ECOSYSTEM DYNAMICS
OF THE BOREAL FOREST

The Kluane Project

Edited by
Charles J. Krebs
Stan Boutin
Rudy Boonstra

OXFORD
UNIVERSITY PRESS
2001
Contents

Contributors  xxii

PART I  INTRODUCTION

1  General Introduction
   CHARLES J. KREBS  3

2  The Kluane Region
   CHARLES J. KREBS & RUDY BOONSTRA  9
   2.1  Geography and Geology, 10
   2.2  Weather and Climate, 12
         2.2.1  Temperature, 12
         2.2.2  Precipitation, 15
   2.3  Study Area and Vegetation, 15
   2.4  Vertebrate Food Web, 18
   2.5  History of Hare Cycles, 21
   2.6  Large Mammals, 22
   2.7  Human Impacts, 23

3  Trophic Interactions, Community Organization, and the Kluane Ecosystem
   A. R. E. SINCLAIR & CHARLES J. KREBS  25
   3.1  Trophic-level Theory, 27
       3.1.1  Community Structure, 27
       3.1.2  Control of Trophic-level Biomass, 27
       3.1.3  Case Studies in Mammalian Communities, 29
   3.2  Interactions of Trophic Levels, 30
       3.2.1  Bottom-up Models, 36
### CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.2.2 Top-down Models, 37</td>
<td></td>
</tr>
<tr>
<td>3.2.3 Herbivore-dominated Models, 37</td>
<td></td>
</tr>
<tr>
<td>3.2.4 Vegetation-dominated Models, 37</td>
<td></td>
</tr>
<tr>
<td>3.2.5 Dilution Models, 37</td>
<td></td>
</tr>
<tr>
<td>3.2.6 Reciprocal Models, 38</td>
<td></td>
</tr>
<tr>
<td>3.3 Experimental Perturbations in the Boreal Forest, 38</td>
<td></td>
</tr>
<tr>
<td>3.3.1 Experiment 1: Application of Fertilizer, 38</td>
<td></td>
</tr>
<tr>
<td>3.3.2 Experiment 2: Addition of Rabbit Chow, 38</td>
<td></td>
</tr>
<tr>
<td>3.3.3 Experiment 3: Exclusion of Carnivores, 41</td>
<td></td>
</tr>
<tr>
<td>3.3.4 Experiment 4: Exclusion of Carnivores and the Addition of Rabbit Chow, 41</td>
<td></td>
</tr>
<tr>
<td>3.3.5 Experiment 5: Exclusion of Hares, 41</td>
<td></td>
</tr>
<tr>
<td>3.3.6 Experiment 6: Exclusion of Hares and the Addition of Fertilizer, 41</td>
<td></td>
</tr>
<tr>
<td>3.3.7 Experiment 7: Removal of Vegetation, 41</td>
<td></td>
</tr>
<tr>
<td>3.4 Discussion, 42</td>
<td></td>
</tr>
<tr>
<td>3.4.1 Limitations of the Models, 42</td>
<td></td>
</tr>
<tr>
<td>3.4.2 Models of Trophic-level Interactions in Different Ecosystems, 42</td>
<td></td>
</tr>
<tr>
<td>3.5 Summary, 43</td>
<td></td>
</tr>
</tbody>
</table>

