</tr>
<tr>
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<tr>
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Table 3.3. Mean daily change (%) in body mass (compared to initial mass) of red-backed voles (*Myodes gapperi*) fed control food (C) and lodgepole pine (*Pinus contorta* (LP)), white spruce (*Picea glauca* (WS)), and subalpine fir (*Abies lasiocarpa* (SF)) seeds over a 14-day period. SF final mass change differs from day 14 mass change due to mortality of voles in this group during the experimental period; hence final mass changes are displayed separately. Within each day, different superscripts denote significant differences among groups based on Tukey’s HSD test (*p* < 0.05). Values in parentheses denote sample sizes.

<table>
<thead>
<tr>
<th>Days</th>
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<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
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<th>11</th>
<th>12</th>
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<th>14</th>
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Table 3.4. Results of ANOVAs comparing daily body mass changes of red-backed voles (*Myodes gapperi*) fed control food and lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*) seeds over a 14-day period. Highlighted values denote data that were not significant (*p* > 0.05).

<table>
<thead>
<tr>
<th>Day</th>
<th><em>F</em> (_{df1,df2})</th>
<th><em>p</em></th>
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<td>5.19(_{3,13})</td>
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</tr>
<tr>
<td>6</td>
<td>3.86(_{3,12})</td>
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<td>7</td>
<td>4.00(_{3,11})</td>
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<td>8</td>
<td>4.21(_{3,11})</td>
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<tr>
<td>9</td>
<td>5.39(_{3,11})</td>
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<td>10</td>
<td>4.05(_{3,11})</td>
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<td>11</td>
<td>3.44(_{3,11})</td>
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<td>13</td>
<td>4.07(_{3,11})</td>
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<tr>
<td>14</td>
<td>4.06(_{3,11})</td>
<td>0.04</td>
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</tbody>
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3.3.4 DM intake

Control DM intake by mice ($F_{13,52} = 0.72, p = 0.74$; Figure 3.2a) and voles ($F_{13,39} = 1.10, p = 0.39$; Figure 3.2b) did not differ among experimental days.

Seed DM intake by mice was similar among the groups on days one ($F_{2,12} = 0.77, p = 0.49$) and two ($F_{2,12} = 2.40, p = 0.13$), but mostly differed from day three onwards ($p < 0.05$; Figure 3.2a). Subalpine fir DM intake was higher than lodgepole pine and white spruce DM intake between days three and fourteen (all $p \leq 0.05$), excluding day four (lodgepole pine: $p = 0.19$; white spruce: $p = 0.16$; Figure 3.2a). There were no daily differences in DM intake between the lodgepole pine and white spruce groups over the experimental period (all $p > 0.05$; Figure 3.2a).

Overall, the average seed DM intake by mice over the experimental period differed significantly among the groups ($F_{2,12} = 10.70, p = 0.002$); mice showed higher subalpine fir DM intake ($4.88 \pm 0.14$ g) than lodgepole pine ($2.97 \pm 0.11$ g; $p = 0.01$) and white spruce ($2.81 \pm 0.09$ g; $p = 0.003$) DM intake over the experimental period. There was no difference between the average lodgepole pine and white spruce DM intake by mice ($p = 0.94$).

Seed DM intake by voles differed significantly among the groups on day one ($F_{2,11} = 18.53, p < 0.001$); subalpine fir DM intake was lower than lodgepole pine ($p < 0.001$) and white spruce DM intake ($p = 0.002$; Figure 3.2b). There were no daily differences in seed DM intake among the groups for the remainder of the experimental period (all $p > 0.05$; Figure 3.2b).
Figure 3.2. Dry matter (DM) intake of (a) deer mice (*Peromyscus maniculatus*) and (b) red-backed voles (*Myodes gapperi*) fed control food (*C*; mice, *n* = 5; voles, *n* = 4) and lodgepole pine (*Pinus contorta* LP; mice and voles, *n* = 5 each), white spruce (*Picea glauca* WS; mice, *n* = 5; voles, *n* = 4), and subalpine fir (*Abies lasiocarpa* SF; mice and voles, *n* = 5 each) seeds over a 14-day period. Data are means ± SE. Within each day, * denotes significant differences from the subalpine fir group based on Tukey’s HSD test (*p* < 0.05).
Overall, there was no difference in the average seed DM intake by voles among the groups (lodgepole pine: $2.92 \pm 0.12$ g, white spruce: $3.08 \pm 0.14$ g, subalpine fir: $3.77 \pm 0.37$ g; $F_{2,11} = 0.51$, $p = 0.61$).

### 3.3.5 Gut dimensions

Total gut length of mice did not vary among the groups ($F_{3,15} = 2.53$, $p = 0.10$), nor did lengths of individual components of the digestive tract (all $p > 0.05$; Figure 3.3a).

Total gut mass of mice was affected by type of food ($F_{3,15} = 13.13$, $p < 0.001$). Gut mass of mice in the control group was 54.6%, 49.4%, and 37.1% higher than those fed lodgepole pine ($p < 0.001$), white spruce ($p < 0.001$), and subalpine fir seeds ($p = 0.003$), respectively (Figure 3.3b). However, no differences in gut mass were seen among the seed groups (all $p > 0.008$). Masses of the stomach ($F_{3,15} = 3.20$, $p = 0.05$), small intestine ($F_{3,15} = 16.68$, $p < 0.001$), caecum ($F_{3,15} = 26.17$, $p < 0.001$), and colon ($F_{3,15} = 5.23$, $p = 0.01$) were all individually affected by type of food as well (Figure 3.3b). Mice fed control food had significantly heavier stomachs than those fed lodgepole pine seeds ($p = 0.001$) and heavier colons than those fed white spruce seeds ($p = 0.005$; Figure 3.3b). Mice fed control food also had significantly heavier small intestines and caeca than mice in each of the other groups (all $p < 0.001$; Figure 3.3b). Similarly, mice fed subalpine fir seeds had significantly heavier caeca than those fed lodgepole pine seeds ($p < 0.001$; Figure 3.3b).

Total gut length of voles did not vary among the groups ($F_{3,13} = 0.59$, $p = 0.63$), nor did lengths of individual components of the digestive tract (all $p > 0.05$; Figure 3.4a).

Similarly, total gut mass of voles ($F_{3,13} = 1.42$, $p = 0.28$) and the masses of the individual
components of the digestive tract (all $p > 0.05$) also did not vary among the groups (Figure 3.4b).

3.3.6 Vital organs

No differences were detected in the masses of the liver, spleen, and kidneys of mice and voles among the groups (all $p > 0.05$).

3.3.7 Blood-glucose concentration

No differences were detected in the blood-glucose concentrations of mice ($F_{3,16} = 2.25, p = 0.13$) and voles ($F_{3,14} = 1.91, p = 0.18$) among the groups.

3.4 Discussion

Subalpine fir seeds possessed the lowest overall nutritional value (lowest crude protein content, highest fibre content) out of the three conifer species tested. Their high ADF content also indicates that they possess low digestible energy. White spruce and lodgepole pine seeds had fairly similar ADF and NDF contents, but lodgepole pine seeds contained considerably more crude protein. Dietary protein limits growth, maturation, and reproduction in mice and voles (Cole and Batzli 1979; Lindroth and Batzli 1984; McAdam and Millar 1999). Therefore, increased protein content could be a major contributor to the preference for lodgepole pine seeds over white spruce seeds observed in many rodent species (Lobo et al. 2009/Chapter 2), and a key reason why both mice and voles fed lodgepole pine seeds were able to maintain body mass.
Figure 3.3. Gut dimensions of deer mice (*Peromyscus maniculatus*) fed control food ((C); *n* = 5) and lodgepole pine (*Pinus contorta* (LP); *n* = 5), white spruce (*Picea glauca* (WS); *n* = 5), and subalpine fir (*Abies lasiocarpa* (SF); *n* = 5) seeds over a 14-day period. (a) Lengths of the total gut and individual components. (b) Masses of the total gut and individual components. Data are means ± SE. Within each category, different letters denote significant differences among groups based on pair-wise Tukey’s LSD tests (*p* < 0.008).
Figure 3.4. Gut dimensions of red-backed voles (Myodes gapperi) fed control food ((C); n = 4) and lodgepole pine (Pinus contorta (LP); n = 5), white spruce (Picea glauca (WS); n = 4), and subalpine fir (Abies lasiocarpa (SF); n = 5) seeds over a 14-day period. (a) Lengths of the total gut and individual components. (b) Masses of the total gut and individual components. Data are means ± SE. Within each category, different letters denote significant differences among groups based on pair-wise Tukey’s LSD tests (p < 0.008).
Overall, the body condition of mice was only slightly affected by seed diets. We observed no major fluctuations in body mass, as was reported for wood mice (*Apodemus speciosus*) (Shimada and Saitoh 2003) and field mice (*Akodon azarae*) (del Valle et al. 2006) fed low quality diets. The body mass of mice in the subalpine fir group decreased early in the experiment, but quickly recovered, coinciding with the pattern of seed DM intake observed. While mice showed similar subalpine fir DM intake as other seeds early in the experiment, they increased their food intake from day three onwards, resulting in higher subalpine fir DM intake than lodgepole pine and white spruce DM intake over the experiment. This prompt shift towards increased ingestion is a common initial response by rodents to low quality diets (Green and Millar 1987; Derting and Bogue 1993; Harju and Tahvanainen 1994; Bozinovic 1995; Bozinovic et al. 1997), and was likely the primary factor that allowed mice in the subalpine fir group to maintain body mass and survive over the experiment.

Mice did not compensate for low quality diet by altering their gut length to increase digestive efficiency, as has been reported in other rodents (Green and Millar 1987; Lee and Houston 1995; Koteja 1996; del Valle et al. 2006). It is possible that the efficacy of increasing food intake to maintain body mass rendered any alteration of gut capacity unnecessary (Derting and Bogue 1993). Gut tissue is metabolically expensive to maintain relative to other body tissues, so animals will only maintain the minimum amount of gut tissue required to meet daily energetic and nutritional needs (Derting and Bogue 1993). The increased masses of the stomach, intestines, and the total gut reflected increased food intake (Green and Millar 1987) for mice in the control group, but this was not the case for mice that were fed subalpine fir seeds. Mice fed subalpine fir seeds did not retain digesta
for long in the stomach, small intestine, or colon, but instead relied more on the caecum (see Green and Millar 1987; Derting and Bogue 1993). An increase in caecum content would facilitate more efficient processing and assimilation of low quality foods through increased microbial degradation, thus allowing higher energy and nutrient extraction (Derting and Bogue 1993; Spinks and Perrin 1995; Bozinovic et al. 1997; del Valle et al. 2006). This strategy appears to maintain digestive efficiency and energy balance in response to the increased ingestion of low quality subalpine fir seeds, without the need for decreasing throughput times and increasing gut capacity (Derting and Bogue 1993).

Previous studies have suggested that increasing retention of digesta by rodents in the small intestine, in addition to the caecum, is also an effective strategy for improved digestion of low quality foods (Sibly 1981; Gross et al. 1985; Koteja 1996; Bozinovic et al. 1997), but we did not observe this (also see del Valle et al. 2006).

The body condition of voles was affected by a diet of white spruce seeds; it appears that they cannot sustain themselves on white spruce seeds for an extended period of time. Voles fed white spruce seeds were in good condition at the beginning of the experiment, but lost mass thereafter. Unlike mice, however, this change in mass did not appear to be influenced by food intake. Voles did not decrease their white spruce DM intake coinciding with the observed loss of body mass, nor did they increase DM intake later to compensate for decreasing body mass. The negative effects of white spruce seed-diets in this study were minor, as we observed no mortality or stress-related behaviours in this group. However, these effects could have escalated if the duration of the experiment was extended (see del Valle et al. 2006). White spruce trees possess small amounts of PSCs
(Bauce et al. 2006) that may have minor negative effects on rodents, which could escalate with prolonged exposure (see Shimada and Saitoh 2003).

Subalpine fir seed-diets had severe negative effects on voles. Voles showed very low subalpine fir DM intake early in the experiment, which likely lead to the corresponding decrease in body mass observed. Herbivorous voles have been shown to have large caeca and colons (Schieck and Millar 1985; Lovegrove 2010), and thus should be able to process foods containing high fibre. It is likely that PSCs played a major role in the deterioration of body condition (Freeland et al. 1985; Hagerman and Klucher 1986) of voles fed subalpine fir seeds, in addition to low food intake, as indicated by the rapid onset of blindness and loss of fur. Both DM intake and body mass increased during the middle of the experiment, but these data only reflect the 40% of voles that were able to consume subalpine fir seeds and did not need to be euthanized prior to 14 days.

Furthermore, unlike mice, voles showed the same subalpine fir DM intake on average as lodgepole pine and white spruce DM intake from the middle of the experiment onwards, and did not compensate for the lower quality food by increasing DM intake above what was observed for higher quality foods (see Green and Millar 1987; Derting and Bogue 1993; Harju and Tahvanainen 1994; Bozinovic 1995; Bozinovic et al. 1997).

An issue with our methodology is that discarded seed coats were not weighed, and their mass was not included when determining the mass of seeds consumed (also see Abbott 1962; Lobo et al. 2009/Chapter 2). This overestimates food intake values for seeds, and should be avoided in future studies. However, since all species of seeds used in this study possessed seed coats and were treated identically, our seed consumption values are still
suitable for comparison purposes when studying the relative use of different species of seeds by rodents.

We observed no changes in the gut dimensions of voles in any of the groups. However, this could have changed if the duration of the experiment was extended. Lee and Houston (1995) found that the rate of change of the gut anatomy of voles in relation to food quality was not constant among species, with bank voles (*Myodes glareolus*) increasing their gut length after one week of feeding on low quality seeds, but field voles (*Microtus agrestis*) showed no response for four weeks. Green and Millar (1987) reported morphological adaptations to low quality diet in the gut of deer mice within 12 days, while del Valle et al. (2006) found similar results in field mice within 33 days. Wild mice feed on a variety of seeds, arthropods, fungi, and plant matter (Jameson 1952; Martell and Macaulay 1981), and may need to respond rapidly to different foods that become available to them (Lee and Houston 1995). On the other hand, the diet of red-backed voles consists mainly of lichens, fungi, and non-seed plant matter (Maser et al. 1978; Martell 1981), so they may take longer to respond to changes in diet and diet quality (Lee and Houston 1995). Similarly, mice may have been able to respond better to subalpine fir seed-diets both behaviourally (increased food intake) and morphologically (increased caecum mass) because they are highly granivorous (Jameson 1952; Martell and Macaulay 1981). Voles are mainly herbivorous in the wild (Martell 1981; Norrie and Millar 1990), and their lack of compensatory responses to low nutritional value and PSCs in subalpine fir seeds most likely caused the dramatic negative effects observed.

Size of vital organs is often associated with the maintenance of body condition (Nespolo et al. 2002), as the efficiency of metabolism is affected by the functioning of the liver and
kidneys (del Valle et al. 2006). However, we observed no differences in the masses of vital organs of mice and voles in this study. The size of the liver and kidneys of rodents is known to increase with higher metabolic energetic demands (Koteja 1996; Nespolo et al. 2002), but their specific responses to food quality and PSCs are unclear. del Valle et al. (2006) reported that field mice fed low quality diet showed larger livers, smaller kidneys, and no change in spleen size compared to control animals. Lindroth and Batzli (1984) also found that kidney-size of prairie voles (*Microtus ochrogaster*) decreased with increasing PSCs in diet, but there were no effects on the liver. On the other hand, Harju and Tahvanainen (1994) found that livers of field voles (*Microtus agrestis*) exposed to PSCs were larger than control animals, but kidneys were not affected. It is clear that further investigation is needed in order to fully understand the specific morphological adjustments of the vital organs of rodents in response to low quality foods and/or PSCs.

Blood-glucose concentration is a good indicator of chronic stress (Boonstra et al. 1998), but the effects of nutritional stress on glucose levels are uncertain (Seal and Hoskinson 1978; Delguidice et al. 1987; Ben-David et al. 1999). Future studies should instead utilize hematocrit and plasma corticosterone concentrations, as they are more reliable indicators of nutritional stress and body condition (see Ben-David et al. 1999 for discussion on body condition measures).

One caveat to consider is that there may have been undetected physiological and biochemical responses occurring during our experiment. Proline-rich proteins are tannin-binding salivary proteins prevalent in small mammals, and provide protection from the harmful effects of tannins by preventing them from interacting with other proteins (especially in the gastrointestinal system) (Hagerman and Robbins 1993; Bennick 2002;
Shimada and Saitoh 2003; Shimada et al. 2006). A few days of tannin-ingestion are needed before proline-rich proteins are induced (Shimada et al. 2006); thus the cessation of mass loss observed in mice and surviving voles in the subalpine fir group indicates that physiological acclimation to PSCs might have been occurring, possibly through proline-rich proteins (Shimada and Saitoh 2003). Similarly, prolonged ingestion of low quality diet and PSCs can also cause the up-regulation of digestive enzymes in the small intestine and caecum (del Valle et al. 2006) and detoxifying enzymes in the liver (Harju and Tahvanainen 1994). We are currently performing a comprehensive analysis of the PSC profiles of lodgepole pine, white spruce, and subalpine fir seeds. While the above-mentioned processes are well-studied in some rodent species (Hagerman and Robbins 1993; Harju and Tahvanainen 1994; Bennick 2002; del Valle et al. 2006; Shimada and Saitoh 2006), it is not known if these, and similar processes are employed by deer mice and red-backed voles during foraging, and should be the focus of future studies.

In conclusion, we found that deer mice increased their food intake and reliance on the caecum to maintain body condition on low quality seed-diets. On the other hand, red-backed voles did not appear to respond sufficiently, and therefore suffered severe consequences. These results indicate that lodgepole pine, white spruce, and subalpine fir seeds can serve as sufficient food resources for mice, but not for voles, if they are the major/only food source available. However, it is unlikely that seeds will be the only food source available to rodents in the wild at any given time. Feeding on a range of foods could help rodents overcome the low nutritional value of subalpine fir seeds, and can possibly prevent overloading of any single detoxification pathway by regulating intake of specific PSCs (Freeland and Janzen 1974). The results of this study provide a clearer
understanding of the response of mice and voles to different quality seed-diets and the potential of different conifer seeds to be a food resource for them, but analyses of PSCs of seeds, long-term seed production and animal population data are still required to fully understand the interactions between conifer seeds and rodents.

3.5 Acknowledgments

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Chapter 4

4 Effects of seed quality and abundance on the foraging behaviour of northern rodents

4.1 Introduction

Caching is commonly practiced by many species of mammals, especially rodents, when they encounter an abundant food source because it provides a reliable supply of food during times when food is scarce (Smith and Reichman 1984; Vander Wall 1990, 2010). The choice between immediate consumption and storage is complex, and is influenced by factors such as food abundance, size, nutritional quality, and plant secondary compounds (PSCs) (Vander Wall 1990; Jansen et al. 2004; Wang and Chen 2009; Vander Wall 2010).

Acorns, nuts, and other types of seeds are commonly cached by rodents (Smith and Reichman 1984; Vander Wall 1990), but their decision to cache is influenced by seed abundance (Vander Wall 2010). Several studies have demonstrated that rodents prefer to store seeds rather than immediately consume them during mast years, while consumption is favoured in non-mast years (Jensen 1985; Vander Wall 1997; Jansen et al 2004).

Caching is also favoured when seed abundance is high under experimental conditions (Zhang et al. 2008). Furthermore, large seeds tend to be stored more frequently than small seeds, with small seeds often being consumed immediately (Jansen et al. 2004; Vander Wall 2010).

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Xiao et al. 2005; Chang et al. 2009; Wang and Chen 2009). Seed size likely acts as a proxy for nutrient content, as larger seeds generally contain more energy (Wang and Chen 2009; Vander Wall 2010). However, the relationship between seed size and nutrient content is complex and inconsistent across plant species (Blate et al. 1998). Nonetheless, several studies have found a positive relationship between seed nutrient content and caching frequency (Jansen et al. 2004; Xiao et al. 2006; Moore et al. 2007; Wang and Chen 2009).

PSCs may influence mammalian foraging decisions, but insights on their importance are mixed. Seeds and other foods containing high levels of PSCs may be preferentially stored rather than consumed (Smallwood and Peters 1986; Dearing 1997; Shimada 2001a; Smallwood et al. 2001; Wood 2005; Xiao et al. 2008) because PSCs in cached foods can degrade over time (Roy and Bergeron 1990; Dearing 1997; Müller-Schwarze et al. 2001; but also see Shimada 2001b; Smallwood et al. 2001; Wood 2005), or may reduce perishability (Hadj-Chikh et al. 1996; Smallwood et al. 2001) and/or delay germination (Smallwood et al. 2001). However, seeds with high levels of PSCs can also be preferentially consumed (Xiao et al. 2006), or have no effect on the choice between consumption and storage (Hadj-Chikh et al. 1996).

The size, nutrients, and PSC contents of seeds reflect their quality to a foraging rodent, and the decision to consume or cache seeds more frequently should be influenced by both the quality and abundance of the seeds encountered. Caching and consumption are not mutually exclusive, but rather one behaviour is performed more frequently than the other depending on the foraging situation (e.g. Jansen et al. 2004; Xiao et al. 2006; Wang and Chen 2009). High-quality seeds may be preferentially cached when they are abundant,
but consumed immediately more often when low quantities are encountered. Low-quality seeds can be ignored by rodents when present in similar or lower quantities than other foods (Abbott 1962; Lobo et al. 2009/Chapter 2). However, rodents can vary their consumption of non-preferred foods with that food’s abundance, even altering relative preferences (Vickery 1984). Therefore, low-quality seeds may be consumed and/or cached to some degree if they are abundant. The combined impact of seed quality and abundance on rodent foraging behaviours is unclear and requires further investigation.

Deer mice (Peromyscus maniculatus) and southern red-back voles (Myodes gapperi) are partially-granivorous North American rodents (Martell 1981; Martell and Macaulay 1981), and in western Canada, they are exposed to conifer seeds of variable abundance and quality. White spruce (Picea glauca) and subalpine fir (Abies lasiocarpa) are two dominant, commonly associated conifer species in western Canada (Alexander et al. 1990); both are masting species (Alexander et al. 1990; Nienstaedt and Zasada 1990), but their seeds differ in size and nutritional quality (Lobo and Millar 2011/Chapter 3). White spruce seeds are small, and contain high protein and low fibre contents, while subalpine fir seeds are approximately twice as large, contain low protein and digestible energy contents, and high fibre content (Lobo and Millar 2011/Chapter 3). Fir seeds also contain high concentrations of PSCs, with monoterpenes such as limonene implicated as most important for defense against predation (Abbott 1962; Smith 1970; Lobo and Millar 2011/Chapter 3; Rubino et al. 2012). Laboratory studies have shown that deer mice and red-backed voles prefer to consume white spruce seeds and avoid subalpine fir seeds when both are equally available (Lobo et al. 2009/Chapter 2). However, deer mice can maintain body condition in the laboratory when their diets are restricted to either conifer
seed (Lobo and Millar 2011/Chapter 3), indicating that both seeds are potentially valuable cache items for use when other foods are scarce. Red-backed voles are unable to maintain body condition on diets restricted to subalpine fir seeds, and only consume them in low amounts (Lobo et al. 2009/Chapter 2; Lobo and Millar 2011/Chapter 3).

Here, we experimentally examined the effects of seed quality and abundance on the foraging behaviour of rodents by observing deer mice and red-backed voles visiting artificial food patches in the field. Patches contained white-spruce or subalpine fir seeds, and we used a standardized variant of giving-up densities (GUDs) to assess the rodents’ perception of the quality of the seeds in the patch. The GUD is the amount of food remaining in a patch when an individual ceases foraging and leaves the patch (Brown 1988). The underlying theory of GUDs, an extension of Charnov’s (1976) marginal value theorem, states that optimal foragers should leave patches when the rate of energy gain balances the risk of predation, and missed-opportunity and metabolic costs of foraging (Brown 1988). When these three factors are held constant, the GUDs of patches containing high-quality seeds should be lower than those containing low-quality seeds, since the rate of energy gain will be higher when feeding on high-quality seeds. Our standardized variant of the GUD, which we have termed the absolute GUD, is not restricted to the amount of seeds remaining in a patch after a single foraging bout, but is rather assessed after the patch has undergone several nights of foraging and the amount of seeds remaining has reached a stable value. The absolute GUD indicates the food density at which rodents categorically stop active foraging for the specific type of seed present in the patch. This experimental design also allowed us to observe how the foraging
behaviours of rodents varied with seed abundance in the experimental patches without artificially manipulating seed abundance beyond the initial amount provided.

We hypothesized that rodents would consider white spruce and subalpine fir seeds as being of different qualities when encountered in the field, which would translate into different foraging strategies based on each seed’s abundance. We predicted that subalpine fir seed patches would have higher absolute GUDs than white spruce seed patches, indicating the lower quality of subalpine fir seeds. Regarding foraging behaviours, we predicted that: (1) both types of seeds would be removed from patches for storage most frequently when experimental seeds were most abundant; (2) rodents would mostly ignore subalpine fir seeds, rather than remove them for storage or consume them, when experimental seed abundance was lower; and (3) rodents would remove white spruce seeds less frequently as experimental seed abundance declined, and instead preferentially consume them within patches. Overall, when comparing foraging behaviours between spruce and fir seed patches, we expected that more in situ consumption of spruce seeds would occur regardless of experimental seed abundance, more removal of fir seeds from patches would occur when experimental seeds were most abundant, and more removal of spruce seeds would occur under lower seed abundance conditions.

