Winter 1997

Foraging strategies of two sympatric lagomorphs: Implications of habitat fragmentation

Douglas Foxall Smith

University of New Hampshire, Durham

Follow this and additional works at: https://scholars.unh.edu/dissertation

Recommended Citation

https://scholars.unh.edu/dissertation/2001

This Dissertation is brought to you for free and open access by the Student Scholarship at University of New Hampshire Scholars' Repository. It has been accepted for inclusion in Doctoral Dissertations by an authorized administrator of University of New Hampshire Scholars' Repository. For more information, please contact nicole.hentz@unh.edu.
Foraging strategies of two sympatric lagomorphs: Implications of habitat fragmentation

Abstract
I studied the effects of variation in food patch quality and predation risk on the foraging patterns and measures of foraging behavior of New England (S. transitionalis) and eastern (S. floridanus) cottontails, and their survivorship and weight change during these experiments. I then superimposed the results of these experiments onto real habitat patches to determine the amount of habitat each species could occupy and maintain similar survivorship. Finally, I measured an adaptation (eye size), and predator detection of both species in an effort to explain the difference in survival between S. floridanus and S. transitionalis.

In outdoor enclosures (5.7 x 45.7-m) I manipulated food quality and predation risk among four food patches. I measured the give-up-density (GUD) of food at each feeder daily, and weighed animals on a weekly basis. I also developed a break-beam sensor device to measure the time cottontails spent foraging at feeders that in predation risk. Neither species varied their behaviors with predation risk, though S. transitionalis spent marginally more total time at risk. During this experiment when no food was available in cover, S. transitionalis had lower survival than S. floridanus. However, when food was available in cover, the survivorship curves of the two species did not differ. When food quality and predation risk varied among food patches, S. floridanus avoided the poorer quality patches and foraged at higher quality patches with greater predation risk, whereas S. transitionalis avoided only the poorest quality food patches. When I applied these foraging patterns onto real habitat patches I found that S. floridanus could occupy 99% of a habitat patch whereas S. transitionalis could only occupy 32% of a patch. As snow accumulated in winter, S. transitionalis lost a significant amount of suitable habitat whereas, S. floridanus did not. One mechanism that may explain the paradox in the survivorship and habitat use of the two species is the bulginess of their eyes and the distance that they can detect an approaching predator. S. floridanus has larger eyes, and can detect an approaching predator at a greater distance than S. transitionalis.

Keywords
Agriculture, Forestry and Wildlife, Biology, Zoology, Biology, Ecology

This dissertation is available at University of New Hampshire Scholars' Repository: https://scholars.unh.edu/dissertation/2001
INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6” x 9” black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.
FORAGING STRATEGIES OF TWO SYMPATRIC LAGOMORPHS:
IMPLICATIONS OF HABITAT FRAGMENTATION

BY

DOUGLAS FOXALL SMITH
BS NORTHLAND COLLEGE, 1980
MS UNIVERSITY OF WISCONSIN, 1992

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy
in

Natural Resources

December 1997
This dissertation has been examined and approved.

[Signatures]

Dx.

Dissertation Director, John A. Litvaitis, Associate Professor

William M. Baum, Professor

Peter J. Pekins, Associate Professor

Michelle T. Scott, Associate Professor

Thomas D. Lee, Associate Professor

Date

September 24, 1997
DEDICATION

This dissertation is dedicated to the memory of my father-in-law, "Papa Jim" Gang. Jim was like a surrogate father when I was in my Master’s program and Kathy in medical school. Jim was an extremely caring man; he loved his family, his church, his town, the local high school sports teams, and the Chicago White Sox, and not always in that order. Jim was the county civil Engineer in Boone County, IL, and held that job all of his life. He was dedicated to his job and to making the town of Belvidere a better place to live for everyone. He would vacuum the office on weekends, take out the trash, and do just about anything to save the taxpayers some money. Jim was always out on the road, surveying his county, checking road signs, noting where accidents frequently occurred, and meeting the needs of future growth. Jim was "at home" in his car, in the county he loved.

Jim was interested in everyone of his son-in-laws as if they were his own. He welcomed us into his home and his family, if not just out of his kindness, then to balance his minority in a house full of five women. Jim enjoyed to hear about my work with wildlife and would describe in detail the latest wetlands statutes affecting road construction or the most recent Discovery show on cable he had seen.

Jim died in my second year of graduate school at UNH, taking his life before his cancer did. Jim was the sort of man who wouldn’t want a dedication, but it is with his spirit of selflessness that I dedicate this dissertation to him. Jim taught me that life is short and we must do what we love with whom we love, and appreciate the simple things in life.

"I had the opportunity to leave several times, but decided to stay... I enjoyed working... where you do everything. There’s satisfaction in seeing a project through, start to finish."

-Jim Gang, at his retirement party
ACKNOWLEDGMENTS

Wow, there are a lot of people who helped me with this project! First, special acknowledgment for my wife, Kathy Gang, you helped me struggle through the most difficult times, and helped celebrate the successes. To my parents Peter and Peggy Smith, and mother-in-law Marge Gang I thank you for your endless supply of support and encouragement.

John Litvaitis, my dissertation advisor, deserves an incredible dedication of his own for allowing me to learn and grow in my own way and in my own direction. He began my program with weekly meetings over lunch or coffee, (he often paid) where we discussed recent and relevant papers. He pushed my butt when I needed a shove and he let go of the rope when he saw me take off. He is an outstanding mentor, advisor, and teacher. John is someone who is equally comfortable discussing metapopulation dynamics as he is the latest recipe he tried, a fine wine or beer, or his recent favorite video tape. I appreciate the incredible amount of common ground we share in science and cooking, and our differences as well.

My dissertation committee I thank for the time they spent helping me, attending meetings, and reading drafts of my proposal and dissertation. Billy Baum was immeasurably helpful in my development. He included me in his behavioral psychology seminars, helped me work out problems with my design, and implementation of behavioral experiments. He and Michelle Scott also put together a seminar on Foraging theory during my tenure which was a wonderful exercise and helped me to pull together all of the recent thinking in foraging theory. Pete Pekins helped me with a side experiment on cottontail basal metabolism and helped revise it with each of the many rejections from peer-reviewed journals. Tom Lee I thank for his guidance, his interest in my work and his contributions on community ecology to my education and development.

Chris Neefus and Will Urban provided assistance with statistics, design, and the many problems I encountered learning SAS language. Chris also helped with C-programming when I needed it and was often available to
bounce ideas off of when I was starting a new set of experiments. Srini Vasan also provided assistance getting my C-programs to run without errors.

My friends, I owe you a lot. You were there to hear me complain, hear my excitement when experiments went well and were part of the community I enjoyed working in everyday. Most helpful were Claire McSweeney, Chief Okoye, Yuriko Yano, Christy Goodale, Maggie Soulia, Jenny Deenik, Sally Turtle, Cassie Ash, Jim Oehler, Brenda Probert, Anne Brown, Roger Coupe, Patty Bedker, Kim Babbitt, Jim Sweeney, and Stuart Leiderman. Thank you for your friendship, your words of advice, and your guidance.

A special thanks to Wayne Smith and the Bioengineering laboratory. Thanks for all of the time you put into on the remote sensors for these experiments. I would hate to calculate how much we paid you on an hourly basis, but your charity is greatly appreciated. Thanks also for helping to write the paper on the system and presenting at the Engineering conference.

Many work study students helped with this project but there were a few that stood out above the rest. Stan Bonis and Shannon Donovan did tremendous work for me and I greatly appreciate their help. Shannon also provided the sometimes daily record of her exploits trapping cottontails. Most times I would be in stitches listening to her tell of the, not first, but second time she locked her keys in her car with the car running, or driving over the lawn at the horticulture farm because the driveway was not yet plowed. Shannon, even if none of the stories are true, and I hope some of them are not, I appreciated your humor.

John McLean and Melissa Sim-Hollister, I greatly appreciate you putting up with my rabbits and me for three years. I looked forward to seeing you everyday to chat about the growing tomatoes, strawberries or pumpkins. I grew my largest pumpkins ever on your good advice and appreciate your friendship, morning coffee, interest in my project.

Sandy Boyle and Bob Taylor, I thank for putting up with me and my rabbits for the last year of the study and for helping me get the mill and the pelletizer running.

There are many more that came and went and I apologize for not naming you. A special thank you to Diana Wright and Faith Sherridan at Complex Systems, John Aber for teaching one of the best courses I’ve ever taken, and for directing a very fine Ph.D. program. Also thanks to Becky Warner for teaching the very best course I have ever taken, and to Karol
LaCroix for her help with graduate student issues, helping me find funding for conferences in Mexico and Europe, and being incredibly supportive.