4 Experimental Design and Practical Problems of Implementation

STAN BOUTIN, CHARLES J. KREBS, VILIS O. NAMS, A. R. E. SINCLAIR, RUDY BOONSTRA, MARK O’DONOGHUE, & CATHY DOYLE 49

4.1 Experimental Design, 50

4.1.1 Choice of Treatments, 50

4.1.2 Size and Spatial Location of Treatments, 52

4.1.3 To Replicate or Not to Replicate, 54

4.2 Practical Problems of Implementation, 55

4.2.1 The Evolution of a Predator-proof Fence, 55

4.2.2 Food Supplementation, 58

4.2.3 Fertilizer, 60

4.2.4 Hare Exclosures, 61

4.3 Organization, Personnel, and Equipment, 61

4.3.1 Organizational Structure, 62

4.3.2 The Problem of Training and Protocols, 63

4.3.3 Seen Sheets, 63

4.3.4 Winter Work at Kluane, 64

4.3.5 Equipment, 64

4.4 Summary, 65

PART II PLANT DYNAMICS

5 Herbs and Grasses

ROY TURKINGTON, ELIZABETH JOHN, & MARK R. T. DALE 69

5.1 Hypotheses Regarding Vegetation, 70

5.2 Study Area, 71

5.3 Tests of Predictions from Three Models, 72

5.3.1 Donor Control Model, 72
<table>
<thead>
<tr>
<th>CONTENTS</th>
<th>xiii</th>
</tr>
</thead>
</table>

5.3.2 Herbivore Control Model, 77  
5.3.3 Combined Top-down Bottom-up Model, 78  
5.4 Which Model Best Describes Boreal Forest Herbs and Grasses? 84  
5.4.1 Transient Dynamics and Stability, 86  
5.4.2 Impacts of Climatic Warming, 87  
5.5 Summary, 88  

6 Shrubs  
CHARLES J. KREBS, MARK R. T. DALE, VILIS O. NAMS, A. R. E. SINCLAIR, & MARK O’DONOGHUE 92  
6.1 The Shrub Community at Kluane, 93  
6.1.1 Species Composition, 93  
6.1.2 Pattern Changes and Succession, 93  
6.1.3 Secondary Chemicals in Kluane Shrubs, 96  
6.2 Biomass Dynamics, 97  
6.2.1 Methods of Estimation, 97  
6.2.2 Impacts of Treatments, 98  
6.3 Growth Rates of Shrubs, 102  
6.3.1 Methods of Estimation, 102  
6.3.2 Impacts of Treatments, 104  
6.4 Losses of Twigs to Browsing and Natural Mortality, 106  
6.4.1 Methods of Estimation, 106  
6.4.2 Impacts of Treatments, 107  
6.5 What Limits Primary Production of Shrubs? 110  
6.5.1 Succession in Boreal Forest Shrubs, 110  
6.5.2 Impact of Hare and Moose Browsing, 112  
6.5.3 Role of Secondary Chemicals, 113  
6.6 Summary, 113  

7 Trees  
MARK R. T. DALE, SHAWN FRANCIS, CHARLES J. KREBS, & VILIS O. NAMS 116  
7.1 Tree Community at Kluane, 117  
7.1.1 Tree Abundance on the Study Area, 118  
7.1.2 Tree Growth, 118  
7.1.3 White Spruce Cone and Seed Production, 120  
7.2 Vegetation Mapping, 122  
7.2.1 Fire History of the Study Area, 123  
7.2.2 Other Forms of Disturbance, 128  
7.3 Succession in the Boreal Forest, 130  
7.4 Fertilizer Effects on Trees, 132  
7.5 Summary, 135  

PART III HERBIVORES  

8 Snowshoe Hare Demography  
KAREN E. HODGES, CHARLES J. KREBS, DAVID S. HIK, CAROL I. STEFAN, ELIZABETH A. GILLIS, & CATHY E. DOYLE 141  
8.1 The Snowshoe Hare Cycle, 142
8.2 Methods, 143
8.3 Demographic Parameters, 145
  8.3.1 Density and Rates of Change, 145
  8.3.2 Sex and Age Structure, 146
  8.3.3 Reproduction, 147
  8.3.4 Survival Rates, 153
  8.3.5 Causes of Death, 162
  8.3.6 Immigration and Emigration, 169
8.4 Impacts of Experimental Treatments, 169
  8.4.1 Impacts on Hare Demography, 171
  8.4.2 Causation of the Hare Cycle, 173
  8.4.3 Efficacy of the Experimental Treatments, 173
  8.4.4 Experimental Scale and Methodological Concerns, 174
8.5 Interactions with Other Species, 175
8.6 Conclusions, 175

9 The Role of Red Squirrels and Arctic Ground Squirrels
RUDY BOONSTRA, STAN BOUTIN, ANDREA BYROM, TIM KARELS, ANNE HUBBS,
KARI STUART-SMITH, MIKE BLOWER, & SUSAN ANTPOEHLER 179
9.1 Natural History, 180
  9.1.1 Red Squirrels, 180
  9.1.2 Arctic Ground Squirrels, 181
9.2 Community Interactions and Factors Affecting Population Dynamics, 181
9.3 Methods, 182
  9.3.1 Red Squirrels, 182
  9.3.2 Arctic Ground Squirrels, 184
9.4 Results, 186
  9.4.1 Red Squirrels, 186
  9.4.2 Arctic Ground Squirrels, 193
9.5 Discussion, 201
  9.5.1 Role of Stochastic Events, 203
  9.5.2 Treatment Effects, 204
  9.5.3 Role of Squirrels in the Boreal Forest Community, 209
9.6 Conclusions, 210