4.2 Methods

4.2.1 White spruce seeds

Foraging data were collected at white spruce seed patches in July and August 2009, August 2010, and July 2011 in the Kananaskis Valley, Alberta, Canada. The study site used in 2009 (51°03.08’N, 114°57.55’W) was composed of a thin stand of mature mixed-
conifer forest. The forest canopy was dominated by white spruce trees, with lower, but fairly equal proportions, of subalpine fir and lodgepole pine trees. Ground cover was mainly composed of conifer needles, moss patches, and fallen logs. A different, but nearby, study site was used in 2010 and 2011 (50°47.16’N, 115°09.52’W) because of very low mouse/vole abundance and major disruption of the experimental setup by North American red squirrels (*Tamiasciurus hudsonicus*) at the original site in those years. The 2010-2011 site was composed of a regenerating stand of mixed-conifer forest which experienced a severe avalanche in approximately 1980. The forest canopy composition was similar to the 2009 study site, although the level of cover was less consistent; patches ranged from dense tree-cover to mostly open. Ground cover was mainly composed of conifer needles and patches of moss/grass. Regular live-trapping revealed that dominant rodent species at both sites were deer mice and red-backed voles. Conifer seed rain in this region occurs from mid-September onward, so experimental addition of seeds substantially increased the availability of this food source at the time and locations of our study, and confounding effects of natural conifer seed availability were not expected.

Two trials were conducted in 2009, and one each in 2010 and 2011. In each trial, 16 experimental food patches were set up using 600 mL plastic food-storage containers (11 × 11 cm along the base). Containers were arranged 4 × 4 with 20 m spacing in 2009, and 2 × 8 with 20 m spacing in 2010 and 2011. Each container was initially filled with 4.00 ± 0.01 g of white spruce seeds mixed with a 1 cm layer of conifer needles. This initial mass of seeds, the highest seed abundance condition, was selected because it exceeded the average daily mass of white spruce seeds consumed by deer mice and red-backed voles in laboratory feeding experiments (3.13 ± 0.25 g; Lobo and Millar 2011/Chapter 3). Sand is
usually used as the substrate in studies that utilize GUDs (e.g. Brown 1988; Andruskiw et al. 2008), but our goal was to create food patches that were as similar to the study site conditions as possible. Lids were secured on each seed container for weatherproofing and to exclude access to birds and larger mammals (e.g. red squirrels). Rodent access was through 4 cm holes cut into two opposite sides of the container. Containers were pre-baited with sunflower (*Helianthus annuus*) seeds for three days in order to encourage rodent visitation and habituation.

Seed containers were placed in the field at approximately 19:00, and were retrieved the following morning at approximately 07:00. They were then transferred to the laboratory at the University of Calgary Biogeoscience Institute, where their contents were sifted, and the masses of remaining intact seeds were weighed (±0.01 g). Seeds were dried at room temperature for at least two hours prior to sifting. Containers were recharged with the remaining intact seeds and conifer needles, placed in its previous location in the field that night, and retrieved the following morning. This process was repeated for each seed container until the mass of intact seeds remaining was constant (±0.02 g) for three consecutive nights, with signs of rodent activity present in the container (e.g. feces). It was considered that the absolute GUD was reached at this point, and the container did not undergo further deployment into the field. The location at which the container was previously present was left empty for the remainder of the trial – until all seed containers reached their absolute GUD. Infrared camcorders (Sony DCR-SR65; Sony of Canada Ltd., Toronto, Ontario) were focused on four randomly selected containers for the duration of each trial in 2009 and 2011, and eight containers in 2010, in order to monitor
the rodent species visiting the container and to observe foraging behaviours of rodents each night, as seed abundance declined.

4.2.2 Subalpine fir seeds

Foraging data were collected at subalpine fir seed patches from June to August 2010, in the same location and employing the same experimental food patches as the 2010 white spruce seed trial. Three trials were conducted; the first utilized 16 seed containers arranged $2 \times 8$ with 20 m spacing, and subsequent trials utilized 12 containers arranged $2 \times 6$ with 20 m spacing. Each container was initially filled with $10.00 \pm 0.01$ g of subalpine fir seeds mixed with a 1 cm layer of conifer needles. This initial mass of seeds, the highest seed abundance condition, was selected because it more than double the average daily mass of subalpine fir seeds consumed by deer mice and red-backed voles in laboratory feeding experiments ($4.06 \pm 0.69$ g; Lobo and Millar 2011/Chapter 3). The experimental procedure used was the same as the white spruce seed trials, except that the absolute GUD for each seed container was established as having been reached when the mass of intact subalpine fir seeds was within $\pm 0.10$ g for three consecutive nights, with signs of rodent activity present in the container. This margin of error was determined based on preliminary experiments observing the mass changes of constant numbers of subalpine fir seeds placed in the field overnight. Infrared camcorders were focused on eight randomly selected containers for the duration of each trial, in order to monitor the rodent species visiting the container and to observe foraging behaviours of rodents each night.
4.2.3 Statistical analysis

We screened all absolute GUD and behavioural data for errors, missing values, outliers, and deviations from normality. Absolute GUD data were log-transformed prior to analyses. Analyses were performed using R version 2.14.2 (R Development Core Team 2012) and SPSS version 16.0 (SPSS Inc. 2007). Unless otherwise stated, we considered differences among groups as being statistically significant at \( p \leq 0.05 \). Excluding foraging behaviours, data are presented as means ± SE.

4.2.3.1 Assessing seed quality

Absolute GUD data from containers visited by species other than deer mice and red-backed voles (e.g. red squirrels) were excluded from the analyses. ANCOVAs, controlling for the number of nights it took each seed container to reach its absolute GUD, were used to test for differences among 2009, 2010, and 2011 white spruce seed absolute GUDs, as well as between each of these and the subalpine fir seed absolute GUDs. Where appropriate, pair-wise Bonferroni-corrected LSD tests were used for post-hoc comparisons. White spruce seed absolute GUDs from all years were also pooled, and compared to subalpine fir seed absolute GUDs using a linear mixed model, with year of trial included as a nominal random factor and the number of nights it took each seed container to reach its absolute GUD as a covariate. The Satterthwaite approximation was used to calculate the denominator degrees of freedom (Satterthwaite 1946).

Since different initial seed masses were employed in the white spruce and subalpine fir seed patches, we also used a standardized metric for additional comparisons between the seed types. The absolute GUD of each seed container was used to calculate the final proportion of seeds consumed and/or removed; these values (arcsine square root
transformed) were then used to test for differences between the white spruce and subalpine fir seed trials analogously to the absolute GUDs.

### 4.2.3.2 Foraging behaviours

Video recordings from 2011 trials were sufficiently clear to identify the species of rodent visiting seed containers, but often could not distinguish among foraging behaviours performed during visits. As such, only video recordings from 2009 and 2010 trials were used to score the foraging behaviours of mice. See Table 4.1 and Figure 4.1 for detailed descriptions of the behavioural scoring.

Contingency tables (loglinear analyses, chi-squared tests, and Fisher’s exact tests with sequential Bonferroni adjustments) were used to test for differences among groups in the proportions of observed rodent visits to seed patches that contained feeding, removal, and neither. These groups included the 2009 and 2010 white spruce seed trials, pooled white spruce seed trials, subalpine fir seed trials, and high- and low-abundance seed patches. We classified low-abundance seed patches as those deployed for the night with less than one-quarter of the initial seed mass provided, and high-abundance patches as anything equal to or higher than this value. This cut-off was selected because it was considerably lower than the average daily mass of spruce (3.1 times lower) and fir (1.6 times lower) seeds consumed by mice in restricted-diet trials in the laboratory (Lobo and Millar 2011/Chapter 3). We also used generalized linear mixed models to examine the relationships between deployed seed abundance and the proportions of mouse visits to the seed patch that contained feeding, removal, and neither. Patch identification number was included as a nominal random factor, and binomial distributions and logit link functions were applied in the analyses.
Table 4.1. Description of foraging behavioural scoring of each rodent visit to seed patches.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>Hind leg-reared feeding behaviour, or pausing with head in substrate and chewing* (Figures 4.1a and 4.1b).</td>
</tr>
<tr>
<td>Removal</td>
<td>Seeds are visibly stored in the rodent’s mouth and the rodent exits without pausing to eat stored seeds, or rodent leaves with distended cheeks** (Figure 4.1c).</td>
</tr>
<tr>
<td>No feeding or removal</td>
<td>Rodent enters the seed container and digs through substrate, but leaves without feeding on or caching seeds.</td>
</tr>
<tr>
<td>Indeterminate</td>
<td>Behaviour is unobservable; e.g. rodent has its back oriented to the camera*** (Figure 4.1d).</td>
</tr>
</tbody>
</table>

* Feeding behaviour outside of the seed container was only included if the seeds were visibly removed from the box.

** Note that under these definitions, a rodent could both feed on and remove seeds in a single visit.

*** Any visits containing indeterminate behaviours were excluded from the analyses.
Figure 4.1. Examples of foraging behaviours of deer mice (*Peromyscus maniculatus*) observed visiting seed containers. Red-backed voles (*Myodes gapperi*) exhibit identical behaviours. (a) Hind leg-reared feeding behaviour; (b) Head in substrate while chewing feeding behaviour; (c) Exiting the seed container with distended cheeks – removal behaviour; (d) Exploring the seed container, but behaviour is indeterminate.
4.3 Results

4.3.1 Assessing seed quality

White spruce seed patches took 5.03 ± 0.26 nights to reach their absolute GUD, while subalpine fir seed patches required 4.16 ± 0.21 nights. White spruce seed absolute GUDs differed among years ($F_{2,57} = 5.07, p = 0.01$); the absolute GUD was higher in 2009 than 2010 ($p = 0.01$) and 2011 ($p = 0.04$), with no difference between 2010 and 2011 ($p = 0.70$; Figure 4.2a). The subalpine fir seed absolute GUD was higher than the white spruce seed absolute GUDs in 2009 ($F_{1,60} = 4.57 \times 10^4, p < 0.001$), 2010 ($F_{1,43} = 4.11 \times 10^4, p < 0.001$), and 2011 ($F_{1,45} = 1.13 \times 10^5, p < 0.001$), as well as the pooled white spruce seed absolute GUD ($F_{1,74.85} = 3.41 \times 10^4, p < 0.001$; Figure 4.2b).

The final proportion of white spruce seeds consumed and/or removed also differed among years ($F_{2,57} = 6.56, p = 0.003$); the final proportion of seeds consumed and/or removed was lower in 2009 than 2010 ($p = 0.001$) and 2011 ($p = 0.05$), with no difference observed between 2010 and 2011 ($p = 0.37$; Figure 4.3a). The final proportion of subalpine fir seeds consumed and/or removed was lower than that of white spruce seeds consumed and/or removed in 2009 ($F_{1,60} = 7.54 \times 10^3, p < 0.001$), 2010 ($F_{1,43} = 3.83 \times 10^3, p < 0.001$), and 2011 ($F_{1,45} = 8.24 \times 10^3, p < 0.001$), as well as the pooled final proportion of white spruce seeds consumed and/or removed ($F_{1,73.83} = 6.16 \times 10^3, p < 0.001$; Figure 4.3b).

4.3.2 Foraging behaviours

There were no differences between years in the proportions of mouse ($\chi^2_2 = 3.13, p = 0.21$) and vole ($\chi^2_2 = 2.82, p = 0.32$) visits to white spruce seed patches where each...
foraging behaviour was observed (feeding, removal, no feeding or removal). Therefore, data from white spruce seed patches were pooled for further analyses.

While we could not determine the exact number of individuals that visited each seed patch in each night, different visitors could often be distinguished based on the presence/absence of ear tags and the location/shape/size of hairless patches on their bodies (small hair samples were obtained from trapped animals for a separate study). As such, we know that several different individuals visited each patch on most nights.

4.3.2.1 Seed quality only

First, we examined the foraging behaviours of rodents in relation to overall seed quality, without partitioning out seed abundance. Within white spruce (high-quality) seed patches, the prevalence of each foraging behaviour differed for both mice ($\chi^2 = 21.00, p < 0.001$) and voles ($\chi^2 = 72.34, p < 0.001$). Mice consumed white spruce seeds within the patch most often (both $p \leq 0.05$), while seed removal occurred least frequently (both $p \leq 0.01$; Figure 4.4). Conversely, voles ignored seeds most often when visiting white spruce seed patches (both $p < 0.001$), with feeding and removal occurring at similar low frequencies ($p = 0.61$; Figure 4.5).

Mice generally ignored seeds when visiting subalpine fir (low-quality) seed patches ($\chi^2 = 83.25, p < 0.001$); minimal seed consumption and no seed removal were observed (both $p < 0.001$; Figure 4.4). Similarly, no voles were observed feeding or removing seeds in subalpine fir seed patches (Figure 4.5).

When comparing mouse foraging behaviours between the two types of seed patches ($\chi^2 = 68.22, p < 0.001$), feeding ($p < 0.001$) and removal ($p < 0.001$) were observed more
frequently in white spruce seed patches, while seeds were ignored more frequently in subalpine fir seed patches \((p < 0.001; \text{Figure 4.4})\). Conversely, voles exhibited similar patterns of foraging behaviour when visiting both types of seed patches \((\chi^2 = 4.81, p = 0.09; \text{Figure 4.5})\).

### 4.3.2.2 Seed quality and abundance

With an initial mass of \(10.00 \pm 0.01\) g of subalpine fir seeds provided per patch, the density of fir seeds in each patch at the beginning of each trial was \(826.45\) g m\(^{-2}\).

Regardless, fir seeds were mostly ignored at this high abundance (Figures 4.4 and 4.5), and thus this experiment did not test the effects of decreased fir seed abundance on rodent foraging behaviours. However, if rodents avoided fir seeds at such a high abundance, it is unlikely that decreased seed abundance would confer greater foraging value on these low-quality seeds and facilitate increased consumption or caching. Among white spruce seed patches, sufficient sample sizes were only available to assess the effects of seed abundance on the foraging behaviours of mice.

Mice in high-abundance \((\geq 1\) g) white spruce seed patches consumed seeds within the patch most often \((\chi^2 = 10.53, p = 0.01; \text{pair-wise both } p < 0.001)\), and removed or ignored seeds at moderate, but similar, frequencies \((p = 0.90; \text{Figure 4.6})\). On the other hand, mice in low-abundance \((< 1\) g) white spruce seed patches rarely removed seeds \((\chi^2 = 31.52, p < 0.001; \text{pair-wise both } p < 0.001)\), and either consumed or ignored seeds at higher, but similar, frequencies \((p = 0.57; \text{Figure 4.6})\).
Figure 4.2. Absolute giving-up densities (GUDs) of rodents visiting seed patches. White spruce seed trials were conducted in 2009 (n = 31), 2010 (n = 14), and 2011 (n = 16), and subalpine fir seed trials were only conducted in 2010 (n = 32). Bars represent means ± SE. (a) Absolute GUDs from the spruce seed trials (close-up). Trials marked with different letters had significantly different (p < 0.05) absolute GUDs from each other. (b) Absolute GUDs from spruce and fir seed trials. Groups marked with an asterisk had significantly lower (p < 0.05) absolute GUDs than fir seed trials.
Figure 4.3. Final proportions of seeds consumed and/or removed by rodents visiting seed patches. White spruce seed trials were conducted in 2009 \( (n = 31) \), 2010 \( (n = 14) \), and 2011 \( (n = 16) \), and subalpine fir seed trials were only conducted in 2010 \( (n = 32) \). Bars represent means ± SE. (a) Final proportions of seeds consumed and/or removed from the spruce seed trials (close-up). Trials marked with different letters had significantly different \( (p < 0.05) \) final proportions of seeds consumed and/or removed from each other. (b) Final proportions of seeds consumed and/or removed from spruce and fir seed trials. Groups marked with an asterisk had significantly higher \( (p < 0.05) \) final proportion of seeds consumed and/or removed than fir seed trials.
Figure 4.4. Proportions of deer mouse visits to white spruce seed \((n = 196\) visits) and subalpine fir seed \((n = 36\) visits) patches that contained feeding, removal, and no feeding or removal behaviours. Within each patch type, groups with different letters are significantly different \((p < 0.05)\) from each other. Within each foraging behaviour, asterisks mark significant differences \((p < 0.05)\) between patch types.
Figure 4.5. Proportions of red-backed vole visits to white spruce seed ($n = 35$ visits) and subalpine fir seed ($n = 27$ visits) patches that contained feeding, removal, and no feeding or removal behaviours. For white spruce seed patches, groups with different letters are significantly different ($p < 0.05$) from each other. For each foraging behaviour, no significant difference ($p > 0.05$) was observed between patch types.
Figure 4.6. Proportions of deer mouse visits to high-abundance ($n = 141$ visits) and low-abundance ($n = 55$ visits) white spruce seed patches that contained feeding, removal, and no feeding or removal behaviours. Within each patch type, groups with different letters are significantly different ($p < 0.05$) from each other. Within each foraging behaviour, asterisks mark significant differences ($p < 0.05$) between patch types.
Overall, varying the abundance of white-spruce seeds mainly affected the frequency of seed removal ($\chi^2 = 23.80, p < 0.001$); mice removed white spruce seeds more frequently when seeds were abundant ($p < 0.001$), but left the patch more often without consuming or removing seeds when seeds were scarce ($p = 0.02$; Figure 4.6). In situ seed consumption occurred at similar frequencies in both high- and low-abundance white spruce seed patches ($p = 0.63$; Figure 4.6). Similarly, generalized linear mixed models showed that the proportion of mouse visits to spruce seed patches that contained seed removal was positively related to the deployed seed abundance ($\beta = 0.67 \pm 0.36; Z = 2.00, p = 0.045$), but seed abundance did not influence the proportions of visits that contained feeding ($Z = 0.08, p = 0.93$) and no feeding or removal ($Z = -1.09, p = 0.27$).

### 4.4 Discussion

Absolute GUDs of white spruce seed patches were consistently lower than those of subalpine fir seed patches, as was expected based on the nutrient contents of seeds (Lobo and Millar 2011/Chapter 3) and the seed preferences of mice and voles in the laboratory (Lobo et al. 2009/Chapter 2). While laboratory studies indicated preferences and utilization of these seeds by rodents under controlled conditions (Lobo et al. 2009/Chapter 2; Lobo and Millar 2011/Chapter 3), the use of experimental patches in the field allowed us to examine their perception of seed quality and utilization of seeds in their native environment, where other natural food sources were readily available.

Rodents may utilize abundant low-quality foods to a higher degree in the field than in the laboratory because unpredictable conditions favour caching food (Vander Wall 2010), they have the opportunity to cache food within their natural territory, and the availability of a mixed diet may allow them to utilize a broader diet containing both high- and low-
quality foods (Freeland and Janzen 1974; Dearing et al. 2000). However, this was not the case in our study, where the low nutrient and high PSC content of subalpine fir seeds appears to have almost completely precluded their use (both consumption and storage) by rodents. Both rodent species visited subalpine fir seed patches, and deer mice sampled small quantities of seeds, but no seeds were removed from patches, and most individuals of both species left the patches without consuming any seeds. High abundance did not confer any value to these low-quality seeds, and even when exaggeratedly abundant relative to naturally available seed densities (Lobo and Millar in press/Chapter 5), subalpine fir seeds had almost no current or future value to foraging rodents. PSCs in some cached plants degrade over time (Roy and Bergeron 1990; Dearing 1997; Müller-Schwarze et al. 2001), but PSCs in cached seeds, containing live tissue may not (Shimada 2001b; Smallwood et al. 2001; Wood 2005); this requires experimental testing in subalpine fir seeds.

White spruce seeds were consumed in situ more frequently than removed by mice in both high- and low-abundance patches. However, the disparity between the two behaviours was considerably lower when seed abundance was high; in situ consumption was observed 1.4 times more frequently than removal when experimental seeds were abundant, compared to 8.3 times more frequently when seeds were scarce. Overall, white spruce seed abundance had the greatest effect on removal behaviour; the frequency of feeding was similar under both high- and low-abundance conditions, but mice removed seeds from patches most frequently when experimental seed abundance was high, and left the patch without consuming or removing seeds most frequently when seed abundance was low. Our results demonstrate a strong interaction between seed abundance and
quality on the foraging decisions of rodents, where caching, but not consumption, rates of high-quality seeds varied with seed abundance, but abundance did not influence the frequency or nature of use of low-quality seeds. Rodents mostly ignored low-quality seeds even when inundated with this food source, demonstrating the relative importance of seed quality in this interaction.

The increased removal of white spruce seeds by mice during high seed-abundance conditions agrees with previous studies on rodent foraging responses to masting (Jensen 1985; Vander Wall 1997; Jansen et al. 2004). However, similar frequencies of in situ consumption between high- and low-seed abundance conditions have not been previously reported. Immediate consumption of seeds typically occurs to a lesser degree when seed abundance is high (Jensen 1985; Vander Wall 1997; Zhang et al. 2008), although Siberian chipmunks (Tamias sibiricus) increase both feeding and caching as the abundance of Korean pine (Pinus koraiensis) seeds increases, indicating that species-specific differences in foraging responses to seed abundance may exist (Yi et al. 2011).

The lack of difference in the frequency of in situ consumption between high- and low-abundance white spruce seed patches may indicate that mice were using their current energetic state to make decisions on the current and future values of the seeds. An animal that has not recently eaten and/or has low energy reserves when it encounters a cacheable food should choose to consume it, since that animal will place great value on immediate acquisition of energy (Kotler et al. 1999). However, an animal that is satiated and/or has high energy reserves will view the food as having low current value, and cache it based on its future value (Kotler et al. 1999). The nightly active period of deer mice in our study area began 100.37 ± 17.28 min before sunset and ended 13.10 ± 9.65 min before
sunrise (Herdman 2005). The average times of sunset and sunrise were 21:32 and 06:06, respectively (±18 min; Environment Canada), and we observed mice visiting seed patches beginning at approximately 20:00 and ending at approximately 06:00. Where we have reliable time data, 70% of the observed visits of mice removing seeds from high-abundance white spruce seed patches \( n = 30 \) occurred later than halfway through the nightly active period. It appears that mice were consuming food early in their nightly activity period, either within seed patches or from outside natural sources, and removed seeds from high-density patches most frequently later in the nightly active period.

One key assumption of our study is that seeds removed by rodents from experimental patches were being stored for future use, and not simply consumed elsewhere. While we did not track the fate of removed seeds, we believe this assumption is valid for multiple reasons: (1) deer mice are known to cache conifer seeds, and are important dispersers of conifer seeds in western North America (Abbott and Quink 1970; Vander Wall 1997; Siepielski and Benkman 2008); (2) the high frequency of in situ seed consumption we observed, which would not have occurred if rodents preferred to consume seeds elsewhere; and (3) several observations of in situ feeding and seed removal in a single visit, where mice would first spend considerable time consuming seeds within the patch.

Measuring absolute GUDs was more appropriate for this study than the traditional method (e.g. Brown 1988) because it controlled for potential confounding effects of the large difference in initial masses of white spruce and subalpine fir seeds provided in patches (e.g. Davidson and Morris 2001). This difference was necessary because we wanted patches to offer a legitimate abundance of seeds to mice and voles, but the maximum daily consumption of subalpine fir seeds was considerably higher than that of
white spruce seeds in laboratory restricted-diet trials (Lobo and Millar 2011/Chapter 3). Furthermore, since all field trials were not conducted within a short period of time, deploying seed patches in the field for several nights reduced the likelihood that short-term adverse weather affected use of the patches (Kotler et al. 1993).

The absolute GUD of white spruce seed patches was higher in 2009 than 2010 and 2011, likely due to differences in rodent abundance. Weekly live-trapping revealed that $7.4 \pm 1.7$ rodents ha$^{-1}$ (Minimum Number Alive) were present at the study site in 2009, compared to $12.9 \pm 2.1$ rodents ha$^{-1}$ in 2010 and $17.4 \pm 1.1$ rodents ha$^{-1}$ in 2011. Low population density indicated less competition for food resources in 2009, likely permitting rodents to leave patches at higher seed-densities (Mitchell et al. 1990; Davidson and Morris 2001). Conversely, annual differences in other factors that affect GUDs (metabolic costs of foraging, missed opportunity costs, predation risk) were relatively minor, and their roles in altering the white spruce seed absolute GUD, were likely less significant. Metabolic costs of foraging should have been similar each year (Brown 1988; Kotler et al. 1993), since the average nightly temperature during trials was similar ($14.2 \, ^{\circ} \text{C}$ in 2009, $14.2 \, ^{\circ} \text{C}$ in 2010, $13.5 \, ^{\circ} \text{C}$ in 2011) and the average precipitation was negligible (Environment Canada). Missed opportunity costs would also have been comparable each year, since the number of experimental patches was consistent (Brown et al. 1992), although we did not quantify variation in natural forage among years. Spruce and fir cone opening occurred after trials were completed, so natural variation in seed rain did not influence our results. Patches were placed in similar microhabitats each year, but the level of canopy cover was more consistent at the 2009 site, which should have translated into lower-risk foraging and lower absolute GUDs that year (Brown 1988;
Andruskiw et al. 2008). However, while we did not measure predator abundance, it is possible that they were more abundant in 2009, which would have resulted in rodents leaving patches at higher seed densities.

The diet of deer mice consists of a variety of arthropods, fungi, and plant matter, but they are also highly granivorous (Jameson 1952; Martell and Macaulay 1981). On the other hand, red-backed vole diets consist mainly of lichens, fungi, and non-seed plant matter, and they are only partially granivorous (Maser et al. 1978; Martell 1981), but can survive on a restricted-diet of white-spruce seeds in the laboratory (Lobo and Millar 2011/Chapter 3). Consequently, the abundance of their preferred natural forage at our study sites was likely the reason why voles mostly ignored both conifer seeds when visiting seed patches.