Also thanks to Van Gould of the University Animal Use and Care Committee. Though Van was the bearer of bad news from time to time, when my proposals for animal research were rejected by the University Animal Use and Care Committee, he always helped me to develop acceptable methods to get the information I needed.
TABLE OF CONTENTS

DEDICATION .........................................................................................................iii

ACKNOWLEDGMENTS ........................................................................................iv

LIST OF TABLES ....................................................................................................xi

LIST OF FIGURES ...............................................................................................xiii

ABSTRACT .............................................................................................................xv

CHAPTER

I. BEHAVIORAL TITRATIONS IN RESPONSE TO FOOD QUALITY AND PREDATION RISK: DIFFERING STRATEGIES AND FITNESS OUTCOMES...................................................................................................1

   Introduction ....................................................................................................1

   Behavioral Titrations ....................................................................................5

   Methods ..........................................................................................................6

      Study Animals ............................................................................................6

      Study Designs ............................................................................................7

      Titration Experiment ................................................................................7

      Foraging Behavior Experiment .............................................................10

      Defining Behaviors ................................................................................12
Survival and Physical Condition ................................................... 14
Results .......................................................................................................... 15
Titration Experiment ....................................................................... 15
   
   S. transitionalis ..................................................................... 15
   
   S. floridanus ........................................................................... 18
Foraging Behavior Described ......................................................... 21
   
   Behavioral Patterns.................................................................. 21
   
   Food Consumption ................................................................ 22
   
   Foraging Events and Search Time.................................... 24
   
   Handling ............................................................................... 30
   
   Vigilance ............................................................................. 30
   
   Total Time at Risk ................................................................. 30
   
   Survival and Weight Change .................................................. 31
Discussion .................................................................................................... 34
   
   Weight Change and Survival .................................................. 37
Conclusion ................................................................................................... 39
Literature Cited .......................................................................................... 43

II. FORAGING IN FRAGMENTED LANDSCAPES: INDIVIDUAL
BEHAVIORS AND POPULATION CONSEQUENCES .................. 48

Introduction ................................................................................................. 48
Methods ........................................................................................................ 53
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study Animals</td>
<td>53</td>
</tr>
<tr>
<td>Trade-Off of Food Quality and Predation Risk</td>
<td>53</td>
</tr>
<tr>
<td>Experimental Design</td>
<td>53</td>
</tr>
<tr>
<td>Patch Use in Southern New Hampshire</td>
<td>56</td>
</tr>
<tr>
<td>Simulation of Foraging Strategies on Real Habitat Patches</td>
<td>57</td>
</tr>
<tr>
<td>Results</td>
<td>59</td>
</tr>
<tr>
<td>New England Cottontails</td>
<td>59</td>
</tr>
<tr>
<td>Eastern Cottontails</td>
<td>59</td>
</tr>
<tr>
<td>Both Species Simultaneously</td>
<td>63</td>
</tr>
<tr>
<td>Survivorship</td>
<td>65</td>
</tr>
<tr>
<td>Implications to Habitat Use</td>
<td>65</td>
</tr>
<tr>
<td>Discussion</td>
<td>66</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>75</td>
</tr>
</tbody>
</table>

### III. DIFFERENCES IN THE EYE SIZE AND PREDATOR DETECTION

DISTANCE OF NEW ENGLAND (*SYLVILAGUS TRANSITIONALIS*)
AND EASTERN (*S. FLORIDANUS*) COTTONTAILS..............78

*Introduction*.................................................................................................78

*Methods*........................................................................................................82

Eye Size............................................................................................82

Predator Detection Ability.................................................................83
LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1. Distance and diet treatment protocols. Every cottontail received, at random, each distance and diet treatment</td>
<td>9</td>
</tr>
<tr>
<td>1.2. Give up densities (GUD) explained by main effects, their interaction, treatment, period and error variance for S. floridanus and S. transitionalis</td>
<td>16</td>
</tr>
<tr>
<td>1.3. Model variables used to describe the variation in food consumption, number of foraging events per night of foraging, time searching, food consumed per foraging event, food consumed per time searching, time handling, food consumed per time handling, vigilance, food consumed per time vigilant, total time at risk, and the food consumed per total time at risk, for New England and eastern cottontails</td>
<td>26</td>
</tr>
<tr>
<td>2.1. Experiment 1: Variables that explain the variation in weight change and give-up-densities (GUDs), among New England cottontails</td>
<td>60</td>
</tr>
<tr>
<td>2.2. Experiment 2: Variables that explain the variation in give-up-densities (GUDs), and weight change among eastern cottontails</td>
<td>62</td>
</tr>
<tr>
<td>2.3. Experiment 3: Variables that explain variation in give-up-densities (GUDs), and weight change, among New England and eastern cottontails simultaneously</td>
<td>64</td>
</tr>
</tbody>
</table>
5.1. Parameter estimate, standard error of estimate, partial correlation, T, and significance of T, for New England cottontails in three different environmental quality specific models.............................................................107

5.2. Parameter estimate, standard error of estimate, partial correlation, T, and significance of T, for New England cottontails in three different environmental quality specific models.............................................................108
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1 Give-up-densities of food for <em>S. transitionalis</em> and <em>S. floridanus</em> at feeders that vary in predation risk (distance to cover) and food quality. Food quality treatments were 40%, 60%, and 100% rabbit chow and the balance being wood chips.</td>
<td>17</td>
</tr>
<tr>
<td>1.2. Comparison of mean (+/- standard error) GUDs and metabolizable energy intake by <em>S. floridanus</em> and <em>S. transitionalis</em> in titration experiment.</td>
<td>19</td>
</tr>
<tr>
<td>1.3. Log relative frequency distribution of pauses between foraging events for <em>S. transitionalis</em> and <em>S. floridanus</em>. Lines fit with non-linear regression.</td>
<td>23</td>
</tr>
<tr>
<td>1.4. Mean food consumption (+/- standard error) by <em>S. floridanus</em> and <em>S. transitionalis</em> from feeders that vary in predation risk.</td>
<td>25</td>
</tr>
<tr>
<td>1.5. Food consumption per time searching, and per event (+/- standard error) by <em>S. transitionalis</em> and <em>S. floridanus</em>.</td>
<td>29</td>
</tr>
<tr>
<td>1.6. Food consumed per total time at risk (+/- standard error) by <em>S. transitionalis</em> and <em>S. floridanus</em> from feeders that vary in predation risk.</td>
<td>32</td>
</tr>
<tr>
<td>1.7. Survivorship functions of <em>S. transitionalis</em> and <em>S. floridanus</em> when food is available in cover and when it has been depleted.</td>
<td>33</td>
</tr>
</tbody>
</table>
1.8. Weight change of *S. floridanus* and *S. transitionalis* that lived and died in experiments.........................................................................................................................35

2.1. Mean give-up-densities (+/- standard error) for New England and eastern cottontails, and both species simultaneously..................................................61

2.2 Changes in cottontail distribution with increasing habitat fragmentation in the landscape.....................................................................................................71

3.1. Experimental set-up to examine the predator-detection distances of *S. transitionalis* and *S. floridanus*...........................................................................84

3.2. Predator detection distance and eye size of *S. transitionalis* and *S. floridanus*...............................................................................................................87

4.1. Experimental set-up of enclosures indicating location of feeders with optical sensors, databus, and data processors.........................................................96

4.2. Log relative frequency distributions of pauses in New England and eastern cottontail foraging described by non-linear (two-phase) regression........100
ABSTRACT

FORAGING STRATEGIES OF TWO SYMPATRIC LAGOMORPHS: IMPLICATIONS OF HABITAT FRAGMENTATION

Douglas Foxall Smith
University of New Hampshire, December 1997

I studied the effects of variation in food patch quality and predation risk on the foraging patterns and measures of foraging behavior of New England (S. transitionalis) and eastern (S. floridanus) cottontails, and their survivorship and weight change during these experiments. I then superimposed the results of these experiments onto real habitat patches to determine the amount of habitat each species could occupy and maintain similar survivorship. Finally, I measured an adaptation (eye size), and predator detection of both species in an effort to explain the difference in survival between S. floridanus and S. transitionalis.