10 Voles and Mice
RUDY BOONSTRA, CHARLES J. KREBS, SCOTT GILBERT, & SABINE SCHWEIGER 215
10.1 Natural History and Food Web Links, 216
10.2 Community Interactions and Factors Affecting Population Dynamics, 217
10.3 Methods, 218
  10.3.1 Small Mammal Trapping, 218
  10.3.2 Data Analysis, 219
  10.3.3 Robustness of Data, 219
10.4 Impacts of the Manipulations, 219
  10.4.1 Northern Red-Backed Vole, 220
  10.4.2 Microtus Voles, 224
10.5 What Limits Mice and Vole Populations at Kluane? 226
  10.5.1 Northern Red-Backed Vole, 227
  10.5.2 Microtus Species, 234
10.6 Summary, 235

11 Forest Grouse and Ptarmigan
KATHY MARTIN, CATHY DOYLE, SUSAN HANNON, & FRITZ MUELLER 240

11.1 The Ecological Role of Forest and Alpine Grouse, 241
  11.1.1 Trophic Position, 241
  11.1.2 Life History, 241
  11.1.3 Habitats, 242
  11.1.4 Current Understanding of Population Dynamics, 243
  11.1.5 Predicted Responses to Experimental Treatments, 243
11.2 Methods, 244
  11.2.1 Duration of Grouse Studies, 244
  11.2.2 Shakwak Valley Population Trends, 244
  11.2.3 Numerical and Reproductive Parameters on Treatment Grids, 244
  11.2.4 Data Robustness and Limitations, 245
11.3 Demography of Grouse, 246
  11.3.1 Population Trends in the Shakwak Valley, 246
  11.3.2 Reproductive Parameters, 247
  11.3.3 Population Trends on Control Plots, 248
  11.3.4 Relationship of Changes to the Snowshoe Hare Cycle, 249
11.4 Response of Forest Grouse to Experimental Treatments, 250
  11.4.1 Fertilizer Addition, 250
  11.4.2 Food Addition, 251
  11.4.3 Predator Exclosure, 252
  11.4.4 Predator Exclosure + Food, 252
11.5 Discussion, 253
  11.5.1 Hypotheses Related to Grouse Population Trends, 253
  11.5.2 Did the Experiments Change the Dynamics for Grouse? 253
  11.5.3 Linkages on the Same Trophic Level, 253
  11.5.4 Linkages to Other Trophic Levels, 254
11.6 Conclusions, 255
  11.6.1 Comparison with Other Studies, 255
  11.6.2 Unexpected Results, 256
  11.6.3 Unanswered Questions, 257

12 Other Herbivores and Small Predators: Arthropods, Birds, and Mammals
JAMES N. M. SMITH & NICHOLAS F. G. FOLKARD 261

12.1 Methods, 263
  12.1.1 Arthropods, 263
  12.1.2 Songbirds and Woodpeckers, 263
  12.1.3 Other Herbivores, 263
12.2 Predicted Responses to Experimental Treatments, 264
12.3 Responses by Species Groups, 264
  12.3.1 Arthropods, 264
12.3.2 Birds, 265
12.3.3 Other Herbivores, 268
12.4 Discussion, 269
  12.4.1 Links to the 10-Year Cycle, 269
  12.4.2 Effects of Fertilization, 269
  12.4.3 Other Patterns in the Food Web, 270
12.5 Summary, 270

PART IV MAMMALIAN PREDATORS

13 Coyotes and Lynx
MARK O'DONOGHUE, STAN BOUTIN, DENNIS L. MURRAY, CHARLES J. KREBS,
ELIZABETH J. HOFER, URS BREITENMOSER, CHRISTINE BREITENMOSER-WÜERSTEN,
GUSTAVO ZULETA, CATHY DOYLE, & VILIS O. NAMS 275