Red-backed voles may have increased their utilization of white spruce seed patches if experiments were conducted in the fall or winter (Barry 1976; Merritt and Merritt 1978), when other natural forage is less abundant. However, this is unlikely for subalpine fir seeds, given that voles are unable to maintain body condition while consuming large amounts of these seeds (Lobo and Millar 2011/Chapter 3). Further research on the interactions between the quality and abundance of seeds, and their impact on foraging decisions, would benefit from concurrent examination of the impact of seasonal changes as well.

The masting-enhanced hoarding hypothesis (Zhang et al. 2008) states that the high abundance of seeds in mast years promotes caching by seed predators, which in turn could benefit seed dispersal and recruitment. Our observations indicate that this
hypothesis, and its subsequent beneficial outcome for the masting species, is unlikely for subalpine fir trees. Rodents are believed to be important predators of subalpine fir seeds (Alexander et al. 1990); however, high seed abundance did not facilitate caching of subalpine fir seeds, and rodents’ almost-complete avoidance of subalpine fir seeds likely plays a role in the high ratio of fir to spruce seedlings observed in mixed forests (Abbott 1962). Given the large resource-investment required for masting (Kelly and Sork 2002), but the efficacy of PSCs in deterring seed predation by rodents, the function of masting by subalpine fir trees requires further consideration.

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Chapter 5

5 Small mammal population responses to northern conifer mast

5.1 Introduction

Resource pulses greatly affect community dynamics and interactions in terrestrial ecosystems (Ostfeld and Keesing 2000). One common terrestrial resource pulse is mast seeding, defined as the intermittent, synchronous production of large seed crops by most reproductive adults in a plant population (Silvertown 1980; Ostfeld and Keesing 2000). The most well-documented hypothesis for the ultimate function of mast seeding is predator satiation; periodic production of large seed crops allows a greater proportion of seeds to escape predation, thereby enhancing the reproductive success of individual plants (Janzen 1971; Silvertown 1980; Kelly and Sork 2002). Selection for high degrees of synchrony should be great, as asynchronous individuals can experience nearly 100% seed predation during years of low neighbouring seed production (Janzen 1971; Curran and Leighton 2000; Schnurr et al. 2002).

While predator satiation enhances relative seed survival, large fluctuations in seed production also affect populations of post-dispersal seed predators (Silvertown 1980; Kelly and Sork 2002), such as small mammals. Tree seeds are an integral component of

\[4\] A version of this chapter has been accepted for publication.

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the diet of many forest rodents, and seed abundance can be a critical limiting factor in the regulation of their populations (Jameson 1952; Silvertown 1980). There is considerable evidence that annual fluctuations of rodent populations in deciduous forests in Europe and eastern North America are directly linked to fall seed production by species of oak (Quercus spp.), maple (Acer spp.), and beech (Fagus spp.; Jensen 1982; Pucek et al. 1993; Ostfeld et al. 1996; Wolff 1996; McCracken et al. 1999; McShea 2000; Ostfeld and Keesing 2000; Schnurr et al. 2002; Selås et al. 2002; Elias et al. 2006; Falls et al. 2007).

Population densities of several species of mice (e.g. Apodemus flavicollis, Apodemus sylvaticus, Peromyscus leucopus, Peromyscus maniculatus) and voles (e.g. Myodes gapperi, Myodes glareolus) increase following fall masting events, primarily because increased seed supply allows individuals to sustain breeding into late fall and winter (Jensen 1982; Pucek et al. 1993; Wolff 1996; Ostfeld and Keesing 2000). Energy requirements of rodents normally exceed the supply of seeds available to them in low seed-production years, but the energy supply available in mast years far exceeds requirements (Wolff 1996). Increased winter survival and earlier onset of spring breeding may also occur following deciduous masting (Hansen and Batzli 1979; Pucek et al. 1993; McCracken et al. 1999). However, low seed production in the fall following a mast year cannot sustain high rodent populations, leading to decreased overwinter survival and low population densities in the subsequent year (Jensen 1982; Pucek et al. 1993; Ostfeld et al. 1996; Wolff 1996; McCracken et al. 1999; Falls et al. 2007).

While the relationship between rodent populations and mast seeding is clear and well-documented in deciduous forests, there is little evidence of consistent effects of fall conifer masting on rodent populations. Gashwiler (1979) and/or Jameson (1953) are
most-often cited as providing evidence of a relationship between small mammal population fluctuations and previous conifer seed crops (e.g. Halvorson 1982; Vessey 1987; McShea and Gilles 1992; McMurray et al. 1996; Duchesne et al. 2000; Falls et al. 2007). However, Gashwiler (1979) found that spring/summer deer mouse (*P. maniculatus*) populations in Oregon did not differ following good and poor fall Douglas fir (*Pseudotsuga menziesii*) seed crops. Instead, population densities were higher in the fall following a mast year, indicating a delayed response to increased seed supply, mainly due to enhanced spring breeding (Gashwiler 1979). Alternatively, Jameson (1953) found a correlation between high fall conifer (Douglas fir, ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*)) seed production and concurrent reproductive activity in deer mice in California, leading to a slightly elevated population in the spring following a masting event, but no effects on survival rates. Breeding began earlier and was more intense two years after the masting event, when the previous fall’s seed production was considerably lower (Jameson 1953). Furthermore, these results were confounded by concurrent heavy crops of oaks, silktassel (*Garrya elliptica*) and manzanitas (*Arctostaphylos* spp.; Jameson 1953).

Other small mammal population studies in coniferous forests are relatively uncommon, and have not found consistent results. Halvorson (1982) reported an increased deer mouse population after a heavy mixed-conifer seed crop, although the mechanisms of population change were unclear. Similarly, Elias et al. (2006) reported that peak red-backed vole (*M. gapperi*) populations were preceded by heavy white pine seed (*Pinus strobus*) crops, but only in four out of five cases, leading to speculation of a spurious correlation. Selås et al. (2002) found that bank vole (*M. glareolus*) populations were
influenced by Norway spruce (*Picea abies*) seed production, but in conjunction with, and to a much lesser degree than, bilberry (*Vaccinium myrtillus*) production. Other studies have shown declines in rodent populations after conifer masting (Stickel and Warbach 1960), or no relationship between conifer seed production and populations (McCracken et al. 1999; Schnurr et al. 2002; Boonstra and Krebs 2006).

Conflicting evidence for an effect of conifer mast seeding on small mammal populations may partly result from concurrent deciduous seed production (Jameson 1953; Selås et al. 2002; McCracken et al. 1999; Schnurr et al. 2002; Elias et al. 2006). This could modify expected population responses because conifer seed crops are typically smaller than deciduous seed crops (Hansson 1971), and rodents prefer deciduous seeds over conifer seeds when both are present simultaneously (Nopp-Mayr et al. 2012). Furthermore, seeds of some conifer species are rarely consumed or cached by rodents, even when abundant (Sullivan 1978; Lobo et al. *in review/Chapter 4*), which could mitigate any population response to mast seeding.

Given the general lack of understanding of how rodent populations are affected by conifer seed production, and the significance of their population fluctuations for structuring bird and insect community dynamics (Elkinton et al. 1996; Ostfeld et al. 1996; McShea 2000; Ostfeld and Keesing 2000), long-term datasets on annual conifer seed production and intensive rodent trapping can provide valuable insights into this important interaction in forest ecosystems. The effect of conifer masting on population dynamics, and its implications for the predator satiation hypothesis, have recently been well-documented for major mammalian pre-dispersal seed predators (*Tamiasciurus hudsonicus, Sciurus vulgaris*; Boutin et al. 2006; Fletcher et al. 2010; Archibald et al.
2012). However, the efficacy of this hypothesis for post-dispersal conifer-seed predators is unclear. A key feature of predator satiation is that populations of seed predators are maintained at low densities during intermast years, allowing greater escape of seeds during the next masting event (Janzen 1971; Kelly and Sork 2002). This requires validation in conifer-rodent interactions.

Here we report on a 10-year study examining the mast seeding patterns of two northern conifers, white spruce (*Picea glauca*) and subalpine fir (*Abies lasiocarpa*), and deer mouse population dynamics in the Canadian Rocky Mountains. White spruce seeds are highly palatable to mice (Radvanyi 1970; Peters et al. 2004; Lobo et al. 2009/Chapter 2), and are cached when encountered in large quantities in the field (Lobo et al. in review/Chapter 4). Diets heavily-comprised of spruce seeds also advance maturation in male bank voles (Eccard and Ylönen 2001). Conversely, fir seeds are avoided if other food options are available (Lobo et al. 2009/Chapter 2; Lobo et al. in review/Chapter 4), likely because they contain high concentrations of plant secondary compounds (Abbott 1962; Smith 1970; Schreiner et al. 2000; Lobo and Millar 2011/Chapter 3; Rubino et al. 2012). Deer mice can maintain body condition on a diet restricted to either conifer seed, but must alter their food intake and digestion patterns in order to persist on subalpine fir seed-diets (Lobo and Millar 2011/Chapter 3).

Based on small mammal population responses to deciduous mast seeding, and our knowledge of interactions between individual mice and conifer seeds, we hypothesized that there would be a positive relationship between mouse populations and white spruce seed production, but no effect of subalpine fir masting. We predicted that the increased food supply from fall spruce masting would consequently enhance the overwinter
survival and spring body condition of mice, and allow for earlier, increased, and extended breeding in the spring and summer following the masting event. These factors should generate increased mouse densities in the spring and summer following spruce masting, relative to years of low seed production.

5.2 Methods

5.2.1 Study area and species

This study was conducted in the Kananaskis Valley in SW Alberta, Canada, a 4200-km² multi-use area located in the front ranges of the Canadian Rocky Mountains. The main tree species in this area are white spruce, subalpine fir, and lodgepole pine (*Pinus contorta*). White spruce and subalpine fir are masting species (Alexander et al. 1990; Nienstaedt and Zasada 1990), while lodgepole pine produces consistent annual seed crops, but in predominately serotinous cones (Despain 2001). Spruce and fir seeds mature in late-summer, and are released when cones open in the fall (Alexander et al. 1990; Nienstaedt and Zasada 1990).

The most abundant rodent species in the study area is the deer mouse, but red-backed voles are also common in densely-forested areas (Millar et al. 1985). Deer mice are omnivorous, and seeds are a significant component of their diet during most of the year (Jameson 1952; Martell and Macaulay 1981). Population densities of mice in the Kananaskis Valley are generally low and show annual cycles; densities typically increase over the summer and decline through the fall and winter (Millar and McAdam 2001). Breeding is highly seasonal and constrained; overwintered adults initiate reproduction in the spring, and females can produce multiple litters in a summer, but breeding by young-
of-the-year is rare (Teferi and Millar 1993; McAdam and Millar 1999a; Millar and McAdam 2001). These populations have a relatively long generation time and slow turnover, with survival and longevity enhanced compared to populations in more temperate environments (Millar 1994; Millar and McAdam 2001).

5.2.2 Cone index

We estimated fall cone production by counting the number of cones visible on one side of the top 3 m of each of 11 white spruce and 8 subalpine fir trees, each year in late August between 2001-2011 (see LaMontagne et al. 2005). The same trees, scattered across the valley, were used each year in order to obtain a representative estimate of the annual variability in cone production in our study area. The number of cones on each tree was ln(x+1) transformed, and these transformed values were averaged among all trees of the same species within each year to derive its cone index for that year (Boutin et al. 2006).

Given the relatively small sample size of trees used, we assessed the precision of our long-term cone indices by comparing these data to the annual average fall cone production of 50-170 random white spruce and subalpine fir trees for 2008-2011. Correlation coefficients assessing the relationship between long-term and random-tree cone indices were strongly positive for both spruce (Spearman’s $\rho = 1.00$) and fir (Spearman’s $\rho = 0.78$, $p = 0.11$).

5.2.3 Seed rain

We measured seed rain on three study sites from 2006-2010 using seed traps constructed from plastic storage bins (0.61 m × 0.40 m × 0.51 m) fitted with a screen net inside to catch seeds. Chicken wire with 0.5-inch diameter openings was placed along the top to
keep animals out, and traps were weighed down with rocks to limit disturbance by wildlife and the elements. 8-13 seed traps were randomly placed beneath the forest canopy at each site in mid-August, and left out over the fall and winter seasons. They were then brought into the lab the following spring, where contents were dried, identified, and weighed.

5.2.4 Small mammal trapping

Deer mouse populations were monitored at a long-term study site (50°45.99’N, 115°08.62W) located in optimum deer mouse habitat (Millar et al. 1985). The effective trapped area was estimated as 1.68 ha (inclusive boundary strip method; Stickel 1954). Trapping was conducted 2-3 times per week from May-September, 2002-2011, using approximately 40 Longworth live traps (one trap per station, 20 m spacing) containing cotton bedding and baited with sunflower seeds and oats. Each mouse was tagged (Monel #1 ear tags affixed to each ear) at first capture. Upon each capture, tag number, mass (nearest 0.5 g, using a Pesola spring balance), sex, age, and breeding condition were recorded. Age was assigned as overwintered adult (OW) or young-of-the-year (YY), based on size and pelage colour. Breeding condition of males was classified as scrotal or non-scrotal, and females as perforate or non-perforate, pregnant, lactating, or pregnant and lactating. First parturition of each breeding female was estimated as the median date between the last capture as pregnant and first subsequent capture as lactating (Millar and Herdman 2004). Since females breed post-partum, and lactation is continuous between litters, subsequent parturitions were identified by a several gram mass loss following pregnancy (Millar and Herdman 2004).
5.2.5 Data analysis

5.2.5.1 Population dynamics

Average Jolly trappability (Jolly 1965; Jolly and Dickson 1983), defined as the probability that an individual in the population will be encountered during a given trapping session (Krebs and Boonstra 1984), was calculated for each year.

5.2.5.1.1 Population density

We used Pollock’s (1982) Robust Design Model, implemented in Program MARK (White and Burnham 1999), to estimate the abundance of deer mice. This model uses closed population models (Otis et al. 1978) to estimate abundance within each primary trapping session, and the Cormack-Jolly-Seber (CJS) open population live-recapture model (Cormack 1964; Jolly 1965; Seber 1965) to estimate the probability of survival between primary trapping sessions. We considered each week as a primary trapping session in our dataset, where the effects of migration, mortality, and recruitment were assumed to be negligible within each week, but not among weeks (Pollock 1982).

We estimated abundance using the Robust Design Model for each year separately. Within each year, we examined a candidate set of eight models that varied time, behaviour, and heterogeneity effects on the probability of capture in all possible combinations (Otis et al. 1978; White and Burnham 1999). All models constrained temporary emigration and immigration rates to be equal, but allowed them to vary as a function of time based on the assumption that the probability of movement changes as populations grow over the breeding season (Fairbairn 1978; Millar and Innes 1983). All models also allowed the probability of survival between trapping sessions to vary as a function of time. The logit link was used for all analyses.
Before comparing models, we assessed the fit of the most fully-parameterized model to the data for each year using a bootstrap goodness-of-fit procedure (White and Burnham 1999). No bootstrap goodness-of-fit test exists for the Robust Design Model in Program MARK, so general goodness of fit was assessed by treating the data as if they were recapture-only (CJS) data (see Lee and Tietje 2005), and confirming that the data fit the CJS model assumptions of equal encounter and equal survival probabilities of all marked individuals within a given sampling period (Cormack 1964; Jolly 1965; Seber 1965; White and Burnham 1999). We generated 1000 simulations of capture histories for each year, and the resulting deviances were compared with the observed deviance from the most fully-parameterized model. There was no evidence of significant deviations from the assumptions of the CJS model in any year (all $p > 0.05$), so no variance inflation factors were applied.

Akaike’s Information Criterion corrected for small sample sizes ($\text{AIC}_c$; Akaike 1987; Hurwich and Tsai 1989) was used for model selection, with the best-supported model having the lowest $\text{AIC}_c$ score (Burnham and Anderson 2002). Models were compared to the best-supported model based on differences in $\text{AIC}_c$ scores ($\Delta\text{AIC}_c$) and $\text{AIC}_c$ weight (Burnham and Anderson 2002). Models with $\Delta\text{AIC}_c$ scores $< 2$ indicate substantial support in the data, and scores of 4-7 indicate weak support; scores $> 10$ show no support in the data (Burnham and Anderson 2002). In order to incorporate model selection uncertainty, we used model averaging in Program MARK to obtain a weighted average for abundance estimates from any models in the candidate set that had $\Delta\text{AIC}_c$ scores $\leq 4$ and $\text{AIC}_c$ weights $\geq 0.10$. Abundance estimates were generated for the full population
each year, as well as OW and YY mice separately. Population densities were calculated by dividing abundance estimates by the effective trapped area.

We also validated our Robust Design Model abundance estimates by testing their relationship with corresponding Minimum Number Alive estimates (Krebs 1966) for the full population. These estimates were highly correlated ($R = 0.91, p < 0.001$).

5.2.5.1.2 Population growth

We calculated population growth as the intrinsic rate of increase week$^{-1}$, $r$:

$$ r = \frac{\ln N_{t+1} - \ln N_t}{\text{Number of weeks elapsed}} $$

Annual summer population growth rates ($N_t =$ average spring density, $N_{t+1} =$ average fall density) were calculated for the full population, as well as for OW mice separately ($N_t =$ average spring density, $N_{t+1} =$ average fall OW density). Annual winter population growth rates ($N_t =$ average fall density, $N_{t+1} =$ average spring density) were also calculated for the full population.

5.2.5.1.3 Overwinter survival

We estimated overwinter survival as the proportion of tagged fall resident YY females that were also trapped the following spring. Female deer mice are highly philopatric (Teferi and Millar 1994), so restricting overwinter survival calculations to females was less likely to confound estimates of mortality and emigration.
5.2.5.2 Body mass

Body masses of females were excluded from analyses in order to avoid potential effects of undetected pregnancies. We averaged multiple body mass recordings of each male, and these values were used to calculate annual average spring, summer, and fall masses of OW males. Annual average mass at first capture of YY males was also calculated. We estimated individual growth rates of juvenile males as the slope of the linear regression of mass on Julian date of capture; growth of juveniles (age 21-42 days) is known to be approximately linear (Millar 1982; Millar and Innes 1983; McAdam and Millar 1999b).

5.2.5.3 Breeding

We estimated annual initiation of breeding as the average of the first recorded parturition of the year and all parturitions within 30 days of the first parturition (Millar and Herdman 2004). Since post-partum gestation is typically 4 weeks (Millar 1989), it is unlikely that our estimate included any second parturitions. General timing of breeding each year was estimated as the average of all parturition dates recorded in the year (Millar and Herdman 2004), while annual cessation of breeding was estimated as the average of the last recorded parturition date and the last recorded date of YY emergence – 21 days (age of independence for YY mice; Millar et al. 1986).

We also calculated the proportions of scrotal OW males in the spring, summer, and fall of each year, as well as the annual proportions of resident OW and YY pregnant females, and the annual proportions of resident OW females that had multiple litters.
5.2.5.4 Cone and seed production

Cone indices are an accurate measure of annual cone production (LaMontagne et al. 2005; Boutin et al. 2006), but likely overestimate the actual amount of seed that becomes available to rodents during the seed rain period because pre-dispersal conifer seed predation can be significant (e.g. Smith 1968; Fletcher et al. 2010). Estimates of average seed rain densities are ideal indicators of seed availability to post-dispersal seed predators. However, our seed rain data were limited to only 5 years, while cone production records extended for 11 years. Given that long-term datasets can reveal ecological relationships that are masked in short-term studies (see McCracken et al. 1999 and Elias et al. 2006), we used the long-term cone index as our indicator of seed production when examining relationships with deer mouse population, body mass, and breeding parameters. However, we first tested the relationship between annual cone indices and average seed rain densities, in order to verify the suitability of using the annual variation in cone production as an indicator of variation in seed availability to mice (see Results section).

5.2.5.5 Statistical analysis

We screened all data for errors, missing values, outliers, and deviations from normality prior to statistical analyses. Proportions were arcsine square root transformed, and other population, body mass, and breeding data were ln(x+1) transformed. Unless otherwise stated, analyses were performed using R version 2.14.2 (R Development Core Team 2012) and SPSS version 16.0 (SPSS Inc. 2007), \( \alpha \) was set to 0.05, and values are presented as means ± SE.
The relationship between 2006-2010 cone indices and average seed rain densities was assessed for white spruce and subalpine fir separately using Spearman’s rank correlations. We used the coefficient of variation (CV) to describe variability in average cone production and seed rain densities among years.

We used information-theoretic methods (Burnham and Anderson 2002) to evaluate 14 plausible linear models explaining annual variation in population densities and growth rates, and overwinter survival of deer mice. The simplest model was a random walk, $y = a + \varepsilon_t$, where $\varepsilon_t$ is a normally distributed random variable with mean zero. In alternate models, we included the previous fall’s spruce, fir, and total cone indices, and previous fall/spring population density as covariates, as well as various biologically-relevant combinations of these factors. We used the CV and the s-index (standard deviation of log$_{10}$($N+1$); Henttonen et al. 1985) to describe variability in average spring and fall population densities among years.

We used CJS models, implemented in Program MARK, to evaluate the relationship between summer survival of OW mice and the previous fall’s spruce, fir, and total cone indices. The probability of survival between trapping sessions was modeled as a function of these covariates and time, while the encounter probability was modeled only as a function of time. Our candidate model set contained 28 models, and model comparison and selection was performed using $\Delta AIC_c$ (described in detail earlier). The logit link was used for these analyses.

Backwards stepwise linear regression models were used to test for the effects of the previous fall’s spruce and fir cone production on all body mass and breeding parameters.
The $\alpha$-to-leave was set to 0.10. Linear regression models were also used to examine the relationships between these parameters and previous total cone production.

5.3 Results

5.3.1 Cone and seed production

There was a significant positive relationship between annual cone indices (Figure 5.1) and corresponding average seed rain densities (Figure 5.2) for white spruce (Spearman’s $\rho = 0.90, p = 0.04$), but not subalpine fir (Spearman’s $\rho = 0.34, p = 0.58$). Average cone production of both species varied considerably among years (spruce CV = 1.34, fir CV = 1.29), but average seed rain densities were less so (spruce CV = 1.01, fir CV = 0.67).

Mast years, based on cone counts, were identified using the standardized deviate method (LaMontagne and Boutin 2007, 2009). White spruce masted in 2001 and 2003, and subalpine fir in 2001 and 2002; cone production was not “all-or-nothing”, with both species producing bumper crops periodically (Figure 5.1). Spruce and fir cone indices were not significantly correlated ($R = 0.55, p = 0.09$).

5.3.2 Population density

Average annual Jolly trappability was high (69.86 ± 3.92 %) over the study period, allowing population sizes to be estimated accurately (Hilborn et al. 1976). Robust Design Model results for deer mouse abundance estimation each year are presented in Appendix A. Average spring population densities ranged from 3.57 to 10.42 ha$^{-1}$, while fall densities ranged from 7.44 to 18.45 ha$^{-1}$ (Figure 5.3).
Figure 5.1. White spruce and subalpine fir cone production in the Kananaskis Valley, Alberta from 2001-2011. Cone indices were calculated by averaging ln(x+1) transformed cone counts of trees across the valley each fall. Dotted lines represent the average cone index for each species over the study period.
Figure 5.2. White spruce and subalpine fir seed rain densities in the Kananaskis Valley, Alberta from 2006-2010. Seed rain was measured using seed traps at three long-term study sites across the valley. Bars represent means ± SE.
Long-term white spruce and subalpine fir cone production, and deer mouse population densities in the Kananaskis Valley, Alberta. Population densities were estimated from mark-recapture data using Pollock’s (1982) Robust Design Model implemented in Program MARK (White and Burnham 1999), and are represented as spring, summer, and fall means ± SE, each year between 2002-2011.
Population variability among years was low, but similar, in the spring (CV = 0.31, s-index = 0.15) and fall (CV = 0.38, s-index = 0.16). Variability in fall YY densities was similar to the full population (CV = 0.37, s-index = 0.16), while variability in fall OW densities was considerably higher (CV = 0.70, s-index = 0.29). Still, the overall degree of population fluctuation among years was quite low (s-index < 0.50; Henttonen et al. 1985) for all groups. Summer population growth was negative in 3 of the 10 years (2004, 2005, 2007; Figure 5.3). Population density typically declined over winter, but positive growth over 2 winters (2004-2005, 2005-2006) indicates that immigration occasionally contributed to the spring densities (Figure 5.3).

Annual variation in average spring and fall population densities were not explained by the previous fall’s white spruce, subalpine fir, or total cone production (Table 5.1). They were also not explained by population densities in the preceding fall or spring, respectively (Table 5.1). However, the most parsimonious model to explain the annual variation in average summer densities contained the previous fall’s fir cone production (Table 5.1); mouse populations were higher in the summers following heavy fir cone crops (Figure 5.4a). We observed the same pattern when considering OW (Figure 5.4b) and YY (Figure 5.4c) densities separately (Table 5.1).