In outdoor enclosures (5.7 x 45.7-m) I manipulated food quality and predation risk among four food patches. I measured the give-up-density (GUD) of food at each feeder daily, and weighed animals on a weekly basis. I also developed a break-beam sensor device to measure the time cottontails spent foraging at feeders that in predation risk. Neither species varied their
behaviors with predation risk, though *S. transitionalis* spent marginally more total time at risk. During this experiment when no food was available in cover, *S. transitionalis* had lower survival than *S. floridanus*. However, when food was available in cover, the survivorship curves of the two species did not differ. When food quality and predation risk varied among food patches, *S. floridanus* avoided the poorer quality patches and foraged at higher quality patches with greater predation risk, whereas *S. transitionalis* avoided only the poorest quality food patches. When I applied these foraging patterns onto real habitat patches I found that *S. floridanus* could occupy 99% of a habitat patch whereas *S. transitionalis* could only occupy 32% of a patch. As snow accumulated in winter, *S. transitionalis* lost a significant amount of suitable habitat whereas, *S. floridanus* did not. One mechanism that may explain the paradox in the survivorship and habitat use of the two species is the bulginess of their eyes and the distance that they can detect an approaching predator. *S. floridanus* has larger eyes, and can detect an approaching predator at a greater distance than *S. transitionalis*.
CHAPTER I

BEHAVIORAL TITRATIONS IN RESPONSE TO FOOD QUALITY AND PREDATION RISK: DIFFERING STRATEGIES AND FITNESS OUTCOMES

Introduction

Predation (Sih et al. 1985) and competition (Hutchinson 1959, MacArthur and Levins 1967, Price 1978, Morin 1984) have long been thought to shape ecological communities. For example, specialist predators may mediate prey coexistence by preferentially consuming competitively superior prey (Paine 1966, Inouye et al. 1980, Morin 1981, 1986, 1987, Wilbur et al. 1983, Steneck et al. 1991). Generalist predators, on the other hand, may reduce the overall abundance of competitors, thus reducing competition among prey (Lubchenco 1986). Predators also may concentrate prey into refuges, and depending on habitat preferences of prey, may indirectly mediate competition among them (Gilliam and Fraser 1988, Kotler and Brown 1988, Kotler and Holt 1989, Walls 1995), or competition among prey in refuges may force less aggressive species to become more susceptible to predation (Garvey et al. 1994). In addition, habitat segregation may occur as a result of differences in
antipredator behavior (Caswell 1978, Sih 1980, Hanski 1983, Werner et al. 1983, Kotler 1984, Hughes et al. 1994). Thus, predation and competition can interact in ways that one process modifies the other (Kotler and Holt 1989).

Vulnerability of prey to predators can increase as landscapes become more fragmented (Brown and Litvaitis 1995). In human-altered landscapes, original habitats are replaced by a mosaic of varying land uses, decreasing the availability of original habitats, reducing the size of patches, increasing landscape diversity, evenness, and habitat edges. Oehler and Litvaitis (1996) demonstrated that the abundance of generalist mammalian predators increased with increased coverage of human-altered habitats (especially agriculture and development). In the context of landscape alteration and increased density of predators, I investigated how two sympatric lagomorphs behaviorally respond to predation risk, and the possible mediating effects of predation on their coexistence.

In the northeastern United States, New England (Sylvilagus transitionalis) and eastern (S. floridanus) cottontails, occupy the same, early successional habitats (Eabry 1968, Smith and Litvaitis unpubl. data). These habitats are ephemeral and therefore populations of cottontails are dependent upon the "birth" of patches as a result of natural or human disturbances. S. transitionalis is endemic to the northeastern United States.
and has declined substantially throughout its range (Chapman and Stauffer 1981), whereas *S. floridanus* has roughly concurrently expanded its range (Johnston 1972, Chapman and Morgan 1973), suggesting possible competition between these lagomorphs (Linkkila 1971, Chapman and Morgan 1973). However, loss of early successional habitats also corresponded with the decline of *S. transitionalis* (Litvaitis 1993), suggesting that the loss of suitable habitat independent of, or combined with competition may be responsible. Probert and Litvaitis (1995) examined whether interference competition may have caused the decline of *S. transitionalis*, but found that neither species was able to exclude the other from either food resources or protective cover in an experimental pen. They suggested, however, that interference competition by *S. floridanus* may limit populations of *S. transitionalis* if they are able to colonize ephemeral patches sooner than *S. transitionalis*.

Previously, Barbour and Litvaitis (1993) evaluated whether populations of *S. transitionalis* were limited by habitat loss. These investigators found that *S. transitionalis* occupying small habitat patches (<2.5 ha) were in poorer physical condition, foraged on lower quality browse, and frequently occupied sites farther from cover than individuals on large patches (>5.0 ha). Rabbits on small patches also had lower winter survival rates. These results
suggested that *S. transitionalis*, occupying resource-limited patches, may use a foraging strategy that balances the risks of predation with their need to forage.

I initiated this study to investigate potential differences in foraging strategies of *S. transitionalis* and *S. floridanus*. Both species occupy similar landscapes, and likely have similar food requirements and predation costs, but one species has been able to persist while populations of the other have declined. I investigated foraging strategies in winter, because cottontail fitness in winter is most strongly influenced by foraging and avoiding predators (Barbour and Litvaitis 1993, Brown and Litvaitis 1995). I examined whether the foraging strategies of the two species differ, and whether their resulting fitness (measured as body weight and survivorship) differed as well. To address these issues, I conducted two experiments. In the first experiment I manipulated the predation risk and food quality of four food patches, and measured the give-up-density of food (GUD, sensu Brown 1988) in a titration experiment (Kotler and Blaustein 1995). In the second experiment, I measured how predation risk affected the amount of search, handling, and vigilance time at feeders that varied in predation risk. To understand the fitness consequences of foraging strategies of both species I compared weight change before and after treatments, and survivorship.
functions of each species from the second experiment and other experiments under similar conditions (Chapter II).

**Behavioral Titrations**

Foraging strategies provide behavioral ecologists with information about how a forager ranks habitats (Kotler and Blaustein 1995, Abramsky et al. 1996, Lima and Dill 1989) in terms of energy intake and safety (Abrahams and Dill 1989). Kotler and Blaustein (1995) described foraging decisions as "behavioral titrations". Based on optimal behavior, a behavioral titration balances marginal costs with marginal benefits and equalizes the marginal values of other activities (Charnov 1976). When the forager ceases to forage in a patch, it is assumed that costs equal gains. The food left in the patch at the time the forager quit the patch is analogous to the chemical titration when anions and cations are balanced in a solution. Therefore, food left over in the food patch is a measure of costs and benefits of patch use. The give-up density (GUD) is directly related to the harvest rate of the animal at the time it quit foraging in the patch (Brown 1988, Kotler and Brown 1990, Kotler and Blaustein 1995). In other words, GUDs should approximate the sum of a forager's energetic, predation, and missed opportunity costs of foraging, if it is behaving optimally (Brown 1988). Therefore, low GUDs (greater patch depletion) indicate low foraging costs, meaning the forager perceived low
predation costs and missed opportunity costs. Large differences in GUDs among patches imply large differences in perceived costs of foraging, predation, and missed opportunity costs. In this paper, I assume costs to be from three sources: the energetic costs of foraging, risk of predation, and missed opportunities of energetic gain at other feeders.

The objectives of this study were to: i) determine the value of predation risk at feeders that vary in distance to cover, ii) compare the effects of predation risk on the search, handling, and vigilance time of S. transitionalis and S. floridanus at feeders that varied in predation risk, iii) and compare the weight change and survivorship of individuals in these experiments and other (Chapter II) experiments.

Methods

Study Animals

I captured S. transitionalis and S. floridanus in Rockingham and Strafford Counties, New Hampshire during October 1994-March 1997. Specific identity was based on pelage and morphological characteristics (Litvaitis et al. 1991). Animals were marked with numbered ear tags, sexed, and weighed when captured. They were housed in individual cages (0.9 x 0.8 x 0.6 m) in a covered outdoor animal facility for 5 - 22 days prior to use in experiments. I maintained animals on a commercial rabbit chow (16% protein, Blue Seal,
Concord, NH) from feeders identical to those used in experiments, and provided water *ad libitum*. I conducted the experimental manipulation of food quality and predation risk for 14 weeks starting in January 1997, and the experiment to measure the allocation of time to patches from December 1995 to March 1996.

**Study Designs**

I conducted all experiments in enclosures (5.7 x 45.7 m) consisting of two microhabitats. Approximately 40% of each enclosure was composed of dense shrubs and the remaining 60% was mowed pasture. The vegetation in the two microhabitats was representative of that occupied by both species in the region. A 1.8-m high fence surrounded the enclosure and a 1.2 m high fence divided the enclosure into 8 replicates and kept rabbits within their individual cells. The exterior fence limited, but did not prevent predator access to the pens. Monofilament line with 1-meter spacing covered the top of the enclosure, to minimize but not eliminate predation by raptors.

**Titration Experiment**

I varied the food quality and distance between the food patch and cover to determine the costs of foraging at risk. In an attempt to determine where foraging costs and missed opportunity costs equalled predation costs, food quality in or next to cover was decreased to the point where cottontails
avoided the feeder.

Eight cottontails were placed in individual enclosures and varied distances from a feeder to cover and food quality were applied to each in a randomized-block design. Two distance and three diet protocols were used (Table 1.1). Each feeder was filled with 80-mL of either commercial rabbit chow (Blue Seal, 16% protein, maintenance ration), or commercial rabbit chow diluted with wood chips. Rabbit chow was diluted with 60%, 40% or 30% wood fiber to decrease the quality of food in or near cover. Rabbit pellets and wood chips were ground in a mill, homogenized, and then repelletized. Each treatment combination lasted for two weeks following an initial month of acclimatization to the pen (December 1995). Four *S. transitionalis* and four *S. floridanus* were used in this experiment, two males and two females of each species. A split-plot general linear model (GLM, SAS Inst. 1986), with time as the split plot, was used to examine how distance to cover and food quality affect GUDs of *S. transitionalis* and *S. floridanus*.

Feeders were replenished each day with 80-mL of chow after measuring the food remaining from the previous day. Volumetric measurement of food was used instead of weight because volume was relatively invariant whereas weight varied with humidity (Smith, pers. observation). Because the energetic value of each diet was different, I converted volume of food
Table 1.1. Distance and diet treatment protocols. Every cottontail received, at random, each distance and diet combination.