13.1 Methods, 278
  13.1.1 Population Monitoring, 278
  13.1.2 Foraging Behavior, 279
  13.1.3 Functional Responses, 280
13.2 Numerical Responses, 282
  13.2.1 Density, 282
  13.2.2 Adult Survival, 283
  13.2.3 Emigration, 286
  13.2.4 Recruitment, 286
13.3 Social Organization, 287
  13.3.1 Home Ranges, 288
  13.3.2 Social Groups, 289
13.4 Foraging Behavior, 289
  13.4.1 Diets, 289
  13.4.2 Scavenging Behavior, 293
  13.4.3 Hunting Tactics, 295
  13.4.4 Group Hunting, 297
  13.4.5 Use of Trails, 297
  13.4.6 Habitat Use, 297
13.5 Functional Responses, 300
  13.5.1 Components of Functional Responses, 301
  13.5.2 Prey Switching, 304
13.6 Synthesis and Conclusions, 307
  13.6.1 Numerical Responses, 308
  13.6.2 Functional Responses, 310
  13.6.3 Total Impact of Predation by Coyotes and Lynx on Hares, 313
  13.6.4 Impact of Predation by Coyotes and Lynx on Alternative Prey, 313
  13.6.5 Coexistence of Coyotes and Lynx, 314
  13.6.6 The Specialist-Generalist Contrast, 316

14 Other Mammalian Predators
MARK O'DONOGHUE, STAN BOUTIN, ELIZABETH J. HOFER, & RUDY BOONSTRA 324

14.1 Methods, 325
CONTENTS xvi

14.2 Red Fox, 325
14.3 Wolf, 327
14.4 Weasel, 329
14.5 Wolverine, 331
14.6 Marten, 332
14.7 Mink and Otter, 332
14.8 Synthesis and Conclusions, 332

PART V AVIAN PREDATORS

15 Great Horned Owls
CHRISTOPH ROHNER, FRANK I. DOYLE, & JAMES N. M. SMITH 339

15.1 Methods, 341
15.1.1 Population Census, 341
15.1.2 Monitoring Diets, 342
15.1.3 Radio Telemetry, 342
15.1.4 Analysis of Telemetry Data, 343
15.1.5 Statistical Analyses, 344

15.2 Demography, 344
15.2.1 Reproduction and Population Productivity, 344
15.2.2 Survival and Emigration, 348
15.2.3 Estimating Numerical Responses, 351

15.3 Foraging Behavior, 351
15.3.1 Diet, 351
15.3.2 Prey Preferences, 354
15.3.3 Estimating Functional Responses and Predation Impact, 355

15.4 Social Organization, 360
15.4.1 Social Status and Vocal Activity, 360
15.4.2 Stability and Size of Home Ranges, 360
15.4.3 Effect of Territoriality on Spacing of Owls, 361
15.4.4 Territorial Behavior and Limitation of Population Increase, 361
15.4.5 Social Behavior and the Time Lag in the Numerical Response, 364

15.5 Responses to Large-Scale Experiments, 366
15.5.1 Space Use in Territories with Experimental Hot Spots of Prey, 366
15.5.2 Predator Movements from Poor Patches to Rich Patches, 368

15.6 Discussion, 368
15.6.1 Large Floating Population When Resources Are Abundant, 368
15.6.2 Factors Affecting Functional Responses and Predation Impact, 369
15.6.3 Limitation of Population Growth at Peaks of Cyclic Prey, 371
15.6.4 Time Lag in the Numerical Response of a Predator of Cyclic Prey, 371
15.6.5 Factors Limiting Spatial Aggregation of Predators, 372

16 Raptors and Scavengers
FRANK I. DOYLE & JAMES N. M. SMITH 377

16.1 Methods, 378
16.1.1 General Approach, 378
16.1.2 Population Surveys: The Intensive Search Area, 380
16.1.3 Reproductive Success, 380
16.1.4 Diets, 380
16.1.5 Data Analysis, 381
16.2 Predicted Responses of Raptors and Corvids, 381
16.3 Responses by Groups and Individual Species, 382
   16.3.1 Large Resident Raptors, 382
   16.3.2 Large Migratory Raptors, 385
   16.3.3 Small Migratory Raptors, 388
   16.3.4 Small Owls, 391
   16.3.5 Corvids, 394
   16.3.6 Other Raptors, 396
   16.3.7 Intraguild Predation, 396
16.4 Discussion, 398
   16.4.1 Functional, Numerical, and Reproductive Responses to Hare Densities, 398
   16.4.2 Resource Partitioning and Diet Width, 400
   16.4.3 Intraguild Predation, 400
   16.4.4 Methodology and Limitations, 401
16.5 Summary, 401