5.3.3 Population growth and survival

Annual variation in summer population growth was not explained by cone production during the previous fall, but was inversely related to the preceding spring population density (Table 5.1; Figure 5.5). Winter population growth and overwinter survival were not related to any of the covariates (Table 5.1).
Evaluation of the parsimony of linear models examining the annual variation in average deer mouse density ($N$), population growth ($r$), and overwinter survival ($\Phi$) relative to previous population density ($N_{t-1}$) and white spruce ($S_{t-1}$), subalpine fir ($F_{t-1}$), and total ($T_{t-1}$) cone indices. Only the most supported models are shown; the complete candidate model set for each population parameter is presented in Appendix A. $\varepsilon_t$ refers to a normally distributed random variable with mean zero, and $K$ is the number of estimable parameters in each model. Model results are provided for the full population, as well as overwintered (OW) and young-of-the-year (YY) mice separately. The best-supported models, based on AIC$_c$ scores, are highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>Full population</th>
<th>OW population</th>
<th>YY population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$K$</td>
<td>AIC$_c$</td>
<td>$\Delta$AIC$_c$</td>
</tr>
<tr>
<td>Population density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$N = a + \varepsilon_t$</td>
<td>3</td>
<td>11.31</td>
<td>0.00</td>
</tr>
<tr>
<td>$N = a + bS_{t-1} + \varepsilon_t$</td>
<td>4</td>
<td>17.36</td>
<td>6.05</td>
</tr>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$N = a + bF_{t-1} + \varepsilon_t$</td>
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<td>8.39</td>
<td>0.00</td>
</tr>
<tr>
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<td>11.06</td>
<td>2.67</td>
</tr>
<tr>
<td>Fall</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$N = a + \varepsilon_t$</td>
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<td>15.17</td>
<td>0.00</td>
</tr>
<tr>
<td>$N = a + bF_{t-1} + \varepsilon_t$</td>
<td>4</td>
<td>19.60</td>
<td>4.43</td>
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<tr>
<td>Population growth</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r = a + \varepsilon_t$</td>
<td>3</td>
<td>-55.36</td>
<td>0.00</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + \varepsilon_t$</td>
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<td>-41.06</td>
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</tr>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r = a + \varepsilon_t$</td>
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</tr>
<tr>
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<td>-35.59</td>
<td>0.00</td>
</tr>
<tr>
<td>Overwinter survival</td>
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<td></td>
</tr>
<tr>
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<tr>
<td>$\Phi = a + bF_{t-1} + \varepsilon_t$</td>
<td>4</td>
<td>19.24</td>
<td>7.06</td>
</tr>
</tbody>
</table>
Figure 5.4. Average summer deer mouse population densities for the (a) full, (b) overwintered (OW), and (c) young-of-the-year (YY) populations in relation to the previous fall’s subalpine fir cone production, the best predictor in models examining annual variation in average summer population densities between 2002-2011.
Figure 5.5. Deer mouse summer population growth (intrinsic rate of increase week\(^{-1}\)) in relation to the preceding spring mouse population density, the best predictor in models examining annual variation in summer population growth rates between 2002-2011.
In the most parsimonious CJS model, summer survival of OW mice was dependent on both the previous fall’s white spruce and subalpine fir cone production (Table 5.2). The probability of survival between trapping sessions was inversely related to previous spruce cone production ($\beta = -0.12 \pm 0.04, 95\% \text{ CI}(\beta) = -0.19, -0.05$), suggesting lower survival of OW mice after heavy spruce cone crops, and positively related to previous fir cone production ($\beta = 0.10 \pm 0.06, 95\% \text{ CI}(\beta) = 0.00, 0.21$), although the confidence interval overlapped zero. The second-ranked model also had substantial support (Table 5.2), but only contained a negative relationship between summer survival and the previous fall’s spruce cone index ($\beta = -0.08 \pm 0.03, 95\% \text{ CI}(\beta) = -0.14, -0.03$).

While the CJS model allowed us to examine the relationship between fall cone production and the probability of survival between trapping sessions in the following summer, we used the summer population growth rate of OW mice as an index of survival over the entire breeding season (spring to fall). Using this metric, annual variation in survival over the entire breeding season was not explained by spring population density or the previous fall’s cone production (Table 5.1).

5.3.4 Body mass

Average spring and fall masses of OW males were not related to the previous fall’s conifer cone production (Table 5.3). However, the final stepwise regression model explaining annual variation in average summer masses of OW males contained a positive relationship with the previous fall’s subalpine fir cone index, and was nearly statistically significant (Table 5.3); this suggests that OW males were heavier in the summers after heavy fir cone crops (Figure 5.6).
Table 5.2. Evaluation of the parsimony of Cormack-Jolly-Seber models examining the relationship between summer survival of overwintered deer mice and the previous fall’s white spruce ($S_{t-1}$), subalpine fir ($F_{t-1}$), and total ($T_{t-1}$) cone indices. The probability of survival between trapping sessions ($\Phi$) was modeled as a function of these covariates and time ($t$), while the encounter probability ($p$) was modeled only as a function of time. A period (".") indicates that the parameter is constant, and $K$ is the number of estimable parameters in each model. The best-supported models, based on $\text{AIC}_c$ scores and $\text{AIC}_c$ weight ($w_i$), are highlighted. Only models with $w_i \geq 0.01$ are shown; the complete candidate model set is presented in Appendix A.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta \text{AIC}_c$</th>
<th>$w_i$</th>
<th>$K$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi(S_{t-1} + F_{t-1}) \cdot p(\cdot)$</td>
<td>7323.88</td>
<td>0.00</td>
<td>0.58</td>
<td>4</td>
</tr>
<tr>
<td>$\Phi(S_{t-1}) \cdot p(\cdot)$</td>
<td>7325.42</td>
<td>1.54</td>
<td>0.27</td>
<td>3</td>
</tr>
<tr>
<td>$\Phi(S_{t-1} + F_{t-1}) \cdot p(t)$</td>
<td>7328.47</td>
<td>4.59</td>
<td>0.06</td>
<td>34</td>
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<tr>
<td>$\Phi(T_{t-1}) \cdot p(\cdot)$</td>
<td>7329.46</td>
<td>5.58</td>
<td>0.04</td>
<td>3</td>
</tr>
<tr>
<td>$\Phi(S_{t-1}) \cdot p(t)$</td>
<td>7329.92</td>
<td>6.04</td>
<td>0.03</td>
<td>33</td>
</tr>
<tr>
<td>$\Phi(\cdot) \cdot p(\cdot)$</td>
<td>7331.65</td>
<td>7.77</td>
<td>0.01</td>
<td>2</td>
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</tbody>
</table>
Table 5.3. Results of linear regression models testing for the effects of the previous fall’s \((t-1)\) white spruce, subalpine fir, and total cone production on various deer mouse body mass and breeding parameters. Simple linear regression models were used when examining relationships with total cone indices, and backwards stepwise regression models were used when examining relationships with spruce and fir cone indices. OW refers to overwintered mice and YY to young-of-the-year. For stepwise models: The \(\alpha\)-to-leave was set to 0.10. Highlighted models included at least one covariate in the final model; \(R^2\) and \(p\)-values are provided for the full models, and partial \(R^2\) and \(p\)-values for the covariates. Models that are not highlighted did not include either covariate in the final model; in this case, \(R^2\), partial \(R^2\), and \(p\)-values are provided for the fully-saturated model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Total cones</th>
<th>Full stepwise model</th>
<th>White spruce(_{t-1})</th>
<th>Subalpine fir(_{t-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(R^2)</td>
<td>(p)</td>
<td>(R^2)</td>
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</tr>
<tr>
<td><strong>Body mass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average OW male, spring</td>
<td>0.06</td>
<td>0.53</td>
<td>0.29</td>
<td>0.36</td>
</tr>
<tr>
<td>Average \textit{OW male, summer}</td>
<td>0.20</td>
<td>0.18</td>
<td>\textbf{0.33}</td>
<td>\textbf{0.08}</td>
</tr>
<tr>
<td>Average OW male, fall</td>
<td>0.02</td>
<td>0.70</td>
<td>0.07</td>
<td>0.80</td>
</tr>
<tr>
<td>Average YY male mass at first capture</td>
<td>0.13</td>
<td>0.30</td>
<td>0.20</td>
<td>0.47</td>
</tr>
<tr>
<td>Average YY male growth rate</td>
<td>0.21</td>
<td>0.18</td>
<td>0.21</td>
<td>0.43</td>
</tr>
<tr>
<td><strong>Breeding</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initiation</td>
<td>0.004</td>
<td>0.87</td>
<td>0.01</td>
<td>0.98</td>
</tr>
<tr>
<td>General timing</td>
<td>0.03</td>
<td>0.63</td>
<td>0.10</td>
<td>0.68</td>
</tr>
<tr>
<td>Length of season</td>
<td>0.11</td>
<td>0.34</td>
<td>0.12</td>
<td>0.64</td>
</tr>
<tr>
<td>Proportion of scrotal OW males, spring</td>
<td>0.04</td>
<td>0.61</td>
<td>0.13</td>
<td>0.65</td>
</tr>
<tr>
<td>Proportion of scrotal OW males, summer</td>
<td>0.01</td>
<td>0.77</td>
<td>0.26</td>
<td>0.35</td>
</tr>
<tr>
<td>Proportion of scrotal OW males, fall</td>
<td>0.09</td>
<td>0.42</td>
<td>0.14</td>
<td>0.65</td>
</tr>
<tr>
<td>\textit{Proportion of pregnant OW females}</td>
<td>0.04</td>
<td>0.59</td>
<td>\textbf{0.74}</td>
<td>\textbf{0.01}</td>
</tr>
<tr>
<td>Proportion of pregnant YY females</td>
<td>0.03</td>
<td>0.64</td>
<td>0.26</td>
<td>0.41</td>
</tr>
<tr>
<td>Proportion of OW females with multiple litters</td>
<td>0.14</td>
<td>0.29</td>
<td>0.17</td>
<td>0.52</td>
</tr>
</tbody>
</table>
Figure 5.6. Average summer mass of overwintered (OW) male deer mice in relation to the previous fall’s subalpine fir cone production, the best predictor in models examining annual variation in average summer body masses between 2002-2011 ($R^2 = 0.33$, $p = 0.08$).
Figure 5.7. The proportion of pregnant resident overwintered (OW) female deer mice (arcsine square root transformed) in relation to the previous fall’s (a) subalpine fir (partial $R^2 = 0.72$, $p = 0.003$), and (b) white spruce (partial $R^2 = 0.37$, $p = 0.02$) cone production. Both parameters were included as covariates in the final backwards stepwise regression model ($R^2 = 0.74$, $p = 0.01$) examining annual variation in the proportions of pregnant resident OW females between 2002-2011.
The average mass at first capture of YY males and the average growth rates of juvenile males were not associated with the previous fall’s spruce, fir, or total cone production (Table 5.3).

5.3.5 Breeding

Annual variation in the initiation of spring breeding, general timing of breeding, and length of the breeding season were not explained by the previous fall’s spruce, fir, or total cone production (Table 5.3). However, the proportion of pregnant resident OW females was positively related to the previous fall’s subalpine fir cone index, and inversely related to previous white spruce cone production (Table 5.3; Figure 5.7). The full model explained 74% of the annual variation in the proportions of pregnant resident OW females, and was mostly influenced by fir cone production (Table 5.3). No other breeding parameters were associated with previous cone production by either conifer species (Table 5.3).

5.4 Discussion

Deer mouse demography was not positively affected by white spruce mast seeding, despite all contrary indications from individual-level experiments (Lobo et al. 2009/Chapter 2; Lobo and Millar 2011/Chapter 3; Lobo et al. in review/Chapter 4). Conversely, we observed an unexpected delayed effect of subalpine fir mast seeding, where increased fall fir seed production did not influence overwinter or spring mouse demography, but instead enhanced summer survival, body masses, and pregnancy rates of overwintered adults. This led to increased summer population densities (full, overwinter adults, and young-of-the-year) in the year following fir mast seeding. Previous total cone
production was not a consistent strong predictor of annual variation in population, body mass, or breeding parameters, highlighting the particular significance of fir seeds in this consumer-resource pulse system.

5.4.1 Cone and seed production

White spruce cone indices and seed rain densities were positively correlated, confirming that variation in cone production was an appropriate indicator of variation in spruce seed availability to deer mice. Conversely, subalpine fir seed rain was not related to cone production, but likely because fir trees were not prevalent in the spruce-dominated study areas where our seed traps were located. Low densities of fir trees would generate low, sporadic measurements of seed rain density, as we observed, and would likely underestimate the true annual variation in seed rain. Variability in fir cone counts over the study period was almost double that of seed rain densities recorded; if we assume that our annual seed rain measurements were truly representative of the quantities produced by subalpine fir trees in the Kananaskis Valley, this high degree of discrepancy between seed-production metrics is only possible if pre-dispersal harvesting of fir cones was rampant. However, this is highly unlikely, as fir cones and seeds are typically avoided by the dominant vertebrate pre-dispersal seed predator in our area, the North American red squirrel (T. hudsonicus).

Red squirrels clip conifer cones from trees prior to cone opening, and store them in underground larder-hoards (Donald and Boutin 2011). While we have observed a few subalpine fir cones in squirrel middens in spruce-fir mixed forests, the number of fir cones found in middens was insignificant compared the number available on trees, and the contents of middens were predominately comprised of white spruce cones, even in
areas dominated by subalpine fir trees (Lobo *unpublished data*). Cafeteria-style preference trials have also shown that squirrels consume large amounts of lodgepole pine (*Pinus contorta*) and white spruce seeds, but mostly avoid fir seeds (Lobo and Millar *unpublished data*). Similarly, Di Pierro et al. (2011) showed that European red squirrels (*S. vulgaris*) alter their habitat use with the availability of Norway spruce (*Picea abies*) cones, but are unaffected by silver fir (*Abies alba*) cone production, and rarely feed on fir seeds.

Given that pre-dispersal harvesting of fir cones is low, we expect that a significant positive relationship between fir cone counts and seed rain densities would have been observed if seed traps were placed in stands containing a higher proportion of fir trees. Fir cone production was typically lower than that of spruce, but the degree of variability over the study period was similar. Therefore, since annual variation in spruce cone counts was a reliable indicator of annual variation in seed rain (also see Dale et al. 2001), we are confident that variation in cone production accurately reflected variation in seed availability to post-dispersal seed predators for both tree species.

### 5.4.2 Population responses to white spruce seed production

Deer mouse populations did not respond to mast seeding by white spruce trees, even though mice consume (Lobo et al. 2009/Chapter 2; Lobo and Millar 2011/Chapter 3) and cache (Lobo et al. *in review*/Chapter 4) large quantities of spruce seeds available to them, and can maintain body condition for an extended period of time on a diet comprised solely of spruce seeds (Lobo and Millar 2011/Chapter 3). Increased spring rodent populations after deciduous masting are a result of both increased fall/winter breeding and higher overwinter survival (Jensen 1982; Pucek et al. 1993; Wolff 1996; Ostfeld and
Keesing 2000). At the very least, we expected that increased fall production of spruce seeds during mast years would have facilitated higher overwinter survival of mice. However, breeding is highly seasonal and more constrained in our northern study area than populations in more temperate environments. The availability of animal protein, in the form of arthropods, appears to play a major role in regulating the initiation (Desjardins 2002; von Blankenhagen et al. 2007) and cessation (Tabacaru et al. 2010) of breeding by northern small mammals. Although white spruce seeds contain abundant crude protein (Lobo and Millar 2011/Chapter 3), the low digestibility and amino acid content of plant protein, compared to animal protein, can reduce the amount of assimilable protein available to rodents (Robbins 1993); this may reduce the efficacy of spruce seeds in extending the breeding season of deer mice in our population.

We hypothesize that pre-dispersal harvesting of cones by red squirrels prevented white spruce mast seeding from effectively enhancing the food supply available to deer mice in the fall and winter, thereby mitigating mouse population responses to heavy cone crops. Red squirrels feed primarily on spruce seeds, and are dominant seed predators, with individuals annually harvesting and hoarding several thousands of spruce cones prior to cone opening (Smith 1968; Fletcher et al. 2010; Donald and Boutin 2011). Although a large proportion of cones produced on a squirrel’s territory can escape hoarding during non-mast and mast years, the degree of cone harvesting is highly variable among individuals and territories, with many spruce trees experiencing complete predation even in mast years (Fletcher et al. 2010; Archibald et al. 2012).

Most of the recent research on white spruce-red squirrel interactions has been conducted in the spruce-dominated forests of the Yukon, Canada (e.g. Boutin et al. 2006; Fletcher et
al. 2010; Donald and Boutin 2011; Archibald et al. 2012). While we have not extensively examined the behaviour of squirrels in our study area, considerably south of the Yukon, indirect evidence suggests that cone harvesting plays a major role in significantly limiting the amount of spruce seed rain produced. First, we found considerably less variation in average spruce seed rain density \((CV = 1.01)\) compared to average cone production \((CV = 1.72)\) during the same period (2006-2010); this discrepancy is likely the result of significant cone harvesting prior to opening. Second, the highest spruce seed rain density recorded from any of our seed traps was 1.85 g m\(^{-2}\), which occurred during the fall/winter of 2007, a bumper cone crop year. Based on previous estimates of spruce seed mass (2.0 mg; Greene and Johnson 1994) and the number of sound spruce seeds per cone (48; Beaulieu et al. 1998), this is the equivalent of seed rain from 19.27 cones m\(^{-2}\). However, individual white spruce trees can produce between 8000 – 12,000 cones in a mast year (Nienstaedt and Zasada 1990), and our average cone count (top 3 m of the tree) in 2007 was 99.00 ± 34.15 tree\(^{-1}\) (range = 4 – 342); therefore, at least 9.50 ± 3.28 g of seed tree\(^{-1}\) would have been produced if no cones were harvested prior to opening. Seed production of this magnitude should have led to significantly higher seed rain density measurements if pre-dispersal cone harvesting was not extensive.

A key assumption of our initial hypothesis that spruce masting would affect mouse populations was that a sufficient amount of the seeds produced during a heavy cone crop would actually end up on the ground for mice to actively forage for them and cache them, in order to use the seeds as a major food resource during the fall and winter. In a previous study (Lobo et al. in review/Chapter 4), we examined the foraging behaviour of rodents in relation to varying abundance of spruce seeds in the field, and determined that the lower
threshold density at which rodents categorically cease active foraging (both consumption and caching) for spruce seeds was $5.60 \pm 0.61$ g m$^{-2}$; this value is 3 times higher than the highest seed rain density recorded from our seed traps. However, the amount of spruce seeds produced tree$^{-1}$ prior to cone harvesting would have easily surpassed this threshold density during a mast year, suggesting that pre-dispersal cone harvesting by red squirrels precludes a sufficient amount of seeds from falling in a mast year to effectively regulate mouse populations. This hypothesis requires experimental testing in the field, either through long-term exclusion of squirrels, or more practically, supplementation of mouse populations with large amounts of spruce seeds (surpassing the foraging threshold seed density) during the typical seed rain period in a non-mast year, in order to observe the effects on mouse survival and breeding (e.g. Jones et al. 1998).

5.4.3 Population responses to subalpine fir seed production

The strong relationship that we observed between subalpine fir seed production and deer mouse densities was unexpected, given that fir seeds contain high concentrations of plant secondary compounds (PSCs; Abbott 1962; Smith 1970; Schreiner et al. 2000; Lobo and Millar 2011/Chapter 3; Rubino et al. 2012), and mice avoid consuming or caching these seeds in the laboratory (Lobo et al. 2009/Chapter 2) and in the field (Lobo et al. in review/Chapter 4). However, the population response to masting was delayed, as we observed no effects on overwinter survival or spring body mass, breeding, and density. Instead, survival, body masses, and pregnancy rates of OW mice were higher in the summer following heavy fir cone crops, leading to increased summer OW and YY densities.
One possible explanation for this delayed population response is that deer mice avoided subalpine fir seeds in the fall and winter, but consumed them in the spring, after the PSCs in the seeds degraded. PSCs in some cut vegetation degrade substantially over time, after which the plant tissue is consumed by mammalian herbivores (Roy and Bergeron 1990; Dearing 1997; Müller-Schwarze et al. 2001). However, this is unlikely to occur in seeds as they are living tissue; high tannin levels in buried acorns have been shown to persist indefinitely (Shimada 2001; Smallwood et al. 2001; Wood 2005). The degradation of PSCs in subalpine fir seeds has not been tested, but if they do degrade, the length of time and conditions required to improve palatability to mice requires consideration. Mice may not cache fir seeds (Lobo et al. *in review/Chapter 4*) immediately after seed rain because of their high PSC contents, but exposure to snow and water over winter may be required to facilitate PSC degradation (Roy and Bergeron 1990; Müller-Schwarze et al. 2001). In this case, high densities of palatable seeds available in the spring following a masting event may be a valuable resource to OW mice. However, even with decreased concentrations of PSCs, the low overall nutritional value of subalpine fir seeds (Lobo and Millar 2011/Chapter 3) are probably insufficient to produce the population responses we observed.

It is more likely that the delayed effect of subalpine fir masting on deer mouse populations was mediated by population responses of invertebrate seed predators. Invertebrate pre-dispersal predators of subalpine fir cones (e.g. *Dioryctria abietivorella*, *Earoymia* spp., *Megastigmus* spp.) are common and have been well-studied, but are unlikely to have produced the delayed population response that we observed. First, the adults are volant, so they would mostly be inaccessible to mice. Second, most species
overwinter as larvae either on the ground or within seeds on the ground, and would be accessible to mice in the fall/winter, causing an overwinter and spring population effect (Kulhavy et al. 1976; Hedlin et al. 1980; Turgeon et al. 1994). Instead, population responses of terrestrial invertebrate post-dispersal seed predators are more likely to have mediated the enhanced summer survival, breeding, and densities of mice that we observed, although the identity and impacts of these species are largely unknown. Based on literature reports of terrestrial invertebrate conifer seed predators (see Nystrand and Granström 2000; Lundgren 2009) and pitfall trapping in our study areas (Lobo unpublished data), the most likely candidates are carabid beetles.

The granivorous nature of carabid beetles is underestimated, with adults and larvae of several genera (e.g. Agonum, Amara, Calathus, Harpalus, Pterostichus, Stenolophus) consuming seeds as part of their diet to varying degrees (see Tooley and Brust 2002; Lundgen 2009; Kotze et al. 2011). Species in the genera Amara and Harpalus are the most granivorous (Tooley and Brust 2002), and some consume large amounts of conifer seeds (Dick and Johnson 1958; Johnson et al. 1966; Nystrand and Granström 2000; references therein), but many are only prevalent in open habitats, weedy patches, and agricultural areas (Lindroth 1968; Tooley and Brust 2002). However, some of the species that are known to consume conifer seeds (e.g. Harpalus cautus) are abundant in forested areas in western Canada (Hatch 1958). Other major post-dispersal conifer seed predators in forested areas include species in the genera Pterostichus (Dick and Johnson 1958; Johnson et al. 1966; Nystrand and Granström 2000; Côté et al. 2005) and Calathus (Nystrand and Granström 2000).
Previous research has shown that population growth of deer mice may be linked to arthropod abundance (Simard and Fryxell 2003; Marcello et al. 2008), and we suggest that summer mouse populations in our study may have been enhanced by increased spring and summer populations of carabid larvae and adults following subalpine fir masting. Reproduction, and consequently populations, of carabid beetles are food-limited (Lövei and Sunderland 1996; Toft and Bilde 2002; Kotze et al. 2011), and many native carabid species in Alberta, including forest-dwelling granivorous species (e.g. *Pterostichus adstrictus*), are spring-breeders (Niemelä et al. 1992). These species may increase reproductive output in response to the enhanced supply of fir seeds available to them in the spring following a masting event. Given that arthropods are a preferred food source of deer mice (Bellocq and Smith 1994) and that animal protein is critical for their reproduction (McAdam and Millar 1999c; Desjardins 2002; Tabacaru et al. 2010), increased spring/summer populations of carabid larvae and adults would certainly enhance summer survival, body mass, and breeding of mice. Most research on invertebrate predation of conifer seeds has focused on pre-dispersal cone and seed predators, but post-dispersal granivory by invertebrates may play an important role in influencing rodent population fluctuations in coniferous forests, which could have further direct and indirect implications for interactions at other trophic levels (Elkinton et al. 1996; Ostfeld et al. 1996; Ostfeld and Keesing 2000). Further examination of the granivorous nature of carabid beetles in coniferous forests, and the relationship between their population fluctuations and conifer masting, would provide significant insights into the validity of this hypothesis.
5.4.4 Fall population dynamics

Summer mouse population responses to fir masting did not carry over into the fall, although the mechanisms for this are unclear. Fall populations are mainly comprised of YY mice, and we observed considerably less variation in fall YY densities (CV = 0.36, s-index = 0.16), which were not related to previous fir cone crops, compared to summer YY population densities (CV = 0.52, s-index = 0.23), which were. We had no measure of emigration by YY mice in our study, but the number of dispersing mice typically increases with density, probably to avoid intraspecific competition and attraction of predators to areas with elevated densities (Fairbairn 1978; Desy and Batzli 1989; Ostfeld 1997). Ostfeld (1997) reported that emigration rates of white-footed mice (*Peromyscus leucopus*) were highest immediately after populations reached peak densities following oak masting. Similarly, increased emigration of YY mice in the late-summer after a subalpine fir mast year, when populations were high, could have decreased the overall variability in fall YY densities, as well as the strength of the relationship between fall densities and previous fir cone crops.

In contrast, fall densities of OW mice were more variable (CV = 0.70, s-index = 0.29) than the full population (CV = 0.38, s-index = 0.16), but were still unrelated to previous fir cone crops. It is possible that the increased food supply in the spring after a mast year, which enhanced the summer survival of OW mice, did not persist into the fall, and was not able to maintain the high summer survival rates for the entire breeding season. In general, the regulation of fall deer mouse populations appears relatively complex (Kalcounis-Rueppell et al. 2002), and also seems to be influenced by density-dependent effects, as witnessed by the negative relationship we observed between summer
population growth and the preceding spring population density. The timing and mechanisms of density-dependence in this short-season, low-density population are unclear and conflicting (see McAdam and Millar 1999c; Millar and McAdam 2001; Kalcounis-Rueppell et al. 2002), and their influence on demography requires further consideration.