<table>
<thead>
<tr>
<th>Feeder</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance treatment 1 0-m(^a)</td>
<td>5-m</td>
<td>13-m</td>
<td>26-m</td>
<td></td>
</tr>
<tr>
<td>diet treatment a</td>
<td>100(^b)</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>diet treatment b</td>
<td>60%</td>
<td>70%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>diet treatment c</td>
<td>40%</td>
<td>70%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>distance treatment 2 2-m</td>
<td>10-m</td>
<td>16-m</td>
<td>20-m</td>
<td></td>
</tr>
<tr>
<td>diet treatment a</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>diet treatment b</td>
<td>60%</td>
<td>70%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>diet treatment c</td>
<td>40%</td>
<td>70%</td>
<td>100%</td>
<td>100%</td>
</tr>
</tbody>
</table>

\(^a\) Distances are labeled as distance from cover.

\(^b\) Diets are labeled as percent commercial rabbit chow. Balance was wood fiber.
consumed into metabolizable energy values for this rabbit chow reported in Walski and Mautz (1977). To determine energetic value of fiber-added diets, I assumed the energetic value of wood fiber to be zero and subtracted the percentage of fiber from the metabolizable energy value of pure rabbit chow. To convert volume to mass, I took five volume samples (i.e., 5, 10, 20, 50, 80-mL) of each diet, and dried pellets in an oven at 56°C for 32 hours. I then weighed the five sample volumes and used linear regression to fit a line to the mass to volume relationship. I used this regression equation to estimate mass from volume measurements obtained from the field (Smith, unpubl. data).

**Foraging Behavior Experiment**

In this experiment one cottontail was randomly assigned to each enclosure for a total of four *S. floridanus* and 4 *S. transitionalis* at any time during the experiment. However, during this 151-day experiment, cottontails were preyed upon by owls (*Srix varia*, and *Bubo virginiana*), therefore a total of 17 *S. floridanus* and 16 *S. transitionalis* were used. Four feeders were available to each rabbit at 3, 9, 15, and 22-m from cover. I used a total of 160-mL of commercial rabbit chow equally divided among four feeders, because this amount was the maximum amount of food consumed in previous trials. Thus, each feeder contained at least 25% of the rabbit's daily requirement.
Each feeder in four of the eight enclosures was equipped with a break-beam signal device that was connected to a microprocessor for data storage and downloading (Smith et al. 1997). When the beam was broken, the microprocessor recorded the time of and the duration (time the rabbit's head was in the feeder) of each event for a 24-hour period. The data were downloaded from the microprocessor to disk and food in feeders was measured and refilled.

The number of events and elapsed time in feeders were tallied for each feeder each night. I considered the elapsed time in feeders to be searching behavior, and pauses between events were used to separate events into discrete bouts of foraging. To characterize handling and vigilance, and differentiate between pauses within and pauses between bouts, pauses between events were calculated by subtracting the next event time from the end of the previous foraging event. For instance, if a rabbit put its head in a feeder at 12:00:00 for three seconds, and its next feeding event occurred at 12:00:50, then the pause between feeding events is 12:00:50-12:00:03 or 47 seconds. Relative frequencies of pauses were then graphed on semi-log plots to determine the shape of the distribution of pauses between foraging events (Machlis 1977). Machlis (1977) described a method of differentiating bouts of behaviors, on the basis of the different slopes in the distribution. Within a
distribution with different slopes, each can be considered a different process. Direct observations were then used to define those processes. I considered events within bouts as those events with pauses with a frequency greater than one. Pauses occurring after this gap were considered alternate activities. Although Slater (1974) suggested that the breakpoint between curves can be approximated by visually inspecting the curves, I used nonlinear (two-phase) regression to determine whether the distribution could be described by one or two regression lines, and the break point between the curves. Nonlinear regression fits least-squares curves to observations, and estimates the breakpoint between curves (Systat 1996).

**Defining Behaviors**

Previous studies have shown that search, handling, and vigilance time vary with predation risk (see review by Lima and Dill 1990). For instance, foragers may increase vigilance time as distance to cover increases (Barnard 1980, Caraco et al. 1980, Holmes 1984), or decrease vigilance time with increasing group size (e.g., Caraco et al. 1980, Lima 1988). However, Lima (1987a) suggested, and later demonstrated (Lima 1987b) that foragers also decease their vigilance time with increasing distance to minimize their overall time at risk. Although these studies of vigilance are largely biased towards social groups of foraging organisms, the relationship between
predation risk and vigilance time for solitary foragers is likely similar. However, I hypothesized that foragers would spend more time vigilant as distance to cover increased, because cottontails are solitary foragers and increasing distance from cover might lessen their probability of escape. Foragers also vary their diet to minimize handling time in risky patches (Lima and Valone 1986) or may shift their diet to items that can be handled while the forager is in a vigilant posture (Lima 1988). Although vigilance and handling may not be mutually exclusive in rabbits (rabbits drop their head to harvest food items but lift their heads to handle it), searching for food items does interrupt vigilance and rabbits may vary their diet or patch depletion rule in order to maximize vigilance time.

In this experiment I was interested in the time that rabbits spent vigilant, handling food, and searching within feeders, the number of feeding events per feeder, and the total time a rabbit spent at risk at the different feeders varying in predation risk. I then examined each dependent measure in relation to distance to cover.

I used a general linear model to determine if differences existed between *S. transitionalis* and *S. floridanus* foraging behaviors. I weighted search, handling, vigilance time, and total time at risk by the amount of food consumed at each feeder per night of foraging to minimize the effect of
decreasing time allocated to feeders farther from cover. I log transformed all foraging parameters, including GUDs because of skew, except handling time, because its distribution did not deviate from normality.

**Survival and Physical Condition**

I used the Kaplan-Meier method of estimating survivorship curves (Cox and Oakes 1984, Muenchow 1986, Pollock et al. 1989) to examine cottontail mortality when food was available in cover (n = 14 *S. floridanus*, n = 17 *S. transitionalis*, Chapter II, unpubl. data) and when food in cover was depleted (n = 17 *S. floridanus*, n = 16 *S. transitionalis*, Experiment 2). I used data from preliminary studies where food was available in cover to increase the sample size of individuals in this survivorship analysis. I compared the survivorship functions of *S. transitionalis* and *S. floridanus* using the log-rank test (Crowley and Breslow 1984, Pyke and Thompson 1986, Pollock et al. 1989). I also compared weight change of individuals to determine if animals that died were in poorer physical condition than those that lived, whether *S. floridanus* and *S. transitionalis* differed in their physical condition, and whether there were differences in weight change between *S. floridanus* and *S. transitionalis* that died with t-tests. I measured body mass of individuals at the beginning of experiments and approximately weekly during experiments.
Results

Titration Experiment

For *S. transitionalis* and *S. floridanus*, give-up-densities of food did not vary significantly with sex of the individual, or the number of days in captivity prior to the experiment ($P > 0.05$).

*S. transitionalis*. Food quality, the distance to the feeder from cover, and their interaction, all affected the GUDs of *S. transitionalis* (Table 1.2). When food quality was the same at all feeders, GUDs increased with increasing distance from cover, indicating that *S. transitionalis* titrate predation and other costs with marginal benefits. However, when food quality in cover declined, this relationship changed. When the poorest quality food (40% rabbit chow, 60% wood chips) was in cover, *S. transitionalis* GUDs increased in cover, and decreased at the intermediate distance feeder station (13 to 16-m from cover, Fig.1.1). By decreasing the quality of food in cover by 60%, their GUD increased three times, suggesting that the marginal value of the patch declined. At the second feeder the marginal value of the patch declined by 30%, and GUDs increased 29%, whereas GUDs at the third feeder decreased by 54% (Fig.1.1). The 40% rabbit chow treatment was the only treatment to increase GUDs in or near cover (first feeder) and decrease GUDs away from cover (third feeder), and no food quality treatment in cover.
Table 1.2. Give up densities (GUD) explained by main effects, their interaction, treatment period and error variance of *S. floridanus* and *S. transitionalis*.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS*</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. floridanus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>diet protocol</td>
<td>1562.51</td>
<td>2</td>
<td>3.92</td>
<td>0.0289</td>
</tr>
<tr>
<td>distance</td>
<td>5208.05</td>
<td>3</td>
<td>8.7</td>
<td>0.0002</td>
</tr>
<tr>
<td>distance*diet protocol</td>
<td>26848.39</td>
<td>6</td>
<td>22.43</td>
<td>0.0001</td>
</tr>
<tr>
<td>Period</td>
<td>5847.07</td>
<td>6</td>
<td>4.88</td>
<td>0.001</td>
</tr>
<tr>
<td>Error</td>
<td>7181.68</td>
<td>36</td>
<td>1.09</td>
<td>0.3681</td>
</tr>
<tr>
<td><em>S. transitionalis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>diet protocol</td>
<td>223.62</td>
<td>2</td>
<td>0.64</td>
<td>0.5346</td>
</tr>
<tr>
<td>distance</td>
<td>27218.36</td>
<td>3</td>
<td>49.5</td>
<td>0.0001</td>
</tr>
<tr>
<td>distance*diet protocol</td>
<td>16731.36</td>
<td>6</td>
<td>15.21</td>
<td>0.0001</td>
</tr>
<tr>
<td>period</td>
<td>4719.33</td>
<td>6</td>
<td>4.29</td>
<td>0.0026</td>
</tr>
<tr>
<td>error</td>
<td>6598.34</td>
<td>36</td>
<td>1.01</td>
<td>0.4752</td>
</tr>
</tbody>
</table>