PART VI COMMUNITY AND ECOSYSTEM ORGANIZATION

17 Testing Hypotheses of Community Organization for the Kluane Ecosystem
   A. R. E. Sinclair, Charles J. Krebs, Rudy Boonstra, Stan Boutin,
   & Roy Turington  407
17.1 Experimental Perturbations of the Boreal Forest, 409
   17.1.1 Direct and Indirect Effects, 409
   17.1.2 The Experiments, 409
17.2 Methods, 411
   17.2.1 Soil Nitrogen, 411
   17.2.2 Vegetation, 411
   17.2.3 Plant Secondary Chemicals, 412
   17.2.4 Herbivore Biomass, 412
   17.2.5 Predator Activity, 412
17.3 Direct Effects of Trophic-level Perturbations, 412
   17.3.1 Fertilizer Addition, 412
   17.3.2 Addition of Hare Food, 413
   17.3.3 Predator Exclosure, 416
   17.3.4 Predator Exclosure and Food Addition, 416
   17.3.5 Hare Exclosure, 419
   17.3.6 Hare Exclosure Plus Fertilizer, 421
   17.3.7 Vegetation Removal, 425
17.4 Indirect Effects of Trophic-level Perturbations, 426
   17.4.1 Fertilizer Addition, 426
   17.4.2 Food Addition, 426
   17.4.3 Predator Exclosure, 426
CONTENTS xix

17.4.4 Food Addition and Predator Exclosure, 427
17.4.5 Hare Exclosure, 427
17.5 Discussion, 427
17.5.1 Direct Effects, 427
17.5.2 Indirect Effects, 428
17.5.3 Top-down versus Bottom-up, 430
17.5.4 Productivity and Biomass Responses, 430
17.5.5 Other Indirect Effects, 431
17.5.6 The Role of Secondary Chemicals, 432
17.5.7 The Dominant Pathways in the Vertebrate Community, 432
17.6 Conclusion, 433
17.7 Summary, 433

18 Vertebrate Community Structure in the Boreal Forest: Modeling the Effects of Trophic Interaction
DAVID CHOQUENOT, CHARLES J. KREBS, A. R. E. SINCLAIR, RUDY BOONSTRA, & STAN BOUTIN 437
18.1 Trophic Interaction and Species Coexistence, 438
18.2 Interaction between Vegetation and Herbivores, 439
18.3 Interaction between Herbivores and Predators, 440
18.4 Modeling, 440
18.4.1 Interaction between Vegetation and Herbivores, 441
18.4.2 Equilibrium Conditions for Snowshoe Hares and Ground Squirrels, 446
18.4.3 Adding Predation to Models of Interaction between Herbivores and Vegetation, 450
18.4.4 The Effect of Herbivore Cycles on Predators, 452
18.5 Discussion, 458
18.5.1 Unresolved Modeling Issues, 458
18.5.2 Mechanisms of Coexistence, 460
18.5.3 Top-down and Bottom-up Influences on Community Structure, 460

19 Trophic Mass Flow Models of the Kluane Boreal Forest Ecosystem
JENNIFER L. RUESINK & KAREN E. HODGES 463
19.1 Questions about the Ecosystem Dynamics of the Boreal Forest, 466
19.2 Modeling the Kluane System, 467
19.3 Methods for Constructing Mass Balance Models, 467
19.3.1 Parameterization of Mass Balance Models, 469
19.4 Results from Mass Balance Models, 474
19.4.1 Consumption of Plant Biomass by Herbivores, 474
19.4.2 Phase of Cycle Models, 476
19.4.3 Seasonal Models, 480
19.4.4 Food Addition and Predator Reduction Models, 480
19.4.5 Partial Food Web Models, 483
19.5 Discussion, 485
19.5.1 Do Predator–Prey Dynamics Structure the Boreal Forest Ecosystem? 485
20 Conclusions and Future Directions
CHARLES J. KREBS, RUDY BOONSTRA, STAN BOUTIN, & A. R. E. SINCLAIR 491

20.1 Primary Findings, 492
   20.1.1 Predator Trophic Level, 492
   20.1.2 Herbivore Trophic Level, 493
   20.1.3 Plant Trophic Level, 494

20.2 Secondary Findings, 494
   20.2.1 Predator Trophic Level, 494
   20.2.2 Herbivore Trophic Level, 495
   20.2.3 Plant Trophic Level, 496

20.3 Opportunities for Further Work, 497
20.4 Unsolved Problems, 498
20.5 Future Boreal Forest Research, 499

Appendix 1 How to Use the Enclosed Kluane CD-ROM 503

Appendix 2 Table of Contents for the Kluane CD-ROM 504

Index 505