5.4.5 Asynchronous cone production

White spruce and subalpine fir cone crops were related in some years, but were not highly synchronous over the entire study period. Synchronous mast seeding should evolve in plant species with shared seed predators in order to effectively satiate predators and regulate their populations (Lalonde and Roitberg 1992; Pucek et al. 1993; Curran and Leighton 2000). However, asynchronous seed production may occur in plant communities when seed production by each species mainly affects different populations of seed predators (Schnurr et al. 2000). The evolution of white spruce mast seeding appears to have been significantly influenced by interactions with red squirrels (Boutin et al. 2006; LaMontagne and Boutin 2007; Fletcher et al. 2010; Archibald et al. 2012), while invertebrates may be the most important pre- and post-dispersal seed predators of subalpine fir trees (Kulhavy et al. 1976; Hedlin et al. 1980). In this case, selection for complete synchrony of seed crops between the two species is unlikely to be very strong, and the moderately synchronous pattern of cone production that we observed is more likely influenced by shared proximate cues for masting such as resource availability and favourable weather conditions (Owens and Molder 1977; Kelly and Sork 2002; LaMontagne and Boutin 2007).
5.4.6 Conclusion

Overall, small mammal population responses to mast seeding appear to be more complex in northern coniferous forests than in temperate deciduous environments, and are potentially confounded by significant pre-dispersal seed predation, indirect/delayed effects on food availability, and constraints on population growth and variability. Rodents can be major conifer seed predators, and have the potential to significantly affect seed survival and recruitment (Radvanyi 1970; Peters et al. 2004), but our data suggest that the predator satiation hypothesis for the evolution of mast seeding is unlikely to apply to conifer-rodent interactions. The characteristic booms and busts of rodent populations in response to deciduous seed crops were replaced by delayed, low-amplitude fluctuations in our study. While rodent population responses to deciduous masting have been shown to have important direct multi-trophic implications (Elkinton et al. 1996; Ostfeld et al. 1996; McShea 2000; Ostfeld and Keesing 2000), similar ecosystem interactions may be more subtle, indirect, and limited in northern coniferous forests. Large-scale field manipulations and intensive long-term demographic studies of other pre- and post-dispersal seed predators are required to further elucidate the key mechanisms regulating rodent population changes in coniferous forests, and to evaluate the importance of species-specific conifer masting on the community dynamics of multiple seed predators.

5.5 Acknowledgments

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Chapter 6

6 Effects of natural food supplementation on a short-season population of deer mice

6.1 Introduction

The importance of food as a constraint on vertebrate populations was emphasized by Lack (1954), and subsequently, a multitude of studies have attempted to understand the role of food availability in regulating the behaviour, life-history traits, population dynamics, and community structure of terrestrial mammals in nature (see reviews in Vessey 1987; Boutin 1990). However, natural food availability is difficult to measure accurately (Boutin 1990), and the most common alternative has been to monitor population responses to large-scale food supplementation. This has been done either independently (e.g. Hansen and Batzli 1978; Taitt 1981; McAdam and Millar 1999a) or in conjunction with the manipulation of other potentially limiting parameters, such as predation (e.g. Krebs et al. 1995; Karels et al. 2000), reproductive investment (e.g. Jonsson et al. 2002), and parasitism (e.g. Murray et al. 1998).

Food addition typically doubles the population density of terrestrial small mammals, mainly through advanced breeding, and increased immigration and breeding intensity (Boutin 1990), although survival (Bendell 1959; Cole and Batzli 1978; Hansen and Batzli

5 A version of this chapter has been accepted for publication.

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1978; Sullivan and Sullivan 1982; Dobson and Kjelgaard 1985) may also be limited by food supply. Typically, supplementation studies provide an excess of unnatural foods (e.g. oats, laboratory chow, catfood, sunflower seeds; but see Jones et al. 1998; Eccard and Ylönen 2001) in order to increase the overall availability of dietary energy (Hansen and Batzli 1978; Sullivan and Sullivan 1982; Teferi and Millar 1993; Jonsson et al. 2002) or protein (Cole and Batzli 1978; McAdam and Millar 1999a; von Blanckenhagen et al. 2007) to individuals in a population. This is a useful approach when the purpose of the study is to determine whether food, in general, has the capacity to limit populations. However, insights gained from responses to these manipulations may be limited because the supplements often fail to mimic the composition of the natural diet, and the populations may be additionally constrained by other nutrients (Wolinsky and Guggenheim 1974; Woolfenden and Millar 1997; McAdam and Millar 1999a). This is important when attempting to determine if natural food availability (in general, or for specific types of foods) is actually limiting populations. In this case, the ecological relevance of the quantity and/or quality of food provided may be suspect, potentially inflating the influence of food supply (overall or specific nutrients) on the natural regulation of individual behaviour and populations.

Conversely, small mammal population responses to natural resource pulses, such as masting, provide strong observational evidence that food abundance can limit populations. Masting, the intermittent, synchronous production of large seeds crops by a plant population (Silvertown 1980; Kelly 1994; Ostfeld and Keesing 2000), can periodically inundate post-dispersal seed predators such as rodents with an integral food resource (Jameson 1952; Silvertown 1980), thereby enhancing the available energy
supply beyond the requirements for breeding and survival (Wolff 1996). Fall masting in deciduous forests leads to enhanced densities of several species of mice and voles the following spring and summer, primarily because increased seed supply allows individuals to sustain breeding into the late fall and winter (Jensen 1982; Pucek et al. 1993; Wolff 1996; Ostfeld and Keesing 2000). Enhanced winter survival and spring breeding may also contribute to population peaks after deciduous masting (Hansen and Batzli 1979; Pucek et al. 1993; McCracken et al. 1999), highlighting the importance of food availability during the non-breeding season. Consequently, low seed supply in the fall following a mast year cannot sustain high populations, leading to decreased overwinter survival and population densities in the subsequent year (Jensen 1982; Pucek et al. 1993; Wolff 1996; McCracken et al. 1999).

In contrast, the effects of natural seed availability on small mammal populations in coniferous forests are more complex and largely inconsistent. Gashwiler (1979) found that fall conifer masting resulted in a delayed increase in rodent populations, but other studies have shown inconsistent population peaks (Jameson 1953; Elias et al. 2006), population declines (Stickel and Warbach 1960), or no response (McCracken et al. 1999; Schnurr et al. 2002; Boonstra and Krebs 2006) in relation to heavy conifer seed crops. Shimada and Saitoh (2006) suggested that conflicting evidence of the relationship between masting and rodent populations may be the result of confounding factors such as the food habits of the specific rodent species, climatic or seasonal limitations on their populations, alternative food availability, and the nutritional characteristics of the seeds. Accordingly, these confounding factors may undermine the key implicit assumptions of masting-rodent population studies: (1) the rodents are highly granivorous; (2) their
populations are limited by food; (3) the seeds are of high nutritional value; and (4) a sufficient amount of seeds are released during a masting event to effectively enhance the food supply to the population.

In a recent long-term study, we found that fall masting by white spruce (*Picea glauca*) trees did not affect deer mouse (*Peromyscus maniculatus*) populations in the Canadian Rocky Mountains (Chapter 5). This was unexpected, as deer mice are highly granivorous (Jameson 1952; Martell and Macaulay 1981), and consume (Radvanyi 1970; Peters et al. 2004; Lobo et al. 2009/Chapter 2) and/or cache (Lobo et al. *in review*/Chapter 4) large quantities of white spruce seeds available to them in the laboratory and in the field. Spruce seeds are rich in protein and digestible energy, and mice can maintain body condition for an extended period of time on a diet comprised solely of these seeds (Lobo and Millar 2011/Chapter 3). Furthermore, supplementation (Teferi and Millar 1993; McAdam and Millar 1999a; Desjardins 2002) and observation-based (Kalcounis-Rueppell et al. 2002; Tabacaru et al. 2010) studies have shown that food quality and quantity play important roles in limiting the breeding and population density of deer mice in our study area. However, it appears that pre-dispersal cone harvesting by North American red squirrels (*Tamiasciurus hudsonicus*), the major white spruce seed predator in northern coniferous forests (Boutin et al. 2006; Fletcher et al. 2010), significantly reduced the quantity of spruce seeds available to mice during the seed rain period. Seed rain produced during heavy cone crops (Chapter 5) was at levels well-below the lower threshold density at which mice cease active foraging (consumption and caching) for spruce seeds (Lobo et al. *in review*/Chapter 4). This suggests that interspecific
competition prevents spruce masting from effectively enhancing the food supply available to mice, thereby mitigating population responses to heavy cone crops.

Our objective was to test the hypothesis that increased availability of white spruce seeds to deer mice during a fall masting event would lead to population-level changes the following spring and summer. This was done by creating a masting event for post-dispersal conifer seed predators. We supplemented a long-term deer mouse population-monitoring grid with an excess of white spruce seeds (almost double the foraging threshold seed density) during the typical seed rain period in a non-mast year, in order to observe the effects of enhanced seed supply on population dynamics. This population was then compared to a control population from a nearby long-term monitoring grid, for several years prior to, and one year after, supplementation. The two grids have historically shown similar annual demographic patterns (Kalcounis-Rueppell et al. 2002). Therefore, we predicted that if seed availability was truly limiting spruce masting from enhancing mouse populations, the population dynamics of the two grids would be similar in most years prior to seed supplementation, but we would observe considerably higher overwinter survival and spring/summer body masses, breeding and population densities of mice on the treatment grid after supplementation.

6.2 Methods

6.2.1 Study area and species

This study was conducted in the Kananaskis Valley in SW Alberta, Canada, a 4200-km$^2$ multi-use area located in the front ranges of the Canadian Rocky Mountains. Two long-term small mammal population-monitoring grids were used; the control (50°45.99’N,
115°08.62W) and treatment (50°47.16’N, 115°09.52’W) grids were approximately 3 km apart, and both located in optimum deer mouse habitat (Millar et al. 1985). The main tree species on both grids were white spruce, subalpine fir (Abies lasiocarpa), and lodgepole pine (Pinus contorta), with spruce trees most prevalent. White spruce is a fall masting species; seeds develop in cones over the summer, mature in late-summer, and are released when cones open in the fall (Nienstaedt and Zasada 1990).

The most abundant rodent species on both grids was the deer mouse. Population densities of mice in the Kananaskis Valley are low and show annual cycles, with densities typically increasing over the summer and declining over winter (Millar and McAdam 2001). Breeding is constrained and highly seasonal; overwintered adults initiate reproduction in the spring, and females can produce multiple litters in a summer, but young-of-the-year rarely breed (Teferi and Millar 1993; McAdam and Millar 1999b; Millar and McAdam 2001). Survival and longevity in these northern populations are enhanced compared to populations in more temperate environments (Millar 1994; Millar and McAdam 2001).

6.2.2 Deer mouse trapping
Mice were trapped at each grid 2-3 times per week from May-September 2004-2011, using Longworth live traps (one trap per station, 20 m spacing) containing cotton bedding and baited with sunflower seeds and oats. The effective trapped area was estimated as 1.68 ha for the control grid and 1.40 ha for the treatment grid (inclusive boundary strip method; Stickel 1954). Each mouse was tagged (Monel #1 ear tags affixed to each ear) at first capture. Upon each capture, tag number, mass (nearest 0.5 g, using a Pesola spring balance), sex, age, and breeding condition were recorded. Age was assigned as
overwintered adult (OW) or young-of-the-year (YY), based on size and pelage colour. Breeding condition of males was classified as scrotal or non-scrotal, and females as perforate or non-perforate, pregnant, lactating, or pregnant and lactating.

6.2.3  Food supplementation

No manipulations were conducted on either grid between May 2004 and September 2010. In late-September 2010, we supplemented the treatment grid with 150 kg of white spruce seeds obtained from the British Columbia Ministry of Forests and Range Tree Seed Centre (6.0 Kcal g\(^{-1}\) (DM), 26.8% (DM) crude protein). Seeds were broadcast by hand in one late-afternoon period, over the entire trapping area as well as a few meters beyond the periphery. The density of seeds supplemented was approximately 10.71 g m\(^{-2}\); this amount is almost double the lower threshold density at which rodents cease active foraging for spruce seeds (5.60 ± 0.61 g m\(^{-2}\); Lobo et al. *in review/Chapter 4*), and almost 6 times the highest spruce seed rain density we recorded in the Kananaskis Valley from 2006-2010 (1.85 g m\(^{-2}\); Chapter 5). However, the amount of seeds produced by white spruce trees in a mast year would have been sufficient to produce this density of seed rain, prior to pre-dispersal cone harvesting by red squirrels (Chapter 5). Spruce cone production was low in 2010 (cone index (\(\ln(x+1)\)) = 0.96, average cone index between 2001-2011 = 2.52, range = 0.28 – 5.51; Chapter 5), so no significant effects of background food availability were expected.

6.2.4  Data analysis

The data from the control grid are a subset of the 10 years of data reported in Chapter 5 of this dissertation. See Chapter 5 for detailed descriptions of the calculations/estimations
of population, breeding, and body mass parameters; these were done for each grid separately.

6.2.4.1 Population dynamics

Average Jolly trappability (Jolly 1965; Jolly and Dickson 1983), defined as the probability that an individual in the population will be encountered during a given trapping session (Krebs and Boonstra 1984), was calculated for each year.

The abundance of deer mice was estimated using Pollock’s (1982) Robust Design Model implemented in Program MARK (White and Burnham 1999). Within each year, we examined a candidate set of 8 models that varied time, behaviour, and heterogeneity effects on the probability of capture in all possible combinations (Otis et al. 1978; White and Burnham 1999). Bootstrap goodness-of-fit testing showed no evidence of significant deviations from model assumptions for either grid in any year (all $p > 0.05$). Akaike’s Information Criterion corrected for small sample sizes ($\text{AIC}_c$; Akaike 1987; Hurwich and Tsai 1989) was used for model selection, with the best-supported model having the lowest $\text{AIC}_c$ score (Burnham and Anderson 2002). Models were compared to the best-supported model based on differences in $\text{AIC}_c$ scores ($\Delta \text{AIC}_c$) and $\text{AIC}_c$ weight (Burnham and Anderson 2002). Abundance estimates were generated for the full population each year, as well as OW and YY mice separately. Robust Design Model abundance estimates were highly correlated with Minimum Number Alive (Krebs 1966) estimates for both the control ($R = 0.96, p < 0.001$) and treatment ($R = 0.94, p < 0.001$) grids. Population densities were calculated by dividing abundance estimates by the effective trapped area.
We calculated population growth as the intrinsic rate of increase week$^{-1}$. Annual summer and winter population growth rates were calculated for the full population, and summer population growth rates were also calculated for OW and YY mice separately.

Overwinter survival was estimated as the proportion of tagged fall resident YY females that were also trapped the following spring, while spring immigration was estimated as the proportion of spring residents that were not part of the resident population the previous fall.

6.2.4.2 Body mass

Body masses of females were excluded from analyses in order to avoid potential effects of undetected pregnancies. We averaged multiple body mass recordings of each male, and these values were used to calculate annual average spring, summer, and fall masses of OW males. For each year, we also recorded the mass at first capture of YY males and estimated individual growth rates of juvenile males.

6.2.4.3 Breeding

We estimated the initiation of breeding, general timing of breeding, and length of the breeding season for each year. We also calculated the annual proportions of scrotal OW males in the spring, summer, and fall, as well as the annual proportions of resident OW and YY pregnant females, and the annual proportions of resident OW females that had multiple litters.

6.2.4.4 Statistical analysis

We screened all data for errors, missing values, outliers, and deviations from normality prior to statistical analyses. The effect of supplementation was examined by comparing
the treatment and control grids in each year before and after supplementation. Since only one treatment and one control grid were used, we could not conduct statistical comparisons of average population densities and growth rates between grids. However, parametric and non-parametric statistics could be used to test the effects of supplementation on other population, breeding, and body mass parameters.

We evaluated whether supplementation affected average spring, summer, and fall mouse population densities using a density effect ratio (see Boonstra and Krebs 2006), comparing the annual average densities on the treatment grid to those on the control grid in each year of the study.

We used contingency tables (log-linear analysis, chi-square tests, Fisher’s exact tests) to evaluate whether supplementation affected overwinter survival, spring immigration, and the proportions of breeding individuals. ANOVAs (parametric and Kruskal-Wallis) and Mann-Whitney U tests were used to examine the effect of supplementation on timing of breeding and body mass parameters. While several breeding and body mass variables were normally distributed, we used non-parametric tests when the sample size of one or more groups was low.

Finally, we used Cormack-Jolly-Seber models (Cormack 1964; Jolly 1965; Seber 1965), implemented in Program MARK, to evaluate whether the summer survival of OW mice varied between grids in each year before and after supplementation. The probability of survival between trapping sessions and the encounter probability were modeled as a function of grid and time, for a total of 15 models in the candidate model set each year.
Model comparison and selection was performed using $\Delta AIC_c$. The logit link was used for these analyses.

Unless otherwise stated, analyses were performed using R version 2.14.2 (R Development Core Team 2012) and SPSS version 16.0 (SPSS Inc. 2007), $\alpha$ was set to 0.05, and values are presented as means ± SE.

# 6.3 Results

## 6.3.1 Overall population density

Average annual Jolly trappability was high for both the control ($75.03 \pm 2.35\%$) and treatment ($68.85 \pm 2.91\%$) grids over the study period, allowing population sizes to be estimated accurately (Hilborn et al. 1976). Robust Design Model results for deer mouse abundance estimation are presented in Appendices A (control grid) and B (treatment grid). Supplementation enhanced population densities in the following breeding season.

Deer mouse populations on the treatment and control grids fluctuated in synchrony prior to supplementation ($R = 0.55$, $n = 21$, $p = 0.01$), with treatment densities typically lower than, or similar to, densities on the control grid (spring density ratio = $0.64 \pm 0.04$, summer density ratio = $0.77 \pm 0.10$, fall density ratio = $0.93 \pm 0.15$; Figure 6.1). However, this trend was reversed after supplementation, with densities on the treatment grid consistently higher than the control grid (spring 2011 density ratio = $1.44$, summer 2011 density ratio = $2.38$, fall 2011 density ratio = $1.63$; Figure 6.1). Consequently, the long-term population fluctuations on the two grids were no longer correlated once the post-supplementation densities were included in the analysis ($R = 0.26$, $n = 24$, $p = 0.23$).
6.3.2 Overwinter population dynamics

Winter population growth on the treatment grid was either similar or lower than growth on the control grid in all years prior to supplementation (Figure 6.2), with the long-term annual fluctuations fairly synchronous between the two grids (Spearman’s $\rho = 0.77$, $n = 6$, $p = 0.07$). However, the treatment population changed very little over winter after supplementation, while the control population declined at a substantially higher rate (Figure 6.2), significantly reducing the strength of the long-term relationship between the grids (Spearman’s $\rho = 0.42$, $n = 7$, $p = 0.35$). In populations with strong seasonal breeding, density changes over winter are a product of survival and/or immigration rates, with immigration often being the main influence in food-supplemented populations (Boutin 1990). This was not the case in our population, as we observed no difference in overwinter immigration between grids in any year of the study (grid × year interaction: $\chi^2_6 = 6.37$, $p = 0.38$; grid main effect: $\chi^2_1 = 0.25$, $p = 0.62$). Instead, supplementation resulted in increased overwinter survival; every YY resident female in the fall of 2010 was recaptured the following spring (Figure 6.3). Log-linear analysis indicated that differences in survival depended on both grid and year ($\chi^2_6 = 14.71$, $p = 0.02$), where no difference between grids was observed in all years prior to supplementation (all $p \geq 0.09$), but overwinter survival was highest on the treatment grid after supplementation ($p = 0.01$; Figure 6.3).
Figure 6.1. Mean ± SE deer mouse population densities on the control and treatment grids in the spring, summer, and early fall of 2004-2011. Population densities were estimated from mark-recapture data using Pollock’s (1982) Robust Design Model implemented in Program MARK (White and Burnham 1999). No manipulations were conducted at either grid from spring 2004 – early fall 2010. The black arrow indicates when the treatment grid was supplemented with white spruce seeds (late fall 2010).
Figure 6.2. Winter deer mouse population growth (intrinsic rate of increase week\(^{-1}\)) on the control and treatment grids from 2004-2011. No manipulations were conducted at either grid from spring 2004 – early fall 2010. The black arrow indicates when the treatment grid was supplemented with white spruce seeds (late fall 2010).
Figure 6.3. Overwinter survival of deer mice on the control and treatment grids from 2004-2011. No manipulations were conducted at either grid from spring 2004 – early fall 2010. The black arrow indicates when the treatment grid was supplemented with white spruce seeds (late fall 2010). The number of tagged fall resident young-of-the-year (YY) females is shown. Within each winter, an asterisk denotes that the grids were significantly different ($p \leq 0.05$) from each other. Error bars represent SE, calculated as in Zanette (2000).
6.3.3 Summer population dynamics

Summer population growth did not appear to be altered by supplementation. Treatment and control populations increased at similar rates in the summer after supplementation (Figure 6.4a), and long-term annual fluctuations were synchronous between the two grids both before (Spearman’s $\rho = 0.86$, $n = 7$, $p = 0.01$) and including the summer after supplementation (Spearman’s $\rho = 0.79$, $n = 8$, $p = 0.02$).

Summer population growth rates of OW mice were used as an index of survival over the entire breeding season (spring to fall). The OW mouse population on the treatment grid declined at a considerably slower rate than the control grid after supplementation, but this trend was also observed in most years (5 of 7) prior to supplementation (Figure 6.4b). CJS analyses indicated that summer survival in the best-supported model differentiated between grids in all years except 2004 (Table 6.1). The combined weight of all models in which survival was dependent on grid was only 0.34 in 2004, but was high (range = 0.62 – 0.97) in all other years prior to supplementation, and 1.00 in the summer after supplementation (Table 6.1). Thus, there is strong support in most years for a difference in summer survival rate between grids, with survival of mice on the treatment grid typically higher than mice on the control grid, both before and after supplementation. Overall, while OW mice in the supplemented population appeared to have a higher survival rate than control mice, it is unclear to what degree this was influenced by a grid effect.

YY mice were typically found in lower or similar densities on the treatment grid than the control grid in most years prior to supplementation (summer density ratio = 0.53 ± 0.13, fall density ratio = 0.88 ± 0.19; Figure 6.5). However, the YY density on the treatment
grid was almost double that of the control grid (density ratio = 1.90) in the summer after supplementation, but this large disparity did not persist into the fall (density ratio = 1.20; Figure 6.5). Both YY populations grew over each summer during the study, but the rate of population growth was higher on the control grid after supplementation, while the opposite trend was observed in most years prior to supplementation (Figure 6.4c).

6.3.4 Timing of breeding

Supplementation did not advance the timing of breeding. We found a significant interaction between grid and year of study when examining annual average dates of first parturition ($F_{7,60} = 6.67, p < 0.001$); breeding began later on the treatment grid (Julian date: $183.88 \pm 6.28$) than the control grid (Julian date: $144.83 \pm 7.53$) in 2005 ($Z = -2.14, p = 0.03$), but we observed no other annual differences between grids in the initiation of breeding, either before or after supplementation ($-1.61 \leq Z \leq -0.34$, all $p \geq 0.11$). We also detected no difference between grids in the general timing of breeding (grid × year interaction: $F_{7,114} = 1.60, p = 0.14$; grid main effect: $F_{1,114} = 0.98, p = 0.33$) throughout the study.

6.3.5 Individual breeding

Supplementation also did not enhance breeding by individual mice. The proportion of scrotal OW males did not differ between the treatment and control grids in the spring (grid × year interaction: $\chi^2_7 = 4.28, p = 0.75$; grid main effect: $\chi^2_1 = 0.24, p = 0.62$) and summer (grid × year interaction: $\chi^2_7 = 4.32, p = 0.74$; grid main effect: $\chi^2_1 = 0.33, p = 0.57$) of any year during the study.
Figure 6.4. Summer deer mouse population growth (intrinsic rate of increase week\(^{-1}\)) of (a) the full population, (b) overwintered adults only, and (c) young-of-the-year only, on the control and treatment grids from 2004-2011. No manipulations were conducted at either grid from spring 2004 – early fall 2010. The black arrow indicates when the treatment grid was supplemented with white spruce seeds (late fall 2010).
Table 6.1. The most parsimonious Cormack-Jolly-Seber models for the analysis of summer survival of overwintered deer mice at the control and treatment grids from 2004-2011. The probability of survival between trapping sessions ($\Phi$) and the encounter probability ($p$) were modeled as a function of grid ($g$) and time ($t$). A period ("\(\cdot\)"") indicates that the parameter is constant. For each model, we show the corrected Akaike Information Criterion ($AIC_c$), the difference in $AIC_c$ from the best-supported model, $AIC_c$ weight ($w_i$), and the number of estimable parameters ($K$). Only models with $w_i \geq 0.01$ are shown; the complete candidate model set is presented in Appendix B.

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<th>Model</th>
<th>$AIC_c$</th>
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<th>$K$</th>
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2011

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Figure 6.5. Ratio of the average summer and fall young-of-the-year population densities of deer mice on the treatment grid to those on the control grid. Ratios of 1 indicate no difference between treatment and control densities. No manipulations were conducted at either grid from spring 2004 – early fall 2010. The black arrow indicates when the treatment grid was supplemented with white spruce seeds (late fall 2010).
However, log-linear analysis indicated that the fall proportion of scrotal OW males was dependent on both grid and year ($\chi^2_7 = 14.52, p = 0.04$), where more males were scrotal on the control grid (3 of 3) than the treatment grid (0 of 4) in the fall of 2005 ($p = 0.03$), but no differences between grids were observed in any other year (all $p \geq 0.17$).

The proportion of OW females that were pregnant or lactating also did not differ between the treatment and control grids in any year before or after supplementation (grid × year interaction: $\chi^2_7 = 6.58, p = 0.47$; grid main effect: $\chi^2_1 = 0.79, p = 0.38$). However, breeding intensity of OW females was dependent on both grid and year ($\chi^2_7 = 14.51, p = 0.04$), with a smaller proportion of breeding females having multiple litters on the treatment grid (4 of 16) than the control grid (4 of 5) in the summer after supplementation ($p = 0.047$), but no difference between grids prior to supplementation (all $p \geq 0.22$).