*Type III sum of squares for unbalanced designs.*
Fig. 1.1. Give-up-densities of food (+/- 1 standard error) for *S. transitionalis*, and *S. floridanus* at feeders that vary in predation risk (distance to cover), and food quality. Food quality treatments were 40%, 60%, and 100% rabbit chow, and the balance was wood chips.
influenced GUDs at the most distant feeder, which had high quality food (Fig. 1.1). *S. transitionalis* harvested the same amount of food on each diet treatment (Table 1.2, Fig. 1.2), but acquired 45% and 46% more energy on the 100% chow diet than on the 40% or 60% diet protocol ($F = 5.68$, $df = 2$, $P = 0.0072$, Fig. 1.2), respectively.

*S. floridanus.* Food quality, distance between cover and the feeder, and their interaction also affected the GUDs of *S. floridanus* (Table 1.2). GUDs of *S. floridanus* also generally increased with increasing distance from cover, but GUDs at the two furthest feeders from cover were not different from each other ($P > 0.05$). *S. floridanus* GUDs at open feeders decreased with both the 60% and the 40% diets in cover (Fig. 1.1). When poorer quality food was available in cover (40% or 60%), *S. floridanus* also avoided the 70% diet at the next nearest feeding station, and foraged 13 to 16-m from cover. This was the nearest feeder with 100% rabbit chow. Decreasing food quality from 100% rabbit chow to 40% rabbit chow in cover increased *S. floridanus* GUDs in cover 700%. The combination of decreasing food quality in cover to 40% and 70% rabbit chow in the second feeder, increased eastern cottontail GUDs at the second feeder 50%, and decreased GUDs at the intermediate feeder (13 to 16-m from cover) 67% (Fig. 1.1).

Although *S. floridanus* harvested the same volume of food on each diet (F

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
Fig. 1.2. Comparison of mean (+/- 1 standard error) GUDs and metabolizable energy intake by *S. floridanus* and *S. transitionalis* over the duration of the entire titration experiment.
= 3.09, df = 2, P = 0.0576, Fig. 1.2.), they acquired 59% and 14% more energy on the 100% chow diet than on the 60% and 40% diets (F = 9.58, df = 2, P = 0.0005, Fig. 1.2), respectively.

For both species, the global environmental quality (diet quality in all feeders) determined the marginal value of feeders. For example, the energetic gain from feeders was not different for *S. transitionalis* when the poorest quality food was available in cover, and 70% chow available at the near-cover feeder. However, when the medium quality chow (60% chow) was available in cover, energetic gain was not different from the near-cover feeder with 100% chow. Similar patterns existed for *S. floridanus* (Fig. 1.1). These results demonstrate that patch depletion depends not only upon the local food quality (local marginal value), but the food quality available to them in their environment. When high quality food is available in cover, the marginal value there is high and costs are low, but when I decreased the the quality of food in cover, the marginal value at risky feeders increased. However, I could not find titrations for every feeder (i.e., where marginal gains were equal among all feeders).

On the highest quality diet, both species had lower GUDs in or near cover than away from cover, suggesting that the foragers were titrating costs and benefits among food patches. When food quality and quantity is equal
among patches, foraging costs are equal and predation costs increase with distance. However, as food quality in cover declined, GUDs away from cover decreased, and the two species diverged in their allocation of time to feeders. *S. transitionalis* accepted lower quality food in cover (60% rabbit chow) instead of foraging from more distant feeders where food quality was higher (feeder three and four), whereas *S. floridanus* avoided the lower quality diets (40% and 60%) and foraged at feeders where food quality was high (feeder three and four). On the poorest quality diet, the marginal costs of foraging in cover were not different from the costs of foraging near cover for *S. floridanus* or *S. transitionalis*. For *S. floridanus* on the 60% diet, foraging costs in cover were not different from foraging costs near cover, and higher than those at medium distances to cover (13-16-m from cover), whereas for *S. transitionalis*, predation costs at the near, medium and far feeders outweighed the increase in foraging costs in cover.

**Foraging Behavior Described**

Behavioral patterns. Nonlinear regressions estimated breakpoints in the distributions of *S. floridanus* and *S. transitionalis* pauses at 16 seconds (11 to 21 sec., 95% CI), and 32 seconds (27 to 38 sec., 95% CI), respectively (Fig. 1.3). Because the distributions for both species were described by two curves, I suggest that the curves represent two behaviors in foraging (Machlis 1977).
I used direct observations to characterize these two behaviors and found that short pauses between foraging events were used for handling food (chewing) whereas longer pauses included time not handling but in a vigilant posture oriented to scan for predators approaching from the cover or open microhabitat. Therefore, I characterized short pauses (< 16 sec. for S. floridanus and ≤ 32 sec. for S. transitionalis) as handling and pauses longer than these as vigilance.

The breakpoint in the two curves and the slope of the left-most curve of the distributions (handling) was different between species. The slope of the "handling" portion of the distribution was not different from zero (t = 0.4, P > 0.05) for S. floridanus. This suggested that there was an equal probability that an eastern cottontail will return to the feeder to forage when pauses are less than 16 seconds. In S. transitionalis, however, the slope of the "handling" portion of the distribution was different from zero (t = -4.0, P < 0.05), suggesting that there was a declining probability of returning to the feeder with increasing pause time. This downward slope may indicate that handling and vigilance were not mutually exclusive and S. transitionalis alternated between handling and vigilance in pauses less than 32 seconds.

Food Consumption. When all feeders were in the open (a scenario that may occur when all food within cover is depleted or energy gained from food in
Fig. 1.3. Log relative frequency distributions of pauses between foraging events for *S. transitionalis* and *S. floridanus*. Lines fit with non-linear regression.
cover is less than the energy gain/costs associated with food patches away from cover, *S. transitionalis* and *S. floridanus* foraged similarly (Table 1.3, Fig. 1.4). Specifically, mean consumption at feeders in the open was not different at all but the most distant feeder from cover. In contrast to previous experiments, consumption did not decrease with increasing distance from cover, though consumption at the most distant feeder was greater than consumption at other feeders for *S. transitionalis* (Fig. 1.4).

The above results indicate that *S. floridanus* and *S. transitionalis* behaved differently when there was no food in cover than in the titration experiment, where there was food in cover (Fig. 1.1 & 1.4). However, I suspected that their behaviors in harvesting food might be influenced by the risk of predation. Therefore, I measured several components of foraging, specifically, search time, handling time, vigilance time, and total time at risk.

**Foraging events and search time.** The number of feeding events per night of foraging, as well as the time searching within a feeder were not different for *S. transitionalis* and *S. floridanus* (Table 1.3). Nor was there a difference between species in the amount of food consumed per event or time searching (Table 1.3, Fig. 1.5). There also were no differences in the mean number of events or time searching for *S. floridanus* or *S. transitionalis* at any feeder.
Fig. 1.4. Mean food consumption (+/- 1 standard error) by *S. floridanus* and *S. transitionalis* from feeders that vary in predation risk.
Table 1.3. Model variables used to describe the variation in food consumption, number of foraging events per night of foraging, time searching, food consumed per foraging event, food consumed per time searching, time handling, food consumed per time handling, vigilance, food consumed per time vigilant, total time at risk, and the food consumed per total time at risk, for *S. transitionalis* and *S. floridanus*.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS*</th>
<th>F*</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Consumption</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>124.58</td>
<td>1.37</td>
<td>0.2553</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>918.96</td>
<td>1.73</td>
<td>0.191</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>388.38</td>
<td>0.73</td>
<td>0.544</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>3709.4</td>
<td>2.05</td>
<td>0.005</td>
</tr>
<tr>
<td><strong>Events</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>64.72</td>
<td>0.10</td>
<td>0.7564</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>3078.68</td>
<td>1.57</td>
<td>0.2272</td>
</tr>
<tr>
<td>Species*feeder</td>
<td>3</td>
<td>1838.38</td>
<td>0.94</td>
<td>0.4412</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>13759.55</td>
<td>2.50</td>
<td>0.000</td>
</tr>
<tr>
<td><strong>Search time</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>39.20</td>
<td>0.01</td>
<td>0.9359</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>37436.3</td>
<td>2.11</td>
<td>0.1295</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>3278.84</td>
<td>0.18</td>
<td>0.9056</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>124229.8</td>
<td>3.69</td>
<td>0.000</td>
</tr>
<tr>
<td>Source</td>
<td>df</td>
<td>SS*</td>
<td>F*</td>
<td>P</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>----</td>
<td>------</td>
<td>-----</td>
<td>------</td>
</tr>
<tr>
<td><strong>mls consumed/foraging</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>event</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>0.37</td>
<td>3.41</td>
<td>0.079</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>0.27</td>
<td>0.82</td>
<td>0.4986</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>0.88</td>
<td>2.69</td>
<td>0.072</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>2.287</td>
<td>0.86</td>
<td>0.6445</td>
</tr>
<tr>
<td><strong>mls consumed/time</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>searching</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>0.88</td>
<td>1.99</td>
<td>0.1727</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>1.58</td>
<td>1.2</td>
<td>0.3353</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>1.05</td>
<td>0.79</td>
<td>0.5128</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>9.26</td>
<td>2.04</td>
<td>0.006</td>
</tr>
<tr>
<td><strong>Handling time</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>428637.87</td>
<td>7.52</td>
<td>0.0122</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>228101.29</td>
<td>1.33</td>
<td>0.2903</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>311055.12</td>
<td>1.82</td>
<td>0.1747</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>1197519.14</td>
<td>2.95</td>
<td>0</td>
</tr>
<tr>
<td><strong>mls consumed/handling</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>time¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>9.35</td>
<td>8.54</td>
<td>0.008</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>0.9</td>
<td>0.27</td>
<td>0.8436</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>5.06</td>
<td>1.54</td>
<td>0.233</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>22.99</td>
<td>2.5</td>
<td>0</td>
</tr>
<tr>
<td><strong>Vigilance time¹</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>1</td>
<td>0.78</td>
<td>0.57</td>
<td>0.4576</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>9.93</td>
<td>2.44</td>
<td>0.0932</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>1.13</td>
<td>0.28</td>
<td>0.8413</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>28.55</td>
<td>1.41</td>
<td>0.1181</td>
</tr>
</tbody>
</table>

### mls consumed/time

#### vigilant

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>1</td>
<td>1.32</td>
<td>0.04</td>
<td>0.8368</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>46.07</td>
<td>0.51</td>
<td>0.6823</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>53.32</td>
<td>0.59</td>
<td>0.631</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>637.16</td>
<td>2.89</td>
<td>0</td>
</tr>
</tbody>
</table>

### Total time at risk

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>1</td>
<td>1836763.06</td>
<td>2.59</td>
<td>0.1223</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>264982.99</td>
<td>2.74</td>
<td>0.0692</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>895216.08</td>
<td>0.92</td>
<td>0.4462</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>6778498.77</td>
<td>3.28</td>
<td>0</td>
</tr>
</tbody>
</table>

### mls consumed/total time at risk

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>1</td>
<td>4.79</td>
<td>3.88</td>
<td>0.0621</td>
</tr>
<tr>
<td>Feeder</td>
<td>3</td>
<td>1.56</td>
<td>0.42</td>
<td>0.7387</td>
</tr>
<tr>
<td>Species*Feeder</td>
<td>3</td>
<td>5.32</td>
<td>1.44</td>
<td>0.2603</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>25.9</td>
<td>2.88</td>
<td>0</td>
</tr>
</tbody>
</table>

*Type III sum of squares for unbalanced designs.

\( ^a \) F obtained from mean square (main effect)/error(split plot).

\(^1\) Log transformed.
Fig. 1.5. Food consumed per time searching, and per event (+/- 1 SE) by *S. transitionalis* and *S. floridanus*. Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
Handling. *S. transitionalis* spent more than twice as much time handling food per night of foraging as *S. floridanus* (Table 1.3). They also spent more time handling food at all but the most distant feeder, suggesting that *S. transitionalis* do not alter their handling efficiency until they are more than 15-m from cover. *S. floridanus* consumed 85% more food per unit of handling time than *S. transitionalis*. Food consumed per handling time differed between species at the three meter and 15-m feeders, and was marginally different (*P* =0.0537) at the 22-m feeder. Although handling is probably the least risky portion of feeding, and cottontails can simultaneously handle food and scan for predators, handling does add to their total time at risk. However, *S. transitionalis* may spend more time handling than *S. floridanus* because handling and vigilance are not discrete behaviors, whereas for *S. floridanus* handling and vigilance seem to be discrete (Fig. 1.3).

Vigilance. Vigilance time did not differ between species (Table 1.3). There also were no differences in the harvest rates per vigilance time between species (Table 1.3), nor between species at any feeder.

Total Time at Risk. To examine the total costs each species incurs at feeders in the open, I summed search, handling, and time vigilant per feeder into a new variable, total time. *S. transitionalis* spent 3 minutes or 42% more time at risk than *S. floridanus*, although this was not statistically
different (Table 1.3). Food consumption per time at risk also did not statistically differ ($P = 0.0621$) between species, although *S. floridanus* consumed 55% more food per time at risk than *S. transitionalis*, and consumed more food per time at risk at the 3-m and 15-m feeder than *S. transitionalis* (Fig. 1.6).

**Survival and Weight Change.** Eighteen *S. transitionalis* and ten *S. floridanus* were killed by owls (*Strix varia, and Bubo virginianus*) during experiment two and other (Chapter II, unpubl. data) experiments. I used data from previous experiments that had an experimental protocol where food was available in cover, to compare to experiment two where no food was available in cover. When there was food in cover (Chapter II), *S. transitionalis* and *S. floridanus* had similar survivorship functions ($\text{Log rank} = 0.15$, $df = 1$, $P = 0.6952$, Fig. 1.7). However, when food in cover was depleted (this experiment) and only food in the open was available, survival differed ($\text{Log rank} = 8.72$, $df = 1$, $P = 0.0031$, Fig. 1.7). Censored animals were those that lived through the experiment and were removed from the enclosure when the experiment ended.

Individuals of both species that were killed by predators lost more weight ($x = -10\%$) than those that lived ($x = +0.1\%$) ($t = -4.28$, $df = 46.9$, $P = 0.0001$). *S. transitionalis* lost more weight than *S. floridanus* ($t = 4.9283$, $df = 47$, $P <$
Fig. 1.6. Food consumed per total time at risk (+/- 1 SE) by *S. transitionalis* and *S. floridanus* from feeders that vary in predation risk.
Fig. 1.7. Survivorship functions of *S. transitionalis* and *S. floridanus* when food is available in cover, and when it has been depleted. Individuals labeled as censored were those that lived through an entire experiment and were removed at its conclusion.
0.0001). Among those animals that died, the percentage of weight that *S. transitionalis* and *S. floridanus* lost was not different (t = 14.0, df = 14, p = 0.2006, Fig. 1.8). However, of the animals that lived through an experiment, weight change of the two species differed (t = 4.2010, df = 31, p = 0.0002, Fig. 1.8), where *S. transitionalis* lost weight and *S. floridanus* gained weight.

**Discussion**

Foraging behavior in cottontail rabbits was responsive to both predation risk and resource quality. My titration experiment illustrated this well. However, when I investigated the individual behaviors employed by foragers, microhabitat seemed to have less of an effect. What is most clear from these experiments is than *S. transitionalis* perceived higher costs than *S. floridanus* when foraging in the open, and thus accepted lower-quality food in cover than *S. floridanus*. Since this strategy constrained their ability to remain on a positive energy budget, they lost weight and became more at risk to predation. Thus, predation risk played an important role in the habitat use of these two sympatric lagomorphs.

GUDs reflected food quality and predation risk at feeders. Differences in GUDs between feeders, when feeders were of equal quality reflected foraging costs due to predation risk from owls. My experiment-wise titration (sensu Kotler and Blaustein 1995) altered the food quality at feeders in or adjacent
Fig. 1.8. Weight change of *S. floridanus* and *S. transitionalis* that lived and died in experiments.
to cover (0 and 2-m from cover) and those near cover (5 and 10-m from cover) until GUDs in cover were higher than those in the open feeders. Resource quality in and adjacent to cover affected GUDs at all but the most distant feeder.

This titration experiment addresses two questions about habitat use. The microhabitat treatments illustrated that perceived predation costs increase with distance from cover, (e.g., GUDs of both species increased with increasing distance from cover). Diet treatments demonstrated that when food quality declines in cover, cottontails quit these patches sooner, and forage where food quality is greater, trading off predation risk for food quality. \textit{S. transitionalis} traded off high foraging costs for higher predation costs when food quality declined by 60%, whereas \textit{S. floridanus} traded off high foraging costs when food quality declined by 40%. \textit{S. transitionalis} lost weight as a result of foraging on lower quality food in cover, and \textit{S. floridanus} maintained or gained weight as a result of avoiding the low quality food in cover. Perhaps, weight loss by \textit{S. transitionalis} during experiments made them more at risk of predation than \textit{S. floridanus} (Lima and Dill 1990).