Additionally, the proportion of YY females that were pregnant or lactating did not differ between the treatment and control grids in any year of the study (grid × year interaction: $\chi^2_7 = 7.81, p = 0.35$; grid main effect: $\chi^2_1 = 3.53, p = 0.06$), and no YY females bred in the summer after supplementation.

### 6.3.6 Body mass

We detected no effect of supplementation on the body mass of mice. While there was a significant interaction between grid and year of study when examining the spring masses of OW males ($F_{7,124} = 3.25, p = 0.003$), this was driven by males on the control grid being heavier than those on the treatment grid in 2008 (control = $21.22 \pm 0.64$ g, treatment = $18.00 \pm 0.67$ g; $Z = -2.81, p = 0.01$) and 2010 (control = $20.32 \pm 0.36$ g, treatment = $16.65 \pm 1.17$ g; $Z = -2.43, p = 0.02$). No differences were observed between the two grids in any other years of the study, before or after supplementation ($-1.15 \leq Z \leq 1.15$).
-0.67, all $p \geq 0.25). We also observed no difference between the treatment and control grids when examining the summer (grid $\times$ year interaction: $F_{7,59} = 1.36, p = 0.24$; grid main effect: $F_{1,59} = 0.10, p = 0.92$) and fall (grid $\times$ year interaction: $F_{7,33} = 0.96, p = 0.47$; grid main effect: $F_{1,33} = 2.04, p = 0.16$) masses of OW males.

Furthermore, the mass at first capture of YY males did not differ between the grids before or after supplementation (grid $\times$ year interaction: $F_{7,133} = 0.35, p = 0.93$; grid main effect: $F_{1,133} = 2.96, p = 0.11$). The growth rate of juvenile males was dependent on both grid and year of study ($F_{6,70} = 2.36, p = 0.04$), where juveniles grew faster on the treatment grid ($0.25 \pm 0.03, n = 4$) than the control grid ($0.09 \pm 0.04, n = 11$) in the summer prior to supplementation ($Z = -1.95, p = 0.05$), but no difference was observed between grids in any other year ($-1.39 \leq Z \leq -0.12, all p \geq 0.17$).

### 6.4 Discussion

Our results indicate that increased fall availability of white spruce seeds to deer mice can lead to enhanced populations in the following spring, summer, and fall. In 8 years of population monitoring, densities on the treatment grid were only consistently higher than the control grid after supplementation with spruce seeds. Overwinter immigration contributed to the high spring density on the treatment grid after supplementation, but the overall proportion of immigrants in both populations was similar. The biggest impact of increased seed availability was on overwinter survival; overwinter survival did not differ between the two grids in any year prior to supplementation, but was significantly enhanced on the treatment grid after supplementation. Survival of OW mice also appeared to be enhanced on the treatment grid in the summer after supplementation, but it
is unclear to what degree this was influenced by differences in external factors between
the grids. While the breeding patterns of individual mice were not affected by food
addition, YY densities were still higher on the treatment grid in the summer after
supplementation. However, similar to most food-addition experiments (Boutin 1990),
overall population growth over summer was not improved by seed supplementation.

Comparing the long-term dynamics of the control and treatment populations prior to
manipulation allowed us to examine for potential grid effects on population trends.
Differences between grids in external factors such as microclimate (e.g. Havelka and
Millar 1997; Kalcounis-Ruepell et al. 2002), predation (e.g. Karels et al. 2000; Fey et al.
2008), microhabitat characteristics (e.g. Sharpe and Millar 1991; Waser and Ayers 2003),
and background food availability had the potential to cloud our interpretation of
population responses to seed supplementation. However, other than the summer survival
of OW mice, grid effects on population, breeding, and body mass parameters were not
prominent. This allowed us to compare the two populations post-supplementation, within
the context of their long-term relationship, in order to identify the effects of seed
availability on both density and the mechanisms driving population responses.

Reproduction by deer mice is energetically demanding and highly seasonal in our study
area (Millar 1979; Millar and Innes 1983), and the initiation (Desjardins 2002) and
cessation (Tabacaru et al. 2010) of their breeding season appears to be limited by the
availability of animal protein. Protein availability is also critical to growth and maturation
of YY mice during the summer (McAdam and Millar 1999a). While the crude protein
content of white spruce seeds used in this experiment was high, the quality and timing of
the excess protein available to mice likely mitigated any breeding response. Plant protein
is less digestible and contains lower amino acid content than animal protein (Robbins 1993); this can reduce the amount of assimilable protein available to rodents, and therefore may not be sufficient to extend the breeding season or advance the initiation of spring breeding of mice in our population. Furthermore, supplementation, and consequently the highest seed availability, occurred in the late fall, after mice had already ceased breeding. Seeds would have been cached and consumed over the winter (Barry 1976), so their availability at the end of winter and in the early spring may not have been sufficient to support earlier and increased reproductive activity by these income breeders (Millar 1979). Supplementation with spruce seeds throughout the winter, or at the end of winter/beginning of spring, would have likely enhanced spring and summer breeding by rodents (see Eccard and Ylönen 2001; Desjardins 2002; von Blanckenhagen et al. 2007), but the timing of seed availability with this experimental design would not be biologically-relevant.

Similarly, the timing of supplementation also likely explains why spring body masses were not enhanced after seed addition. Food supplementation over winter has led to increased body masses of some rodents (e.g. Taitt 1981; Yunger 2002; Ylönen and Eccard 2004; von Blanckenhagen et al. 2007), but these studies administered excess food to populations throughout the winter at fairly regular intervals, as opposed to a single-occasion supplement that individuals cache to use over winter. Caches deplete over time, and thus would not provide the same excess of food throughout the winter as in the case of prolonged supplementation. It appears that increased caching of spruce seeds with seed availability (Lobo et al. in review/Chapter 4) provided a fall and winter food supply that
met the energy requirements of mice, thereby increasing their probability of survival over winter, but not enhancing body masses.

Although individual breeding patterns were not affected by spruce seed supplementation, we still observed more YY mice on the treatment grid than the control grid in the summer after supplementation. Supplemented females did not breed earlier or produce more litters than control females, but the higher OW female density on the treatment grid would nevertheless lead to more YY being produced, which is the main contributor to summer and fall populations. Thus, even if the only effect of increased fall spruce seed availability on mice is to improve overwinter and summer survival, masting could still significantly enhance summer densities through overall increased juvenile production.

Nest mortality also significantly influences the number of YY mice in our study area (Millar and McAdam 2001; Kalcounis-Rueppell et al. 2002), and thus may have contributed to our observations of higher summer YY densities on the treatment grid than the control grid after supplementation. However, we do not have estimates of nestling survival in our study, and the proximate causes and extent of nest mortality in small mammal populations tends to be highly variable and largely unknown (Millar 2007). Lower survival of dams on the control grid could have enhanced nest mortality (Millar 2007), but this is unlikely to have significantly reduced early-summer recruitment since a high proportion of resident control dams lived long enough to have multiple litters. Nestling predation and infanticide can also affect nest mortality rates (Millar 2007), but their density-dependent nature should have resulted in higher nest mortality on the treatment grid after supplementation. Overall, nestling survival likely was not
significantly influenced by seed supplementation, and also likely did not differ considerably between grids.

While YY density was still higher on the treatment grid than the control grid in the fall after supplementation, there was little disparity between the two populations at the end of the breeding season. Both YY populations grew over the summer, but the rate of increase was higher on the control grid, indicating that juvenile production was higher on the treatment grid early in the summer, but relatively more YY entered the control population as the breeding season progressed. This may be partially explained by the enhanced breeding intensity of control OW females, as higher per capita juvenile production through second and third litters can contribute to increased YY population growth, and consequently similar YY densities between grids by the end of the breeding season. However, dispersal of YY mice may have also influenced the patterns of population growth on each grid. We had no measure of emigration by YY mice in our study, but the number of dispersing mice typically increases with population density, probably to avoid intraspecific competition and attraction of predators to areas with elevated densities (Fairbairn 1978; Desy and Batzli 1989; Ostfeld 1997). Therefore, while the actual number of YY mice on the treatment grid was increasing over time, a potentially higher emigration rate on this high-density grid in the late-summer could have resulted in reduced population growth, and in conjunction with mortality of OW mice, the observed population decline on the treatment grid between summer and fall. Immigration of YY mice onto the relatively sparsely-populated control grid could have also played a role in altering population growth over the breeding season (see Ostfeld 1997). Deer mouse demography in our study area has historically been assumed to operate independently of
density-effects (Teferi and Millar 1993; Millar and McAdam 2001) because population
densities are relatively low, but there is mounting evidence that overwinter survival
(McAdam and Millar 1999a; Kalcounis-Rueppell et al. 2002) and summer population
growth (Chapter 5) may be density-dependent; the timing and mechanisms of density-
dependence in relation to survival, movement, and breeding in this short-season
population requires further consideration.

While mouse population density was enhanced by spruce seed supplementation, the
population increase we observed was much less dramatic than population responses to
oak masting (e.g. Pucek et al. 1993; Wolff 1996; Ostfeld and Keesing 2000) and
experimental supplementation of acorns (Jones et al. 1998). Large rodent population
peaks in response to natural and experimentally-enriched acorn availability are driven by
increases in both survival and fall/winter breeding (Pucek et al. 1993; Wolff 1996; Jones
et al. 1998; Ostfeld and Keesing 2000). However, only survival was impacted by
increased spruce seed availability in our study, as greater environmental constraints on
breeding are present in our northern study area than in temperate deciduous forests.
Furthermore, the food-energy available to rodents is enhanced to a greater degree by
increased availability of acorns than conifer seeds, as deciduous seed crops are typically
larger than those of conifers (Hansson 1971), and individual acorns are also larger than
conifer seeds and contain very high fat and low fibre contents (Shimada and Saitoh
2006). Thus, similar types of seed-rodent interactions can occur in both ecosystems, but
the specific timing, mechanisms, and amplitude of rodent population fluctuations are
directly influenced by the nature of both the populations and seeds involved.
Active foraging and caching of spruce seeds is necessary for mouse populations to numerically respond to increased seed availability. The density of seeds used in our supplementation experiment was selected because it exceeded the lower threshold density at which rodents cease active foraging of spruce seeds (Lobo et al. *in review*/Chapter 4). However, the amount of seeds produced in a mast year would be sufficient to produce this density of seed rain if pre-dispersal seed predation was less prevalent (Chapter 5). Our results showed clear survival and population responses to increased spruce seed availability. Therefore, we conclude that fall masting by white spruce trees has the potential to influence deer mouse populations, but under natural conditions, population responses to variable spruce seed production are not observed because of intervention by red squirrels. Pre-dispersal cone harvesting by this specialist seed predator appears to prevent spruce masting from releasing enough seeds onto the ground to effectively enhance the food supply available to mice, thereby limiting its ability to regulate their populations.

### 6.5 Acknowledgments

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Chapter 7

7 General discussion

The main goal of this dissertation was to investigate the effects and implications of conifer seed production on the foraging and population dynamics of northern small mammals. While several studies have examined the severity of post-dispersal conifer seed predation by rodents (e.g. Abbott 1961; Radvanyi 1970; Pank 1974; Sullivan and Sullivan 1982; Duchesne et al. 2000; Côté et al. 2003), little was known about the foraging dynamics of individual rodents in relation to varying nutritional quality and abundance of conifer seeds, as well as how these factors contributed to rodent population fluctuations. Combining the results of the studies presented in this dissertation, I have provided an integrative, comprehensive perspective on several of the major trends and specific mechanisms and assumptions underlying bottom-up interactions between conifer seeds and small mammals. However, as with most large-scale ecological interactions, the picture is more complex than originally expected, and the results of my studies have generated new questions about this system of direct and indirect plant-animal interactions, foraging behaviour, population responses, interspecific competition, and biochemical processes. Detailed discussions of specific experimental and observational results are presented in the relevant chapters. Here, I summarize the cumulative findings of my dissertation, and describe remaining important knowledge gaps and future research directions.
7.1 Foraging dynamics of conifer-rodent interactions

The results of the studies reported in Chapters 2-4 indicate that the foraging dynamics of rodents in relation to conifer seeds depend heavily on the quality of the seed and the granivorous nature of the rodent species being studied. These studies include examining seed quality and palatability of commonly-associated conifers, the effects of seed quality and abundance on the frequency of consumption and caching by rodents, and the efficacy of low- and high-quality conifer seeds as major food resources to different rodents.

7.1.1 Preferential foraging and seed quality

When seed abundance and availability were held constant in cafeteria-style feeding experiments (Lobo et al. 2009/Chapter 2), conifer seed preferences of small mammals were not species-specific, but rather the overall and relative patterns of selection were mostly similar. In the laboratory, the deer mouse (*Peromyscus maniculatus*), southern red-backed vole (*Myodes gapperi*), long-tailed vole (*Microtus longicaudus*), and meadow vole (*Microtus pennsylvanicus*) all showed a distinct preference for lodgepole pine (*Pinus contorta*) seeds and avoidance of subalpine fir (*Abies lasiocarpa*) seeds, with intermediate consumption of white spruce (*Picea glauca*) seeds. Deer mice and red-backed voles showed similar seed consumption and preference patterns in the field as well. Only the heather vole (*Phenacomys intermedius*), which is almost exclusively herbivorous (Côté et al. 2003), behaved differently from other rodents in that it did not show a preference among seed species, mainly because individuals rarely consumed seeds at all. Although long-tailed voles are also primarily herbivorous, their low microhabitat segregation and high niche overlap with heather voles (Millar et al. 1985) may be partially explained by differential rates of seed consumption.
Since seed availability and abundance were kept constant and rodents were held captive under controlled conditions in the laboratory- and field-based preference experiments, individuals selected seeds based on their overall quality. The quality of a seed can be influenced by both its external and internal characteristics, such as size, nutritional value, and defence compounds (e.g. Kerley and Erasmus 1991). Seed size generally acts as a proxy for nutrient content, and larger seeds tend to be preferentially consumed and/or cached by rodents (Hulme 1998; Wang and Chen 2009; Vander Wall 2010). However, given that subalpine fir seeds are considerably larger than lodgepole pine and white spruce seeds, other characteristics play a larger role in influencing rodent foraging patterns. Subalpine fir seeds contain relatively high fibre content and low nutritional value (Lobo and Millar 2011/Chapter 3), which may contribute to their avoidance by rodents (e.g. Chen et al. 2012). However, plant secondary compounds (PSCs) are a powerful defence strategy employed by fir seeds (Smith 1970; Lobo and Millar 2011/Chapter 3; Rubino et al. 2012), and appear to be primarily responsible for deterring seed predation in this genus (e.g. Abbott 1962; Grodzinski and Sawicka-Kapusta 1970; Smith 1970; Rubino et al. 2012; Lobo unpublished data). Monoterpenes such as limonene have recently been speculated as being the most efficacious PSCs for reducing predation rates in fir seeds, but this requires further experimental testing (Rubino et al. 2012).

Protein content also plays an important role in seed selection, as high protein lodgepole pine seeds (Lobo and Millar 2011/Chapter 3) were selected over white spruce seeds by rodents, even though the latter contained higher overall energy (Grodzinski and Sawicka-Kapusta 1970; Lobo unpublished data) and digestible energy (Lobo and Millar
2011/Chapter 3) contents. However, spruce seeds also contain small amounts of PSCs (Rubino et al. 2012; Lobo unpublished data), while lodgepole pine appears to invest very few resources into chemical defences in seeds (Lobo unpublished data), and instead employs serotiny as its major defence strategy against pre- and post-dispersal seed predators (Despain 2001). Given that spruce seeds are highly palatable to many rodent species (Lobo et al. 2009/Chapter 2), the amount of PSCs in spruce seeds is not sufficient to prevent large losses to post-dispersal seed predators, as they are in subalpine fir seeds. Conversely, even the small amounts of PSCs in spruce seeds appear to have negative effects on less granivorous voles over an extended period of time, but do not impact the body condition of highly granivorous mice (Lobo and Millar 2011/Chapter 3). Thus, PSCs may have also played some role in the relative preferences of lodgepole pine and white spruce seeds (Lobo et al. 2009/Chapter 2), although the role of PSCs as a feeding deterrent in spruce seeds has been poorly studied.

7.1.2 Effects of seed abundance on foraging behaviour

Seed abundance influenced the specific foraging behaviours performed by some rodents, but did not alter relative usage patterns of seeds as dictated by seed quality. Since animals can utilize seeds by both consuming and/or caching them (Vander Wall 2010), I used artificial food patches in the field to examine individual deer mouse and red-backed vole use of subalpine fir and white spruce seeds under different abundance conditions (Lobo et al. in review/Chapter 4). This was different from the seed preference experiments conducted in the field (Lobo et al. 2009/Chapter 2) because rodents were no longer held captive in livetraps with conifer seeds as their only food options. Instead, they had unrestricted access to other naturally-available foods, and they were free to cache
experimental seeds within their natural territory. Rodents perceived subalpine fir seeds as being of low quality in the field, as indicated by the high absolute giving-up densities (GUDs; Brown 1988) of fir seed patches. I originally predicted that rodents would remove fir seeds from seed patches for storage when they were abundant in spite of their low palatability, since unpredictable conditions typically favour caching food from abundant sources (Vander Wall 2010), and the availability of a mixed diet in the field would allow individuals to utilize a broader diet incorporating low-quality foods when necessary (Freeland and Janzen 1974; Dearing et al 2000). However, fir seeds were mostly ignored by mice and voles throughout the study, with very few seeds consumed and none cached. Seeds were provided in exaggeratedly abundant quantities compared to natural seed rain densities (Lobo and Millar in press/Chapter 5) in order to generate some value for the food patch, given that the intrinsic value of each seed was minimal; however, the low nutrient and high PSC contents of fir seeds almost completely preclude their use by rodents, regardless of seed abundance. Thus, under both artificial and natural conditions, fir seeds have almost no direct current or future value to foraging rodents. This may be because PSCs in living tissues such as seeds do not degrade over time (e.g. Shimada 2001; Smallwood et al. 2001) as they do in cut vegetation in caches (e.g. Roy and Bergeron 1990; Dearing 1997), but this requires experimental testing in subalpine fir seeds.

Seed abundance affected the frequency of removal of white spruce seeds; these seeds were perceived as being of high quality by rodents, as indicated by the low absolute GUDs of spruce seed patches. Overall, mice consumed seeds in high- and low-abundance patches at a similar frequency, but seed removal mostly occurred when seed abundance
was high. Seed removal also predominantly occurred late in the nightly active foraging period, indicating that mice were using their current energetic state to make short- and long-term foraging decisions. Based on personal observations and literature reports (Abbott and Quink 1970; Vander Wall 1997; Siepielski and Benkman 2008), I assumed that removed seeds were being stored for future use, and not simply immediately consumed elsewhere. However, the ultimate fate of removed seeds was not tracked, and this is necessary to determine whether increased caching of seeds during white spruce masting would benefit seed dispersal and recruitment (Zhang et al. 2008), or if cached seeds are mostly harvested prior to germination (e.g. Abbott and Quink 1970). The high palatability and preferential consumption of white spruce seeds under high- and low-abundance conditions indicates that any benefits of increased seed caching in mast years would likely be minimal.

The granivorous nature of the rodent species did affect their usage of seeds in their natural environment. Red-backed voles mostly ignored both the low-quality subalpine fir seeds and high-quality white spruce seeds present in food patches. However, this is likely because their summer diets consist mainly of lichens, fungi, and non-seed plant matter (Maser et al. 1978; Martell 1981), which were abundant in the study areas during the experiments. Red-backed voles may utilize spruce seeds to a greater degree in the fall, as the availability of their preferred summer food sources declines. The impact of seasonal diet shifts on foraging decisions by rodents in relation to conifer seed quality and abundance requires further consideration.
7.1.3 The efficacy of conifer seeds as major food resources

The effects of conifer seed quality and abundance on rodent foraging dynamics were also examined by determining if and how deer mice and red-backed voles can use low- and high-quality seeds as major food resources if the seeds are abundantly available (Lobo and Millar 2011/Chapter 3). Based on the relative palatability of seeds previously observed (Lobo et al. 2009/Chapter 2), I hypothesized that rodents would be able to maintain body condition on a diet restricted to either lodgepole pine or white spruce seeds, but would suffer substantial negative effects on subalpine fir seed-diets. Again, the granivorous nature of the rodent species determined their response to diet quality. Voles did not compensate for the low quality of fir seed-diets behaviourally or morphologically, and suffered severe negative consequences including rapid weight loss, lethargy, loss of fur, and blindness. These symptoms indicated that PSCs, rather than low nutritional value, were responsible for the major antifeedant responses to these seeds. Voles were able to maintain body condition when their diets were restricted to pine seeds, but were unable to do so on spruce seed-diets in the long-term, once again stressing the important role that PSCs play as a defence against predation in conifer seeds.

On the other hand, deer mice were able to maintain body condition on all seed-diets. However, in order to use subalpine fir seeds as a major food source, mice had to increase their seed intake and retain more digesta in the caecum, a component of the gut that facilitates efficient degradation and assimilation of low quality foods (e.g. Green and Millar 1987; Derting and Bogue 1993). This strategy allowed mice to maintain digestive efficiency and energy balance without the need for increasing the length and capacity of the gut, which is more metabolically-expensive to maintain than other body tissues.
Undetected physiological and biochemical detoxification mechanisms such as salivary proline-rich proteins and enzyme activity in the small intestine, caecum, and liver may have also played a role in mitigating the negative effects of PSCs on mice (e.g. Freeland and Janzen 1974; Harju and Tahvanainen 1994; Shimada and Saitoh 2003; del Valle et al. 2006; Shimada et al. 2006), but this requires further examination.

7.2 Conifer seed production and small mammal populations

In Chapters 5 and 6 (Lobo and Millar *in press*), I investigated the effects of conifer seed availability on the population dynamics of deer mice. Consumer populations are directly linked to previous or current resource availability (Bayliss and Choquenot 2002), and intermittent resource pulses such as mast seeding can often have dramatic effects on the population dynamics of consumers (e.g. Ostfeld and Keesing 2000). While this has been comprehensively studied and well-documented in deciduous forests (e.g. Jensen 1982; Pucek et al. 1993; Wolff 1996; McCracken et al. 1999; Ostfeld and Keesing 2000; Falls et al. 2007), small mammal population studies in coniferous forests are relatively limited, and have not shown consistent effects of conifer masting (e.g. Jameson 1953; Stickel and Warbach 1960; Gashwiler 1979; Boonstra and Krebs 2006).

7.2.1 Assumptions of population-level interactions

While the laboratory and field experiments described in Chapters 2-4 provided important insights into the patterns and underlying bases of post-dispersal conifer seed predation by rodents, they also examined fundamental assumptions of the hypothesis that rodent populations should fluctuate with mast seeding in coniferous forests: (1) the rodents
being studied are highly granivorous; (2) their populations are limited by food; (3) the seeds are of high nutritional value; and (4) a sufficient amount of seeds are released during a masting event to effectively enhance the food supply to the population.

Deer mice are highly granivorous (assumption 1; Chapters 2-4), and food quality and quantity play important roles in limiting their breeding and population densities in our study area (assumption 2; McAdam and Millar 1999; Desjardins 2002; Tabacaru et al. 2010). Mice consume (Chapters 2-4) and cache (Chapter 4) large amounts of white spruce seeds available to them, but mostly avoid subalpine fir seeds if other food options are available (Chapters 2 and 4) because of their low nutritional value and high PSC content (assumption 3; Chapter 3). Both seeds have the potential to be a viable major food resource to mice, but they must alter their food intake and digestion patterns in order to persist on fir seed-diets (Chapter 3). These factors led us to hypothesize that there would be a positive relationship between mouse populations and white spruce seed production, but no effect of subalpine fir masting.

### 7.2.2 Population responses to conifer mast seeding

I examined the spring, summer, and fall demography of deer mice in the Kananaskis Valley in relation to the previous fall’s white spruce and subalpine fir seed production over a 10-year period (Lobo and Millar in press/Chapter 5). Annual seed production of the two conifer species was not significantly correlated, but both conifer species masted twice during the study period, and produced bumper crops intermittently.

Surprisingly, I observed a strong relationship between summer mouse population dynamics and the previous fall’s subalpine fir seed production. However, the population
response to fall fir mast seeding was delayed, as no effects on overwinter survival or spring body mass, breeding, and density were observed. Instead, survival, body masses, and pregnancy rates of overwintered mice were enhanced in the summer following a heavy cone crop, leading to increased summer overwintered and young-of-the-year mouse densities. One possible explanation for this delayed response is that mice avoided fir seeds in the fall and winter, but consumed them in the spring, after their PSCs degraded. However, this is unlikely, given that PSCs in seeds are resistant to degradation over time (e.g. Shimada 2001; Smallwood et al. 2001) unlike in some cached vegetation (e.g. Roy and Bergeron 1990; Dearing 1997), and the low nutritional value of subalpine fir seeds (Lobo and Millar 2011/Chapter 3) is probably insufficient to enhance survival and breeding in rodents. It is more likely that the delayed response to fir masting observed in Chapter 5 (Lobo and Millar in press) was mediated by terrestrial invertebrate post-dispersal conifer seed predators. I hypothesize that spring and summer larval and adult populations of carabid beetles were enhanced following heavy fall fir cone crops, leading to enhanced survival, body masses, breeding, and summer densities of mice. Further examination of the relationship between the population dynamics of carabid beetles and conifer masting are necessary to validate the efficacy of this hypothesis, and can provide important insights into key direct and indirect multi-trophic ecosystem interactions in northern coniferous forests.

It was also unexpected that annual variation in deer mouse demography was not positively related to previous white spruce seed production. However, mice are not the only vertebrate seed predator in our study area. The North American red squirrel is a major pre-dispersal white spruce seed predator, and harvests and hoards several
thousands of spruce cones prior to cone opening (Smith 1968; Fletcher et al. 2010; Donald and Boutin 2011). Based on the disparity between cone production and seed rain densities recorded, I hypothesized that pre-dispersal cone harvesting by red squirrels prevented spruce masting from effectively enhancing the food supply available to mice in the fall and winter, thereby mitigating mouse population responses to heavy fall cone crops; assumption 4 of the hypothesis that rodent populations should fluctuate with conifer mast seeding. The highest spruce seed rain density I recorded was considerably less than what would have been produced if pre-dispersal cone harvesting was not extensive, and was 3 times lower than the absolute GUD recorded for spruce seeds (Lobo et al. in review/Chapter 4), the lower threshold density at which rodents cease active foraging for spruce seeds. However, the amount of seeds produced prior to cone harvesting would have easily surpassed this threshold density during a mast year, suggesting that a sufficient amount of seeds would have dispersed during the seed rain period in a mast year to effectively regulate mouse populations if pre-dispersal cone harvesting was less severe.

I tested the hypothesis that increased fall spruce seed availability to deer mice would lead to enhanced spring and summer populations by supplementing a long-term mouse population monitoring grid with an excess (almost double the absolute GUD) of white spruce seeds (Lobo and Millar in press/Chapter 6); this population was then compared to a historically-similar control population before and after supplementation. Population densities on the treatment grid were either lower or similar to the control grid in all years prior to supplementation. However, overwinter survival on the treatment grid was considerably higher than the control grid post-supplementation, leading to a higher spring
density on the supplemented grid. Individual breeding patterns were not affected by seed supplementation, but the higher spring density of overwintered females after supplementation led to more young-of-the-year also being produced on the treatment grid than the control grid. These results indicate that white spruce seed production can provide a fall and winter food supply that meets or exceeds the energy requirements of deer mice, and that spruce masting has the potential to enhance mouse populations, but under natural conditions, population responses to variable spruce seed production are not observed because of intervention by red squirrels.

7.3 Key future research directions

7.3.1 Conifer recruitment and regeneration

The results of my seed preference experiments (Lobo et al. 2009/Chapter 2) clearly show that differential rates of seed predation by small mammals have the strong potential to significantly influence the community structure of mixed conifer forests, and the success of both natural and artificial regeneration projects. While the negative effects of rodents on the survival and recruitment of lodgepole pine (Radvanyi 1971; Lindsey 1975) and white spruce (Radvanyi 1970; Peters et al. 2004) seeds have been documented, this has not been experimentally tested in the field for subalpine fir. Future studies examining the recruitment rates of naturally-produced or experimentally-placed seeds in rodent-exclosures (e.g. Peters et al. 2004) would provide strong insights into the importance of palatability and post-dispersal seed predation to the regeneration of this species. Furthermore, this experimental design could be used with multiple species of seeds in order to elucidate the significance of preferential seed predation by rodents on the community structure of mixed coniferous forests. A long-term study of this nature would
determine the relative importance of seed predation to other potentially-limiting stages of recruitment (Hulme 1998). The results of these studies would be very useful for forest management programs; this is especially important in western Canada, where widespread regeneration projects are conducted in conifer stands affected by natural resource development and/or mountain pine beetle (*Dendroctonus ponderosae*) infestation.

### 7.3.2 Physiological ecology of rodent foraging dynamics

I used restricted seed-diets to show that deer mice alter their food intake and digestive patterns in order to utilize subalpine fir seeds as a major food source (Lobo and Millar 2011/Chapter 3). Future studies should also examine the role of physiological and biochemical responses by mice to PSC-rich conifer seed-diets, as they can play important roles in the nutritional and population ecology of small mammals. For example, the induction of salivary proline-rich proteins and tannase producing bacteria allows Japanese wood mice (*Apodemus speciosus*) to persist on diets containing PSC-rich acorns (*Quercus crispula*; Shimada and Saitoh 2003; Shimada et al. 2006); consequently, *A. speciosus* can utilize these acorns as a major food source, while other rodent species cannot, and only their populations have been observed to increase following mast seeding by *Q. crispula* (Saitoh et al. 2007). Given that the ecology of *Apodemus* and *Peromyscus* are often very similar (Montgomery 1989), these mechanisms and their potential influence on conifer-rodent interactions at multiple scales are an exciting, untapped area of research. Similarly, further study is required on the use of digestive and detoxifying enzymes, and morphological adjustments of the vital organs by rodents in order to mediate the effects of PSCs in conifer seeds, important mechanisms in the response of herbivorous rodents to plant defences (e.g. Lindroth and Batzli 1984; Harju and
Tahvanainen 1994; del Valle et al. 2006). While my dissertation has provided important insights into the nutritional and population interactions between conifer seeds and rodents, the physiological and biochemical interactions in this system remain largely unknown.

7.3.3 Plant secondary compounds in conifer seeds

It is clear that PSCs are an important defence strategy employed by conifers, significantly influencing both pre- and post-dispersal seed predation. However, the PSC profiles of conifer seeds are largely unknown, especially compared to acorns and other deciduous seeds, which mainly rely on tannins to deter seed predators (e.g. Smallwood et al. 2001; Shimada and Saitoh 2003). A wide variety of PSCs can be found in conifer seeds, but several of them do not actually deter feeding by rodents (Lobo et al. unpublished data). Tannins are also not prevalent in PSC-rich conifer seeds, and are likely not very important feeding deterrents in this system (Rubino et al. 2012). I have been using a process of bioassay-guided fractionation, with deer mice, to isolate and identify the specific classes of PSCs that cause feeding deterrence in subalpine fir seeds. However, this has turned out to be an extremely complicated study, and could legitimately form the basis of a PhD project on its own. Rubino et al. (2012) recently reported that silver fir (Abies alba) seeds contain very high concentrations of limonene, and speculated that this monoterpene may be responsible for deterring feeding by European red squirrels (Sciurus vulgaris). This requires further experimental testing for this species, as well as in other true fir species, which also rely heavily on chemical defences (Abbott 1962).

Furthermore, as I stated previously in this dissertation, experimental testing of the stability of PSCs in conifer seeds over time is required, as well as the conditions required
to facilitate PSC-degradation to improve palatability to rodents. These factors have important implications for understanding the bases and mechanisms underlying the foraging (Lobo et al. *in review*/Chapter 4) and population (Lobo and Millar *in press*/Chapter 5) responses of rodents to subalpine fir seed availability. The overall significance of PSCs in high quality conifer seeds, such as white spruce seeds, also requires further consideration. Clearly, more research is required to identify and quantify the biologically-active PSCs in different species of conifer seeds, and characterize their influence on the nutritional ecology of rodents and other conifer seed predators. This is a direction I will continue to pursue in my future research, and one that has great potential to provide important, multifaceted insights into interactions between conifer trees and several pre- and post-dispersal seed predators at basic, applied, and evolutionary levels.

7.3.4 Post-dispersal conifer seed predation by invertebrates

The delayed mouse population response to subalpine fir mast seeding that I reported in Chapter 5 (Lobo and Millar *in press*) suggests that granivorous carabid beetles may play an important role in multi-trophic interactions in coniferous forests, and should be the focus of further study. The granivorous nature of these invertebrates have been underestimated for several decades (Tooley and Brust 2002; Lundgen 2009), and their interactions with conifer seeds are poorly studied (but see Dick and Johnson 1958; Johnson et al. 1966; Nystrand and Granström 2000). Deciduous masting has been shown to negatively influence invertebrate populations by enhancing the density of rodents, one of their major predators (e.g. Elkinton et al. 1996; Ostfeld and Keesing 2000); however, similar multi-trophic community dynamics in coniferous forests appear to be inverted, and the patterns and mechanisms of these interactions can be further elucidated with
population-level studies of carabid beetles in relation to conifer mast seeding. This system is ideal for the types of large-scale, integrative, multi-disciplinary ecosystem studies that ecologists are encouraged to pursue (e.g. Krebs et al. 2001). Future studies should investigate the granivorous food habits of carabid beetles in coniferous forests, the mechanisms used by beetles to utilize PSC-rich conifer seeds, and the relationship between their population fluctuations and conifer mast seeding. While there is some evidence that rodent populations may be influenced by arthropod abundance (Simard and Fryxell 2003; Marcello et al. 2008), this requires further observational and experimental testing.

7.3.5 Multiple plant defences

Given the large investment into PSCs in subalpine fir seeds, and their effectiveness in limiting predation, the function of mast seeding in this species requires further consideration. Fir trees may be utilizing a bet-hedging strategy, whereby PSCs are used to deter seed predation by vertebrates (Lobo et al. 2009/Chapter 2; Di Pierro et al. 2011; Lobo et al. in review/Chapter 4), while masting may be used to satiate invertebrate pre- and post-dispersal seed predators. As mentioned previously, future studies should investigate the interactions between subalpine fir seed production and granivorous invertebrates. Also, it is unknown whether there is a trade-off between the volume of seed production and PSC concentrations. I have collected subalpine fir seeds from the 2007-2011 cone crops in the Kananaskis Valley, and intend to test this relationship and its implications for seed predation.
7.3.6 Interactions between pre-dispersal seed predators and rodents

Pre-dispersal cone harvesting by specialist red squirrels has significantly influenced the evolution of mast seeding by white spruce trees (LaMontagne and Boutin 2007; Fletcher et al. 2010; Archibald et al. 2012), and prevents spruce masting from influencing generalist rodent populations in our study area (Lobo and Millar *in press*/Chapters 5 and 6). However, in white spruce forests without red squirrels, it is unknown to what degree mast seeding is utilized to satiate major seed predators such as rodents. Given the large resource-investment required for mast seeding (Kelly and Sork 2002) and the efficacy of PSCs in deterring seed predation by rodents, masting may be less prominent as a defense strategy in areas without red squirrels, with spruce trees in these areas relying more on PSCs. The geographic mosaic of coevolution (see Benkman et al. 2001) between white spruce and its major vertebrate seed predators is an exciting avenue for future research.

7.3.7 Natural food supplementation studies

I found only three other studies (Krebs et al. 1986; Jones et al. 1998; Eccard and Ylönen 2001) that used a natural food source as a food supplement in order to elucidate the influence of natural food availability on small mammal population and/or breeding dynamics. Future food-addition studies with this goal should also aim to utilize natural foods in ecologically-relevant quantities, as the use of unnatural high-quality foods in unjustified excess quantities in food supplementation experiments is useful to determine if food has the capacity to limit populations, but may provide misleading insights into the importance of food supply (in general, or for specific foods) on natural population fluctuations. This will be more challenging than the traditional experimental model, as
researchers will have to monitor the natural availability of a food source for a sufficient amount of time and specifically define the “excess” amount to be supplemented based on this. This is most feasible for systems containing a key specific food, and it may be difficult and costly to acquire sufficient quantities of the appropriate natural food for experimental purposes. However, the power and certainty of insights provided by this experimental model substantially justify the extra time, consideration and resources required.

7.4 Concluding remarks

Individual- and population-level interactions between small mammals and seed production have been the focus of intensive studies in deciduous forests in eastern North America, western Europe, and northern Japan for many years, but prior to the results presented in this dissertation, similar relationships in coniferous forests have largely been ignored. This is a non-trivial knowledge gap, given the importance of both conifers and small mammals in forest ecosystems, and the severe impact that small mammals can have on conifer seed survival, recruitment, and community structure. The results of my dissertation have provided a comprehensive picture of the nutritional, foraging, and population ecology of northern rodents in relation to conifer seed production, new information that is of both basic and practical importance to rodent biology and forest management and regeneration. These studies also provide the foundation for future work with rodents and other vertebrate and invertebrate conifer seed predators in this system, as well as related systems including similar rodent species in more temperate North American coniferous forests (e.g. Peromyscus leucopus), and northern rodents in European and Asian coniferous forests (e.g. Apodemus spp., Myodes glareolus). Finally,
it is my goal that this dissertation has highlighted the importance of not only documenting large-scale patterns when examining consumer-resource systems, but also identifying and testing the mechanisms and assumptions underlying these observations using intensive field and laboratory observations, experiments, and manipulations.

7.5 References


Lindroth RL and Batzli GO. 1984. Plant phenolics as chemical defenses: effects of natural phenolics on survival and growth of prairie voles (Microtus ochrogaster). Journal of Chemical Ecology, 10: 229-244.


Lobo N and Millar JS. 2011. The efficacy of conifer seeds as major food resources to deer mice (Peromyscus maniculatus) and southern red-backed voles (Myodes gapperi). Mammalian Biology, 76: 274-284.


Appendices

Appendix A: Chapter 5 supplementary material

Table A.1. Pollock’s (1982) Robust Design Model results for deer mouse abundance estimation for 2002-2011. Models varied time (t), behaviour (b), and heterogeneity (h) effects on the probability of capture in all possible combinations, as per Otis et al. (1978). All models constrained temporary emigration and immigration rates to be equal, but allowed them to vary as a function of time, and allowed the probability of survival between trapping sessions to vary as a function of time. The best-supported models, based on AICc scores and AICc weight (wi), are highlighted. K is the number of estimable parameters in each model. See the Methods section of Chapter 5 for details on the model selection and averaging procedures used to obtain abundance estimates.

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<tr>
<td><strong>2011</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M&lt;sub&gt;0&lt;/sub&gt;</td>
<td>152.33</td>
<td>27.35</td>
<td>0.00</td>
<td>29</td>
</tr>
<tr>
<td>M&lt;sub&gt;t&lt;/sub&gt;</td>
<td>146.21</td>
<td>21.23</td>
<td>0.00</td>
<td>50</td>
</tr>
<tr>
<td>M&lt;sub&gt;b&lt;/sub&gt;</td>
<td>164.79</td>
<td>39.81</td>
<td>0.00</td>
<td>34</td>
</tr>
<tr>
<td>M&lt;sub&gt;h&lt;/sub&gt;</td>
<td>175.86</td>
<td>50.88</td>
<td>0.00</td>
<td>40</td>
</tr>
<tr>
<td>M&lt;sub&gt;tb&lt;/sub&gt;</td>
<td><strong>124.99</strong></td>
<td><strong>0.00</strong></td>
<td><strong>0.39</strong></td>
<td><strong>48</strong></td>
</tr>
<tr>
<td>M&lt;sub&gt;th&lt;/sub&gt;</td>
<td><strong>126.19</strong></td>
<td><strong>1.20</strong></td>
<td><strong>0.22</strong></td>
<td><strong>48</strong></td>
</tr>
<tr>
<td>M&lt;sub&gt;bh&lt;/sub&gt;</td>
<td>157.19</td>
<td>32.20</td>
<td>0.00</td>
<td>42</td>
</tr>
<tr>
<td>M&lt;sub&gt;tbh&lt;/sub&gt;</td>
<td><strong>124.99</strong></td>
<td><strong>0.00</strong></td>
<td><strong>0.39</strong></td>
<td><strong>48</strong></td>
</tr>
</tbody>
</table>

**References:**


Table A.2. Evaluation of the parsimony of several alternate linear models examining the annual variation in average spring deer mouse population density \((N)\) relative to the previous fall’s average population density \((N_{t-1})\) and white spruce \((S_{t-1})\), subalpine fir \((F_{t-1})\), and total \((T_{t-1})\) cone indices. \(\varepsilon_t\) refers to a normally distributed random variable with mean zero, and \(K\) is the number of estimable parameters in each model. The best-supported model, based on \(\text{AIC}_c\) scores, is highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>(K)</th>
<th>(\text{AIC}_c)</th>
<th>(\Delta\text{AIC}_c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N = a + \varepsilon_t)</td>
<td>3</td>
<td>11.31</td>
<td>0.00</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + \varepsilon_t)</td>
<td>4</td>
<td>18.51</td>
<td>7.20</td>
</tr>
<tr>
<td>(N = a + bT_{t-1} + \varepsilon_t)</td>
<td>4</td>
<td>17.78</td>
<td>6.47</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cT_{t-1} + \varepsilon_t)</td>
<td>5</td>
<td>29.74</td>
<td>18.43</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cT_{t-1} + d(N_{t-1} \times T_{t-1}) + \varepsilon_t)</td>
<td>6</td>
<td>51.06</td>
<td>39.75</td>
</tr>
<tr>
<td>(N = a + bS_{t-1} + \varepsilon_t)</td>
<td>4</td>
<td>17.36</td>
<td>6.05</td>
</tr>
<tr>
<td>(N = a + bF_{t-1} + \varepsilon_t)</td>
<td>4</td>
<td>18.45</td>
<td>7.14</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + \varepsilon_t)</td>
<td>5</td>
<td>29.29</td>
<td>17.98</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + d(N_{t-1} \times S_{t-1}) + \varepsilon_t)</td>
<td>6</td>
<td>52.08</td>
<td>40.77</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cF_{t-1} + \varepsilon_t)</td>
<td>5</td>
<td>30.45</td>
<td>19.14</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cF_{t-1} + d(N_{t-1} \times F_{t-1}) + \varepsilon_t)</td>
<td>6</td>
<td>52.84</td>
<td>41.53</td>
</tr>
<tr>
<td>(N = a + bS_{t-1} + cF_{t-1} + \varepsilon_t)</td>
<td>5</td>
<td>29.22</td>
<td>17.91</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + \varepsilon_t)</td>
<td>6</td>
<td>53.12</td>
<td>41.81</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + e(N_{t-1} \times (S_{t-1} + F_{t-1})) + \varepsilon_t)</td>
<td>8</td>
<td>156.10</td>
<td>144.79</td>
</tr>
</tbody>
</table>
Table A.3. Evaluation of the parsimony of several alternate linear models examining the annual variation in average summer deer mouse population density \((N)\) relative to the preceding spring’s average population density \((N_{t-1})\) and previous fall’s white spruce \((S_{t-1})\), subalpine fir \((F_{t-1})\), and total \((T_{t-1})\) cone indices. \(\varepsilon_t\) refers to a normally distributed random variable with mean zero, and \(K\) is the number of estimable parameters in each model. Model results are provided for the full population, as well as overwintered (OW) and young-of-the-year (YY) mice separately. The best-supported models, based on \(AIC_c\) scores, are highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>Full population</th>
<th>OW population</th>
<th>YY population</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N = a + e_t)</td>
<td>3</td>
<td>13.13</td>
<td>4.74</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + e_t)</td>
<td>4</td>
<td>18.83</td>
<td>10.44</td>
</tr>
<tr>
<td>(N = a + bT_{t-1} + e_t)</td>
<td>4</td>
<td>11.06</td>
<td>2.67</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cT_{t-1} + e_t)</td>
<td>5</td>
<td>19.99</td>
<td>11.60</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cT_{t-1} + d(N_{t-1} \times T_{t-1}) + e_t)</td>
<td>6</td>
<td>34.78</td>
<td>26.39</td>
</tr>
<tr>
<td>(N = a + bS_{t-1} + e_t)</td>
<td>4</td>
<td>14.91</td>
<td>6.52</td>
</tr>
<tr>
<td>(N = a + bF_{t-1} + e_t)</td>
<td>4</td>
<td><strong>8.39</strong></td>
<td><strong>0.00</strong></td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + e_t)</td>
<td>5</td>
<td>23.87</td>
<td>15.48</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + d(N_{t-1} \times S_{t-1}) + e_t)</td>
<td>6</td>
<td>38.87</td>
<td>30.48</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cF_{t-1} + e_t)</td>
<td>5</td>
<td>17.25</td>
<td>8.86</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cF_{t-1} + d(N_{t-1} \times F_{t-1}) + e_t)</td>
<td>6</td>
<td>24.15</td>
<td>15.76</td>
</tr>
<tr>
<td>(N = a + bS_{t-1} + cF_{t-1} + e_t)</td>
<td>5</td>
<td>17.11</td>
<td>8.72</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + e_t)</td>
<td>6</td>
<td>32.07</td>
<td>23.68</td>
</tr>
<tr>
<td>(N = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + e(N_{t-1} \times (S_{t-1} + F_{t-1})) + e_t)</td>
<td>8</td>
<td>138.01</td>
<td>129.62</td>
</tr>
</tbody>
</table>
Table A.4. Evaluation of the parsimony of several alternate linear models examining the annual variation in average fall deer mouse population density ($N$) relative to the preceding spring’s average population density ($N_{t-1}$) and previous fall’s white spruce ($S_{t-1}$), subalpine fir ($F_{t-1}$), and total ($T_{t-1}$) cone indices. $\epsilon_t$ refers to a normally distributed random variable with mean zero, and $K$ is the number of estimable parameters in each model. Model results are provided for the full population, as well as overwintered (OW) and young-of-the-year (YY) mice separately. The best-supported models, based on AIC$_c$ scores, are highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>Full population</th>
<th>OW population</th>
<th>YY population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>$K$</td>
<td>AIC$_c$</td>
<td>ΔAIC$_c$</td>
</tr>
<tr>
<td>$N = a + \epsilon_t$</td>
<td>3</td>
<td>15.17</td>
<td>0.00</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>21.16</td>
<td>5.99</td>
</tr>
<tr>
<td>$N = a + bT_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>21.17</td>
<td>6.00</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cT_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>30.16</td>
<td>14.99</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cT_{t-1} + d(N_{t-1} \times T_{t-1}) + \epsilon_t$</td>
<td>6</td>
<td>44.83</td>
<td>29.66</td>
</tr>
<tr>
<td>$N = a + bS_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>20.48</td>
<td>5.31</td>
</tr>
<tr>
<td>$N = a + bF_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>19.60</td>
<td>4.43</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cS_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>29.44</td>
<td>14.27</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cS_{t-1} + d(N_{t-1} \times S_{t-1}) + \epsilon_t$</td>
<td>6</td>
<td>44.35</td>
<td>29.18</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cF_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>28.45</td>
<td>13.28</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cF_{t-1} + d(N_{t-1} \times F_{t-1}) + \epsilon_t$</td>
<td>6</td>
<td>43.39</td>
<td>28.22</td>
</tr>
<tr>
<td>$N = a + bS_{t-1} + cF_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>22.27</td>
<td>7.10</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + \epsilon_t$</td>
<td>6</td>
<td>37.13</td>
<td>21.96</td>
</tr>
<tr>
<td>$N = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + e(N_{t-1} \times (S_{t-1} + F_{t-1})) + \epsilon_t$</td>
<td>8</td>
<td>151.92</td>
<td>136.75</td>
</tr>
</tbody>
</table>
Table A.5. Evaluation of the parsimony of several alternate linear models examining the annual variation in population growth ($r$) relative to the preceding population density ($N_{t-1}$) and previous fall’s white spruce ($S_{t-1}$), subalpine fir ($F_{t-1}$), and total ($T_{t-1}$) cone indices. $\varepsilon_t$ refers to a normally distributed random variable with mean zero, and $K$ is the number of estimable parameters in each model. Model results are provided for the full population for winter ($N_{t-1}$ = average fall young-of-the-year population density) and summer ($N_{t-1}$ = average spring population density) population growth, as well as overwintered (OW) mice separately for summer population growth. The best-supported models, based on AIC$_c$ scores, are highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>Winter</th>
<th>Summer (Full population)</th>
<th>Summer (OW population)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r = a + \varepsilon_t$</td>
<td>3</td>
<td>-55.36</td>
<td>-32.92</td>
<td>2.67</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + \varepsilon_t$</td>
<td>4</td>
<td>-41.06</td>
<td>-35.59</td>
<td>0.00</td>
</tr>
<tr>
<td>$r = a + bT_{t-1} + \varepsilon_t$</td>
<td>5</td>
<td>-31.38</td>
<td>-23.98</td>
<td>8.92</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + CT_{t-1} + \varepsilon_t$</td>
<td>6</td>
<td>-9.73</td>
<td>45.63</td>
<td>22.96</td>
</tr>
<tr>
<td>$r = a + bS_{t-1} + \varepsilon_t$</td>
<td>4</td>
<td>-38.23</td>
<td>-17.13</td>
<td>6.82</td>
</tr>
<tr>
<td>$r = a + bF_{t-1} + \varepsilon_t$</td>
<td>5</td>
<td>-36.37</td>
<td>-27.18</td>
<td>8.41</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + cS_{t-1} + \varepsilon_t$</td>
<td>5</td>
<td>-31.84</td>
<td>23.53</td>
<td>7.52</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + cS_{t-1} + dN_{t-1} \times S_{t-1} + \varepsilon_t$</td>
<td>6</td>
<td>-8.17</td>
<td>47.19</td>
<td>21.49</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + cF_{t-1} + \varepsilon_t$</td>
<td>5</td>
<td>-29.76</td>
<td>25.60</td>
<td>7.73</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + cF_{t-1} + dN_{t-1} \times F_{t-1} + \varepsilon_t$</td>
<td>6</td>
<td>-7.38</td>
<td>47.98</td>
<td>22.73</td>
</tr>
<tr>
<td>$r = a + bS_{t-1} + cF_{t-1} + \varepsilon_t$</td>
<td>5</td>
<td>-26.48</td>
<td>28.88</td>
<td>12.52</td>
</tr>
<tr>
<td>$r = a + bS_{t-1} + cF_{t-1} + dF_{t-1} + \varepsilon_t$</td>
<td>6</td>
<td>-7.84</td>
<td>47.52</td>
<td>14.78</td>
</tr>
<tr>
<td>$r = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + e(N_{t-1} \times (S_{t-1} + F_{t-1})) + \varepsilon_t$</td>
<td>8</td>
<td>92.85</td>
<td>148.21</td>
<td>95.34</td>
</tr>
</tbody>
</table>
Table A.6. Evaluation of the parsimony of several alternate linear models examining the annual variation in overwinter deer mouse survival ($\Phi$) relative to the previous fall’s young-of-the-year population density ($N_{t-1}$) and white spruce ($S_{t-1}$), subalpine fir ($F_{t-1}$), and total ($T_{t-1}$) cone indices. $\epsilon_t$ refers to a normally distributed random variable with mean zero, and $K$ is the number of estimable parameters in each model. The best-supported model, based on AIC$_c$ scores, is highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>AIC$_c$</th>
<th>$\Delta$AIC$_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi = a + \epsilon_t$</td>
<td>3</td>
<td>12.18</td>
<td>0.00</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>19.25</td>
<td>7.07</td>
</tr>
<tr>
<td>$\Phi = a + bT_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>18.89</td>
<td>6.71</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + cT_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>30.78</td>
<td>18.60</td>
</tr>
<tr>
<td>$\Phi = a + b(T_{t-1} + N_{t-1}) + \epsilon_t$</td>
<td>6</td>
<td>54.24</td>
<td>42.06</td>
</tr>
<tr>
<td>$\Phi = a + bS_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>18.76</td>
<td>6.58</td>
</tr>
<tr>
<td>$\Phi = a + b(S_{t-1} + \epsilon_t$</td>
<td>4</td>
<td>19.24</td>
<td>7.06</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + cS_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>30.59</td>
<td>18.41</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + cS_{t-1} + d(N_{t-1} \times S_{t-1}) + \epsilon_t$</td>
<td>6</td>
<td>54.54</td>
<td>42.36</td>
</tr>
<tr>
<td>$\Phi = a + bS_{t-1} + cF_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>31.16</td>
<td>18.98</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + cF_{t-1} + d(N_{t-1} \times F_{t-1}) + \epsilon_t$</td>
<td>6</td>
<td>54.52</td>
<td>42.34</td>
</tr>
<tr>
<td>$\Phi = a + bS_{t-1} + cF_{t-1} + \epsilon_t$</td>
<td>5</td>
<td>30.74</td>
<td>18.56</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + \epsilon_t$</td>
<td>6</td>
<td>54.50</td>
<td>42.32</td>
</tr>
<tr>
<td>$\Phi = a + bN_{t-1} + cS_{t-1} + dF_{t-1} + e(N_{t-1} \times (S_{t-1} + F_{t-1})) + \epsilon_t$</td>
<td>8</td>
<td>157.53</td>
<td>145.35</td>
</tr>
</tbody>
</table>
Table A.7. Evaluation of the parsimony of Cormack-Jolly-Seber models evaluating the relationship between summer survival of overwintered deer mice and the previous fall’s white spruce ($S_{t-1}$), subalpine fir ($F_{t-1}$), and total ($T_{t-1}$) cone indices. The probability of survival between trapping sessions ($\phi$) was modeled as a function of these covariates and time ($t$), while the encounter probability ($p$) was modeled only as a function of time. A period (“.”) indicates that the parameter is constant, and $K$ is the number of estimable parameters in each model. The best-supported models, based on AIC$_c$ scores and AIC$_c$ weight ($w_i$), are highlighted.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC$_c$</th>
<th>$\Delta$AIC$_c$</th>
<th>$w_i$</th>
<th>$K$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi(S_{t-1} + F_{t-1}) p(\cdot)$</td>
<td>7323.88</td>
<td>0.00</td>
<td>0.58</td>
<td>4</td>
</tr>
<tr>
<td>$\phi(S_{t-1}) p(\cdot)$</td>
<td>7325.42</td>
<td>1.54</td>
<td>0.27</td>
<td>3</td>
</tr>
<tr>
<td>$\phi(S_{t-1} + F_{t-1}) p(t)$</td>
<td>7328.47</td>
<td>4.59</td>
<td>0.06</td>
<td>34</td>
</tr>
<tr>
<td>$\phi(T_{t-1}) p(\cdot)$</td>
<td>7329.46</td>
<td>5.58</td>
<td>0.04</td>
<td>3</td>
</tr>
<tr>
<td>$\phi(S_{t-1}) p(t)$</td>
<td>7329.92</td>
<td>6.04</td>
<td>0.03</td>
<td>33</td>
</tr>
<tr>
<td>$\phi(\cdot) p(\cdot)$</td>
<td>7331.65</td>
<td>7.77</td>
<td>0.01</td>
<td>2</td>
</tr>
<tr>
<td>$\phi(F_{t-1}) p(\cdot)$</td>
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Appendix B: Chapter 6 supplementary material