In the second experiment, \textit{S. transitionalis} GUDs did not differ from \textit{S. floridanus} at any but the most risky feeder, nor did their behaviors with the exception of handling. \textit{S. transitionalis} spent twice as much time handling
food in the open as *S. floridanus*, but my measure of handling for *S. transitionalis* may have included vigilance time. The slope of the handling portion of the distribution of pauses between foraging events suggests that vigilance and handling are not discrete behaviors in *S. transitionalis*. Therefore, the overall time at risk may be the best measure for comparison of the two species at feeders that vary with predation risk. *S. transitionalis* and spent more overall time at risk, though only marginally significant. This marginal difference in time at risk however, may help explain the difference in survival rates of the two species.

**Weight Change and Survival**

Two scenarios may explain the pattern of weight loss in those that lived and those that died. Either predators select the animals in poorer physical condition (Errington 1946, Slobodkin 1968, Curio 1976, Morse 1980, Temple 1987) or animals in poor physical condition are forced to take greater risks to prevent starvation (Lima and Dill 1990, Sinclair and Arcese 1995, Villafuerte et al. 1997). Villafuerte et al. (1997) demonstrated that *S. transitionalis* on resource-limited patches decline in body condition faster and to a lower point than *S. transitionalis* on large, resource rich patches. Cottontails on small patches also had lower survival rates than those on large patches (Villafuerte et al. 1997). In my study, there was no difference in the weight change of *S.*
transitionalis that lived and died, suggesting that predators were not selecting the animals in poorer physical condition. However, *S. floridanus* that lived through experiments gained, or maintained weight whereas those that were killed lost about 8% of their body mass. Because most of the predation was done by barred owls (*Strix varia*, pers. observation of evidence at kill sites) and their body mass is about ½ that of cottontails (Craighead and Craighead 1969), I suggest that barred owls may select individuals in poorer physical condition, but these individuals also may be foraging at times when predation risk is highest. I attempted to determine whether individuals that were killed by predators behaved differently than individuals that lived, but the sample size was inadequate and variance in daily use of feeders too great to quantify a difference.

*S. transitionalis* had lower survivorship than *S. floridanus* when food in cover was depleted, which could be explained by their poor physical condition. *S. transitionalis* lost approximately 10% of their body mass, whereas *S. floridanus* maintained their weight. Lima and Dill (1990), Brown (1988), and Kotler (1997) suggested that foragers in poorer physical condition should accept higher risks of predation. I suggest that *S. transitionalis* was slow to accept the predation risk in the open arena or weighted it too heavily, thereby actually increasing risk when they did accept it. For example,
weighting the risk of predation too high may have forced the animals to remain in cover and consume poor quality food, causing them to lose weight. After losing weight, they had to forage in the open to avoid starvation, thereby increasing their risk of predation. An alternative strategy utilized by S. floridanus was to forage from feeders that would maintain small variance around their physical condition, and would allow them to chose when to forage at risk. S. floridanus maintained weight throughout experiments, had GUDs that did not differ among risky feeders, and had higher survivorship than S. transitionalis. In terms of fitness (physical condition and survival), the strategy used by S. transitionalis proved too costly. S. floridanus avoided the costs of predation, harvested more food than S. transitionalis from feeders in the open, and maintained their physical condition.

**Conclusion**

*S. transitionalis* apparently evolved in landscapes that were primarily forested, and inhabited early successional patches and disturbed sites within this homogeneous landscape (Litvaitis 1993). Predators occupying such landscapes were likely less diverse and more specialized on particular prey than in fragmented landscapes. For instance, *S. transitionalis* were a major prey item of bobcats (*Felis rufus*) in the 1950s but their importance as predators of *S. transitionalis* declined in the 1960s (Litvaitis et al. 1984).
Currently, coyotes and foxes (Vulpes) are important predators of S. transitionalis (Barbour and Litvaitis 1993, Brown and Litvaitis 1995), and their abundance has been shown to increase with increasing landscape fragmentation (Oehler and Litvaitis 1995). Raptors have not been important predators of S. transitionalis (Litvaitis, Barbour, and Brown, unpublished data) but are important predators of S. floridanus (Trippensee 1948, Korschgen and Stuart 1972, Petersen 1979). S. floridanus are the most wide-ranging member of their genus, and are presumably adapted to many habitat types and the predators there, whereas S. transitionalis have a small geographic range, and occupy a narrow range of habitats. Because S. transitionalis evolved in landscapes where predation risk was presumably lower than in fragmented landscapes, they may not have anti-predator behaviors to use risky patches without incurring significant predation costs. This was evident in these experiments. S. transitionalis avoided risky patches when food quality was the same among feeders, and when food in cover was removed, S. transitionalis suffered significant predation costs. S. floridanus, on the other hand, evolved in more open landscapes where predation from a more diverse predator guild likely existed. This species shows an adaptation to more risky habitat, where it minimizes its predation costs by minimizing its time at risk. In this study, this strategy conferred
higher fitness (physical condition and survival); *S. floridanus* maintained weight by foraging from higher quality food, and paid lower predation costs.

In a separate experiment (Chapter III), I found that *S. floridanus* had larger eyes, and could detect an approaching predator sooner than *S. transitionalis*. This result, along with the behavioral adaptations described above, may suggest that *S. floridanus* is better adapted to foraging in risky habitats.

The coexistence of *S. floridanus* and *S. transitionalis* is a recent phenomenon, and patterns in distributions of the two species suggests that *S. floridanus* are replacing *S. transitionalis* in landscapes that *S. transitionalis* once dominated. Although Litvaitis (1993) suggested that *S. transitionalis* may have a declined as a result of loss of early successional habitat in New England, this would not explain the population expansion in *S. floridanus*. I suggest that landscape changes (i.e., increases in fragmentation, human-altered cover types, and generalist predators) have favored populations of *S. floridanus* because of their behavioral and morphological adaptations to foraging in risky habitat. *S. floridanus* are well-adapted to the increased vulnerability to predation in fragmented landscapes whereas *S. transitionalis* are not. Therefore, predation may act to mediate competition between cottontails in these altered landscapes. In these experiments I demonstrated
that *S. floridanus* evaluate their foraging options based more on resource quality, whereas *S. transitionalis* based their foraging decisions on predation costs. This difference in foraging strategies may partition the resources of these two sympatric lagomorphs, but recent population trends in both species, and our survival data suggest that *S. transitionalis* have lower fitness associated with this strategy, and *S. floridanus* may be out competing them in human-altered landscapes.
LITERATURE CITED


CHAPTER II

FORAGING IN FRAGMENTED LANDSCAPES: INDIVIDUAL BEHAVIORS AND POPULATION CONSEQUENCES

Introduction

Although much is known about how populations respond to habitat fragmentation, relatively little is known about how individuals might respond (Lima and Zollner 1996, Yahner and Mahan 1997). Behavioral ecologists have studied habitat selection of animals, patch and prey choice, and movement rules, but have done so at limited spatial scales (Lima and Zollner 1996). A union of these two disciplines is needed to understand the mechanisms that cause the patterns exhibited by animals in fragmented landscapes.

As landscapes become fragmented by human land uses, several results of fragmentation contribute to a decline in biological diversity, including: loss of original habitat, reduction in patch size, isolation of remnant patches, and introduction of new cover types (Wilcox 1980). In these landscapes predation may be a dominant process controlling populations on fragmented habitat patches (Wilcove 1985, Soulé et al. 1988, Barbour and Litvaitis 1993, Brown and Litvaitis 1995, Oehler and Litvaitis 1996). Generalist predators
increase in fragmented landscapes (Andrén 1992, Oehler and Litvaitis 1996), and there also may be a functional response of predators at edges, or on small patches of habitat, where prey concentration is high enough to increase predator efficiency.

In an effort to understand predator-prey interactions, prey were typically modeled with little or no variation in response to the numeric or functional responses of predators (e.g., Lotka 1922, Volterra 1926, Holling 1965). However, recent studies have investigated how predators cause adaptive shifts in prey behavior, known as "risk effects" (Schmitz et al. 1997). Several authors have suggested that risk effects of predators may be as important as lethal direct effects to trophic interactions (Kotler and Holt 1989, Lima and Dill 1990, Schmitz et al. 1997). For example, a predation event only impacts an individual prey animal per unit time, whereas the risk introduced by the presence of a predator may affect the activity of many prey animals in the same period of time (Schmitz et al. 1997). Schmitz (1997) found that direct predation effects were only compensatory to risk effects.

Recent models of foraging with predation risk have suggested that animals balance the costs of predation with the gains from foraging and choose the option with the lowest risk-to-reward ratio (Gilliam and Frasier 1989, Brown 1991), or balance predation, foraging, and missed-opportunity costs with energy gains (Kotler 1997). In fragmented landscapes, animals
likely experience greater variance in predation risk associated with food patches than in unfragmented landscapes. In addition, foragers may not be adapted to increased predation risks, or risks from predators not associated with contiguous habitat in which they evolved. Also, the adaptive behaviors used to avoid one predator may put them at risk of another predator (Kotler et al. 1992).