Table B.1. Pollock’s (1982) Robust Design Model results for deer mouse abundance estimation for 2004-2011 at the treatment population-monitoring grid. Models varied time (t), behaviour (b), and heterogeneity (h) effects on the probability of capture in all possible combinations, as per Otis et al. (1978). All models constrained temporary emigration and immigration rates to be equal, but allowed them to vary as a function of time, and allowed the probability of survival between trapping sessions to vary as a function of time. The best-supported models, based on AICc scores and AICc weight (\(w_i\)), are highlighted. \(K\) is the number of estimable parameters in each model. See the Methods sections of Chapters 5 and 6 for details on the model selection and averaging procedures used to obtain abundance estimates.

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<th>(K)</th>
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Table B.2. The most parsimonious Cormack-Jolly-Seber models for the analysis of summer survival of overwintered deer mice at the control and treatment grids from 2004-2011. The probability of survival between trapping sessions ($\Phi$) and the encounter probability ($p$) were modeled as a function of grid ($g$) and time ($t$). A period (".") indicates that the parameter is constant. For each model, we show the corrected Akaike Information Criterion ($\text{AIC}_c$), the difference in $\text{AIC}_c$ from the best-supported model, $\text{AIC}_c$ weight ($w_i$), and the number of estimable parameters ($K$).

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<tr>
<td>( \Phi(t) p(t) )</td>
<td>1443.42</td>
<td>413.72</td>
<td>0.00</td>
<td>35</td>
</tr>
<tr>
<td>( \Phi(t) p(g \times t) )</td>
<td>1447.66</td>
<td>417.96</td>
<td>0.00</td>
<td>64</td>
</tr>
</tbody>
</table>
Appendix C: Permission to reproduce published material

A version of Chapter 2 was published in the *Canadian Journal of Zoology*. As per NRC Research Press copyright policy, authors retain the right, “To reuse all or part of their manuscript in other works created by them for noncommercial purposes, provided the original publication in an NRC Research Press journal is acknowledged through a note or citation.” (www.nrcresearchpress.com/page/authors/information/rights)

A version of Chapter 3 was published in *Mammalian Biology*. As per Elsevier GmbH copyright policy, authors retain “the right to include the journal article, in full or in part, in a thesis or dissertation;” (www.elsevier.com/wps/find/authorsview.authors/rights)

A version of Chapter 4 has been submitted to the *Journal of Mammalogy* for publication. As per American Society of Mammalogists copyright assignment policy, “ASM grants back to the Author the right to use or republish, with a citation to the source of the published article, all or part of the material from the published manuscript in oral presentations and future published works written or edited by the author.” (American Society of Mammalogists copyright assignment and author disclosure form)

A combined version of Chapters 5 and 6 has been accepted for publication in the *Journal of Animal Ecology*. As per John Wiley and Sons Inc. copyright policy, “AUTHORS – If you wish to reuse your own article (or an amended version of it) in a new publication of which you are the author, editor or co-editor, prior permission is not required (with the usual acknowledgements).” (http://www.wiley.com/bw/permis.asp?ref=0021-8790&site=1)
Appendix D: Animal use protocol approvals

Dear Dr. Miller:

Your Animal Use Protocol form entitled:

Population of Red-backed Voles and Deer Mice in Relation to Diet

has been approved by the Animal Use Subcommittee.

This approval is valid from 03.31.07 to 03.31.08

The protocol number for this project remains as 2004-026-03

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
4. If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
5. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 1 YR. - Highest Pain Level: B

<table>
<thead>
<tr>
<th>Species</th>
<th>Other Detail</th>
<th>Housing/Use Locations</th>
<th>Animal # Total for 1 Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Other, add to detail</td>
<td>Deer Mouse, MF</td>
<td>Field Station</td>
<td>150</td>
</tr>
<tr>
<td>Other, add to detail</td>
<td>Voles</td>
<td>Field Station</td>
<td>150</td>
</tr>
</tbody>
</table>

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

e.c. Approved Protocol - J. Millar, J. Wasylenko, Dept. Office
   Approval Letter - J. Wasylenko, Dept. Office

The University of Western Ontario
Animal Use Subcommittee/University Council on Animal Care
Health Sciences Centre • London, Ontario • CANADA - N6A 5C1
Phone: 519-661-2111 ext. 86770 • Fax: 519-661-2028 • www.uwo.ca/animal
Western

March 2, 2008

This is the Original Approval for this protocol
*A Full Protocol submission will be required in 2012*

Dear Dr. Millar:

Your Animal Use Protocol form entitled:
The Ecology of Small Mammals

Funding Agency: NSERC - Grant [Redacted]

has been approved by the University Council on Animal Care. This approval is valid from March 2, 2008 to March 31, 2009. The protocol number for this project is 2008-001-03 and replaces #2004-026-03.

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
4. If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.

4. Purchases of animals other than those approved for this system must be cleared through the ACVS Office. Health certificates will be required.

ANIMALS APPROVED FOR 1 YR.

<table>
<thead>
<tr>
<th>Species</th>
<th>Strain</th>
<th>Other Detail</th>
<th>Pain Level</th>
<th>Animal # Total for 1 Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Other, add to detail</td>
<td>Deer Mice</td>
<td></td>
<td>B</td>
<td>500</td>
</tr>
<tr>
<td>Other, add to detail</td>
<td>Red-backed Voles</td>
<td></td>
<td>B</td>
<td>300</td>
</tr>
<tr>
<td>Other, add to detail</td>
<td>Meadow Voles, Long-tailed Voles, Heather Voles</td>
<td></td>
<td>B</td>
<td>50 of each</td>
</tr>
</tbody>
</table>

STANDARD OPERATING PROCEDURES

Procedures in this protocol should be carried out according to the following SOPs. Please contact the Animal Use Subcommittee office (661-2111 ext. 66770) in case of difficulties or if you require copies.

SOPs are also available at http://www.uwo.ca/animal/acvs

320 Euthanasia
321 Criteria for Early Euthanasia/Rodents

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

cc. Approved Protocol [J. Millar, J. V. Weber]

Approval Letter [J. Weber, D.]

The University of Western Ontario
Animal Use Subcommittee/University Council on Animal Care
Health Sciences Centre, • London, Ontario • CANADA • N6A 5C1
PH: 519-661-2111 ext. 86770 • F: 519-661-2028 • www.uwo.ca/animal
Dear Dr. Millar:

Your Animal Use Protocol form entitled:

**The ecology of small mammals**

has had its yearly renewal approved by the Animal Use Subcommittee.

This approval is valid from **April 1, 2009 to March 31, 2010**

The protocol number for this project remains as **2008-001**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
4. If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

**c.c. Approved Protocol**

- J. Millar, J. Wasylenko, D. Cheshuk

**Approval Letter**

- J. Millar, J. Wasylenko, D. Cheshuk

---

*The University of Western Ontario*

Animal Use Subcommittee / University Council on Animal Care

Health Sciences Centre, London, Ontario • CANADA – N6A 5C1

PH: 519-661-2111 ext. 86770 • FL 519-661-2028 • www.uwo.ca / animal
Dear Dr. Millar

Your Animal Use Protocol form entitled:

The ecology of small mammals

has had its yearly renewal approved by the Animal Use Subcommittee.

This approval is valid from **04.01.2010** to **04.01.2011**

The protocol number for this project remains as **2008-001**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
   If the application for funding is not successful and you wish to proceed with the project, request that an internal
   scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health
   certificates will be required.

**REQUIREMENTS/COMMENTS**

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar
with the contents of this document.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety
components (biosafety, radiation safety, general laboratory safety) comply with institutional safety
standards and have received all necessary approvals. Please consult directly with your
institutional safety officers.

c.c. S. Warr, W. Lagerwerf

---

*The University of Western Ontario*

Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, 1 University Avenue, London, Ontario, CANADA N6A 5C1
PH: 519-661-2111 ext. 86770  FL 519-661-2028  www.uwo.ca/animal
Dear Dr. Millar:

Your Animal Use Protocol form entitled:

The ecology of small mammals

has had its renewal approval by the Animal Use Subcommittee.

This approval is valid from April 1, 2011 to March 31, 2012

The protocol number for this project remains as 2008-001

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
4. If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
5. Purchases of animals other than through this system must be cleared through the AVS office. Health certificates will be required.

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

c.c. Approved Protocol - J. Millar, J. Wasylenko, D. Chessuk
Approval Letter - J. Millar, J. Wasylenko, D. Chessuk

The University of Western Ontario
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre - London, Ontario • CANADA N6A 5C1
Ph: 519-661-2111 ext. 66770 • FL 51861-2029 • www.uwo.ca/animal
Appendix E: Research permits

RESEARCH PERMIT

FEE $ NIL

PERMITTEE: Dr. J. S. Millar

ADDRESS: University of Western Ontario, London, ONT

IS AUTHORIZED TO:
Conduct research on small mammals

DATE OF ISSUE: April 01, 2007

DATE OF EXPIRY: March 31, 2008

Signature of Permittee

For Minister of Alberta Sustainable Resource Development

IN ACCORDANCE WITH:
- Collection Licence 27927 and conditions
- Approved application & protocol on file with Fish and Wildlife Division

**IMPORTANT
District Office instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Permittee
Copy to – Wildlife Management, Edmonton HQ
Copy to – Licensing & Revenue Services, Edmonton HQ
Copy for – Issuing District
COLLECTION LICENCE

NAME: Dr. J.S. Millar
ADDRESS: University of Western Ontario, London, ONT

Is authorized to collect the following wildlife: Shrews, jumping mice, long tailed and meadow voles, squirrels, chipmunks, red backed voles and deer mice (Up to 20 of each species)

This licence authorizes the use of the following equipment and methods: Longworth traps and

Analgesics for blood collection, as per Animal Care Committee Class Protocol 007.

This licence is valid (location): In Kananaskis Valley

EFFECTIVE DATE: 01 April 2007 DATE OF EXPIRY: 31 March 2008

Collections are to conducted by: Licencsee, Y.T. Hwang, T. Slettrud, C. Tabacaru, J. Smith & summer assistant

Date of issue: 26 March 2007

Signature of Licencsee (not valid unless signed by Licencsee) Licence must be carried while collecting.

                  FGF PAster of Alberta Sustainable Resource Development

Conditions:
1. The licencsee must keep the appropriate Fish and Wildlife Officer informed of collection activities as they occur.
2. This licence is not transferable.
3. Persons collecting under the authority of this licence must produce a copy of the licence on the request of a Fish and Wildlife Officer when carrying out collection activities.
4. If any information obtained from the collection of any wildlife under this licence is used in a report or publication of any kind, the licencsee shall forward a copy of such publication to the Director of Wildlife.
5. Within 7 days of the expiry of the licence, the licencsee shall complete the table below, and any other records required by this licence, and return licence and records to the Director of Wildlife.

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>Species</th>
<th>Sex/M/F</th>
<th>Location</th>
<th>Disposition</th>
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IMPORTANT

District Office instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Licencsee

Copies to: Licensing Services-Edmonton HQ, Region, Issuing District
RESEARCH PERMIT

FEE $NIL

PERMITTEE: Dr. J. S. Miller

ADDRESS: University of Western Ontario

IS AUTHORIZED TO:
Conduct research on small mammals

DATE OF ISSUE: Apr 18, 2008 DATE OF EXPIRY: Mar 31, 2009

Signature of Permittee

For Minister of Alberta Sustainable Resource Development

IN ACCORDANCE WITH:
- Collection Licence # 34142
- Approved application & protocol on file with Fish and Wildlife Division

**IMPORTANT**
District Office instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Permittee
Copy to – Wildlife Management, Edmonton HQ
Copy to – Licensing & Revenue Services, Edmonton HQ
Copy for - Issuing District
COLLECTION LICENCE

FEE $ NIL

NAME: Dr. J. S. Miller

ADDRESS: University of Western Ontario, London, Ont.

Is authorized to collect the following wildlife: Deer mouse, red-backed vole, spotted skunk, long-tailed weasel, jumping mice, chipmunks, squirrels

This licence authorizes the use of the following equipment and methods: Longworth traps

This licence is valid (location): In Kananaskis Valley

EFFECTIVE DATE: Apr 18/08 DATE OF EXPIRY: Mar 31/09

Collections are to conducted by Dr. J. S. Miller and assistance under direct supervision.

Date of issue: Apr 18/08

Signature of Licencee (not valid unless signed by Licencee) Licence must be carried while collecting

For Minister of Alberta Sustainable Resource Development

Conditions:
1. The licencee must keep the appropriate Fish and Wildlife Officer informed of collection activities as they occur.
2. This licence is not transferable.
3. Persons collecting under the authority of this licence must produce a copy of the licence on the request of a Fish and Wildlife Officer when carrying out collection activities.
4. If any information obtained from the collection of any wildlife under this licence is used in a report or publication of any kind, the licencee shall forward a copy of such publication to the Director of Wildlife.
5. Within 7 days of the expiry of the licence, the licencee shall complete the table below, and any other records required by this license, and return licence and records to the Director of Wildlife.

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>Species</th>
<th>Sex M/F</th>
<th>Location</th>
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IMPORTANT

District Office Instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Licencee Copies to: Licensing Services – Edmonton HQ Region, Issuing District
RESEARCH PERMIT

FEE $ NIL

PERMITTEE: Dr. J. S. Millar

ADDRESS: University of Western Ontario, London, ONT

IS AUTHORIZED TO:

Conduct research on small mammals

DATE OF ISSUE: May 8, 2009
DATE OF EXPIRY: Mar 31, 2010

For Minister of Alberta Sustainable Resource Development

IN ACCORDANCE WITH:

- Collection Licence #40809
- Approved report on research activities on file
- Alberta Wildlife Animal Care Committee
  Class Protocol #007

**IMPORTANT
Office instructions:**

Please photocopy this document once it is issued and forward copies to:

Original – Permittee
Copy to – Wildlife Management, Edmonton HQ
Copy to – Licensing & Revenue Services, Edmonton HQ
COLLECTION LICENCE

FEE $ NIL

NAME: Dr. J. S. Miller

ADDRESS: Dept of Biology, 1151 Richmond S. W. London, ON T N6A 5B7

Is authorized to collect the following wildlife: Shrews, jumping mice, long-tailed voles, meadow voles, squirrels, chipmunks, red-backed voles, deer mice (up to 20 species)

This licence authorizes the use of the following equipment and methods: Longworth traps and anaesthetics for blood sampling - according to class approval 007

This licence is valid (location) : Kananaskis Valley

EFFECTIVE DATE: May 1, 2009 DATE OF EXPIRY: Mar 31, 2010

Collections are to be conducted by: Licenclee, Nikhil Lobo and assistants under direct supervision

Date of issue: May 5, 2009

Signature of Issuer (Valid unless signed by Licenclee) Licence must be carried while collecting

For Minister of Alberta Sustainable Resource Development

Conditions:
1. The licenclee must keep the appropriate Fish and Wildlife Officer informed of collection activities as they occur.
2. This licence is not transferable.
3. Persons collecting under the authority of this licence must produce a copy of the licence on the request of a Fish and Wildlife Officer when carrying out collection activities.
4. If any information obtained from the collection of any wildlife under this licence is used in a report or publication of any kind, the licenclee shall forward a copy of such publication to the Director of Wildlife.
5. Within 7 days of the expiry of the licence, the licenclee shall complete the table below, and any other records required by this licence, and return licence and records to the Director of Wildlife.

<table>
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<th>Collection Date</th>
<th>Species</th>
<th>Sex M/F</th>
<th>Location</th>
<th>Disposition</th>
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IMPORTANT

District Office instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Licenclee Copies to: Licencing Services-Edmonton HQ, Region, Issuing District
RESEARCH PERMIT

FEE $ NIL

PERMITTEE: John S. Millar

ADDRESS: Dept of Biology University of Western Ontario, London, ON, N6A 5B7

IS AUTHORIZED TO: Conduct research on small mammals

DATE OF ISSUE: Apr 12, 2010 DATE OF EXPIRY: Mar 31, 2011

Signature of Permittee

For Minister of Alberta Sustainable Resource Development

IN ACCORDANCE WITH:

Collection Licence #40828
Approved Protocol #007 Small Mammals

**IMPORTANT
Office instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Permittee
Copy to – Wildlife Management, Edmonton HQ
Copy to – Licensing & Revenue Services, Edmonton HQ.
**COLLECTION LICENCE**

**NAME:** John S. Millar  
**ADDRESS:** Dept of Biology University of Western Ontario, London, ON N6A 3B7

**Licence – CN**  
**Southern Rockies Area**

Is authorized to collect the following wildlife: Deer mice/redbacked voles

This licence authorizes the use of the following equipment and methods: Longworth traps

This licence is valid (location): Southern Rockies Area

**EFFECTIVE DATE** April 12, 2010 **DATE OF EXPIRY:** Mar 31, 2011

Collections are to be conducted by: Personnel/Students under J.S. Millar’s supervision

**Signature of Licencee:** [Redacted] **Date of issue:** Apr 12, 2010

**Conditions:**
1. The licencee must keep the appropriate Fish and Wildlife Officer informed of collection activities as they occur.
2. This licence is not transferable.
3. Persons collecting under the authority of this licence must produce a copy of the licence on request of a Fish and Wildlife Officer when carrying out collection activities.
4. If any information obtained from the collection of any wildlife under this licence is used in a report or publication of any kind, the licencee shall forward a copy of such publication to the Director of Wildlife.
5. Within 7 days of the expiry of the licence, the licencee shall complete the table below, and any other records required by this licence, and return licence and records to the Director of Wildlife.

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>Species</th>
<th>Sex/MF</th>
<th>Location</th>
<th>Disposition</th>
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**IMPORTANT**

**District Office Instructions:**
Please photocopy this document once it is issued and forward copies to:

Original – Licencee  
Copies to: Licensing Services-Edmonton HQ, Region, Issuing District
Government of Alberta
Sustainable Resource Development
Fish and Wildlife Division

General Permit – GP

RESEARCH PERMIT

District: Calgary

FEE $ NIL

PERMITTEE: John S. Millar

ADDRESS: Dept of Biology - University of Western Ontario; London, ON, N6A 5B7

IS AUTHORIZED TO: Conduct research on small mammals


Signature of Permittee

For Minister of Alberta Sustainable Resource Development

IN ACCORDANCE WITH:

Collection Licence #47867
Approved Protocol #007 Small Mammals

**IMPORTANT
District Office Instructions:

Please photocopy this document once it is issued and forward copies to:

Original – Permittee
Copy to – Wildlife Management, Edmonton HQ
Copy to – Licencing & Revenue Services, Edmonton HQ
Copy for – Issuing District
COLLECTION LICENCE

NAME: John S. Millar

Is authorized to collect the following wildlife: Deer mice/redbacked voles

This licence authorizes the use of the following equipment and methods: Longworth traps

This licence is valid (location) Southern Rockies Area

EFFECTIVE DATE: April 5, 2011

DATE OF EXPIRY: Mar 31, 2012

Collections are to be conducted by Personnel/Students under J.S. Millar’s supervision

Date of issue: Apr 5, 2011

Signature and photo of licencse (not valid unless signed by licencsee) Licence must be carried while collecting

For Minister of Alberta Sustainable Resource Development

Conditions:
1. The licencsee must keep the appropriate Fish and Wildlife Officer informed of collection activities as they occur.
2. This licence is not transferable.
3. Persons collecting under the authority of this licence must produce a copy of the licence on the request of a Fish and Wildlife Officer when carrying out collection activities.
4. If any information obtained from the collection of any wildlife under this licence is used in a report or publication of any kind, the licencsee shall forward a copy of such publication to the Director of Wildlife.
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<th>Sex M/F</th>
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IMPORTANT

District Office instructions:
Please photocopy this document once it is issued and forward copies to:

Original – Licencsee

Copies to: Licensing Services, Edmonton HQ, Region, Issuing District
# Curriculum Vitae

**Name:** Nikhil Lobo

**Post-secondary Education and Degrees:**
University of Western Ontario  
London, Ontario, Canada  
2007-2013 Ph.D.

University of Toronto  
Mississauga, Ontario, Canada  

**Selected Honours and Awards:**
Natural Sciences and Engineering Research Council Canada Graduate Scholarship – Doctoral  
2011-2013

J.D. Detwiler Award  
2011-2012

Province of Ontario Graduate Scholarship  
2010-2011, 2011-2012 (Declined)

Ruth Horner Arnold Fellowship  
2010-2011, 2011-2012

American Society of Mammalogists Grant-in-Aid of Research  
2010

Centre for Environment & Sustainability Excellence Award  
2009-2010, 2010-2011

Robert and Ruth Lumsden Graduate Award in Science  
2009-2010

Department of Biology Graduate Student Teaching Award  
2009-2010

Graduate Teaching Assistant Union Community Service Award  
2009-2010

Dr. Irene Uchida Fellowship in Life Sciences  
2008-2009, 2009-2010
Related Work

Experience:
Teaching Assistant
University of Western Ontario
2007-2012

Course Instructor
University of Western Ontario
2010

Faculty of Science Learning Development Graduate Fellow
University of Western Ontario
2009

Publications:

Submitted

Lobo N, Green DJ and Millar JS. Effects of seed quality and abundance on the foraging behavior of northern rodents. *Journal of Mammalogy*.

Accepted

Lobo N and Millar JS. Indirect and mitigated effects of pulsed resources on the population dynamics of a northern rodent. *Journal of Animal Ecology*.


Published