The New England cottontail (*Silvilagus transitionalis*) is endemic to the northeastern United States, and populations have declined substantially throughout its range during the past four decades (Chapman and Stauffer 1981). Previous research suggested that the decline was in response to loss of habitat (Litvaitis 1993) and expanding populations of eastern cottontails (*Linkkila 1971, Chapman and Morgan 1973*). Eastern cottontails (*S. floridanus*) extended their range into much of New England, facilitated by intentional introductions to increase game populations (Johnston 1972, Chapman and Morgan 1973). At the same time, early successional habitats were advancing into more mature forest stands (Litvaitis 1993). Therefore, either competition or the combined effects of competition and loss of suitable habitat may have caused the decline. Probert and Litvaitis (1995) examined the hypothesis that interference competition may have caused the decline of New England cottontails, but found that neither species was able to exclude the other from either food resources or protective cover. They suggested that
interference competition by eastern cottontails may limit populations of New England cottontails if easterns are able to colonize ephemeral patches sooner than New England cottontails.

Barbour and Litvaitis (1993) demonstrated that New England cottontails sequestered to small patches of habitat were in poorer physical condition, foraged at sites further from cover, with greater predation risk, and foraged on poorer quality food than those on larger patches. In addition, these individuals experienced predation rates twice the rate of individuals on larger patches. These data suggest that New England cottontails trade-off predation risk for energetic gains, and that the value of energy gain for residents of small patches is greater than for individuals on large patches (e.g., they take greater risks).

Gilliam and Frasier (1987) modeled a similar phenomenon with juvenile creek chubs (*Semotilus atromaculatus*). Their model predicted that 1.) foragers would choose foraging sites that minimized the risk of predation:reward ratio, subject to an energetic constraint that described the foragers' minimal overall harvest rate, 2.) when the value of energy was high, animals would accept greater risks to obtain food, and 3.) when there was a refuge from predators, foragers would balance the risks of predation (in a particular food patch) plus the missed opportunity costs of remaining in the refuge, with the energetic gain from foraging. The results of Barbour and
Litvaitis (1993) qualitatively agree with the predictions of Gilliam and Frasier (1987). The patterns of foraging reported by Barbour and Litvaitis (1993) suggested that New England cottontails minimize the risk-to-reward ratio. For example, cottontails accepted greater risks when the value of food was high (e.g. residents of small-patches in poor condition foraged further from cover than large-patch residents in better condition). Despite their balancing of risks and rewards, New England cottontails on smaller patches suffered nearly twice the predation rate of individuals on larger patches. This suggests that New England cottontails on small patches might forage in safe patches subject to some threshold of physical condition (Villafuerte et al. 1997), and below this threshold, they forage on higher quality food where they are more vulnerable to predation.

To investigate the processes that might explain the New England cottontail decline and eastern cottontail population expansion, I conducted experiments on the foraging strategies of New England and eastern cottontails in winter. The objectives of this study were to: i) investigate how New England and eastern cottontails trade-off food quality for predation risk in a two-patch system and to compare the survival rates of New England and eastern cottontails, and ii) apply the spatial distribution of foraging from these experiments to real patches to determine what proportion of patches can be exploited by New England and eastern cottontails and maintain
similar survival rates.

Methods

Study animals

New England and eastern cottontails were captured in Rockingham and Strafford Counties, New Hampshire, during October 1993 to March 1994. Specific identity was based on pelage and morphological characteristics (Litvaitis et al. 1991). All captured animals were marked with numbered ear tags. Mass and sex were determined prior to placing rabbits in individual cages (0.9 x 0.8 x 0.6 m) within a covered outdoor enclosure. Animals were in captivity from five to 22 days prior to use in experiments, provided water ad libitum and fed commercial rabbit chow (16% protein) from feeders identical to those used in experiments.

Trade-Off of Food Quality and Predation Risk

Experimental Design

All experiments were conducted in enclosures (5.7 x 45.7 m) consisting of two microhabitats. Approximately 40% of each enclosure was dense shrub cover, and the remaining 60% was mowed grass. The vegetation in the two microhabitats was representative of the species and structure of early successional habitats in the region. A 1.8-m fence surrounded the enclosure to limit, but not prevent predators access to the pens, and a 1.2-m fence kept rabbits separated into 8 enclosures. Monofilament line with one meter
Spacing covered the top of the enclosure, in an effort to minimize, but not eliminate predation by raptors.

Before initiating experiments, one cottontail was placed in each enclosure for four weeks to remove ambient browse in enclosures. Following this period, eight, newly captured cottontails were placed in individual enclosures for five, one-week periods. Each treatment combination lasted for one week following an initial week of acclimatization (week 1). Fixed treatment levels were randomly applied to rabbit enclosures (x 8 replicates). Two diet and four distance treatments were used. Low-quality food consisted of commercial rabbit chow diluted with 30% wood chips and high-quality food was diluted with 10% wood chips. Wood chips and rabbit chow were milled and homogenized, then reprocessed into pellets. This technique prevented rabbits from selectively foraging on the components of the chow. Distance between the feeder (food patch) and cover also varied weekly as an index of predation risk. Four distances (3, 8, 11, and 18-m) were considered real distances that a cottontail would forage from cover, and represented increasing risk of predation with increasing distance from cover (Barbour and Litvaitis 1993). Two food patches (feeders) were available for each treatment week, one in cover and another at one of the above described distance treatments. Two, 2 x 4 randomized blocks were used to apply treatments to experimental units (rabbits). Feeders were filled at approximately the same
time each day with 210 mL of rabbit chow, and their contents measured the following day. Volumetric measurement of food was used instead of weight, because volume was relatively invariant whereas weight varied with humidity (pers. observation). At the end of each treatment week, rabbits were captured, weighed and treatments were changed according to randomized blocks.

I used the give-up density of food (GUD, sensu Brown 1988) as a measure of the predation costs and energetic gains from foraging, because GUDs are directly related to the harvest rate of the forager when it quits a patch (Brown 1988, Kotler and Brown 1990, Kotler and Blaustein 1995). Therefore, GUDs should equal the sum of energetic, predation, and missed opportunity costs of foraging (Brown 1988). Low GUDs (greater patch depletion) should indicate low foraging costs, meaning the forager perceives low predation, energetic costs of foraging, and missed opportunity costs. Large differences in GUDs among feeders indicate differences in these costs. In this paper, I assumed all costs to be from predation and missed opportunities at other feeders and time in refuge (cover). I also assumed that foraging costs among feeders of similar food quality are equal.

I repeated this experiment three times. The first of the series was conducted with New England cottontails in January 1994, the second trial was run with eastern cottontails in February 1994, and the third trial was
run with new individuals of both species (n = 4 each) in March 1994.

Animals were weighed before the week of acclimation in the enclosure and at the end of each treatment week. I used the weight change during the treatment week, and the weekly mean GUD of food as dependent variables in the analyses. A split-plot general linear model (GLM, SAS Inst. 1986), with time as the split plot, was used to examine how distance to cover and food quality affect GUDs and weight change of cottontails.

**Patch Use in Southern New Hampshire**

Based on the results of this study and personal observations, I wanted to investigate the implications of the foraging behaviors of both species. Specifically, I was interested in the availability of suitable habitat to both species, and temporal changes in availability due to snow cover. Early successional habitat patches are easily delineated from surrounding habitat but have a high degree of heterogeneity within the patch (Barbour and Litvaitis 1993). For instance, dense brush is patchily distributed within the habitat and separated by open field with sparsely distributed trees and shrubs. There is also variation in the frequency and density of brush within the habitat patch (Barbour 1993).

Brown and Litvaitis (1995) suggested that New England cottontail mortality increases with the number of days snow covers the ground. Snow accumulation prevents cottontails from remaining cryptic, and may also
hinder their escape. If they use sites far from cover, they suffer higher predation rates than if they remain near cover (Barbour and Litvaitis 1993, Chapter I). However an alternative strategy to using sites away from cover is to use sites near cover and avoid sites in the open. To evaluate the difference in area available to New England and eastern cottontails given this strategy, I randomly selected four early successional habitat patches (> 2.5-ha), exclusively occupied by New England cottontails in Strafford County, New Hampshire. These habitat patches were used in previous studies (Barbour and Litvaitis 1993, and Brown and Litvaitis 1995) and are described in Barbour (1993) and Brown (1995). To determine how snow accumulation changes the availability of food and cover, I sampled patches in the beginning of winter (December 1993-January 1994), and at the end of winter (March 1994) following the methods of Barbour and Litvaitis (1993). I randomly sampled understory stem density (< 7-cm dbh), availability of stems and stems browsed (<0.5-m from ground or snow surface, < 10-mm diam.) within a 2 x 5-m plot, pellets and tracks in a 1-m radius plot nested within the understory density plot, and distance from plot center to nearest cover (1.0-m² patch of vegetation that would obscure > 50% of a foliage density board at a height of 0.5-m).

**Simulation of Foraging Strategies on Real Habitat Patches**

To simulate the consequences of the foraging strategies of these two
species in temporally and spatially heterogeneous habitat, I imposed a habitat-selection rule on habitat data collected in this study and from Barbour (1993). Barbour (1993) measured the use, availability, and distance from cover of a random sample of locations (sample plots) on 20 patches of early successional habitat in Strafford County, NH that ranged 0.5 - 30 ha in size, and totaled 104 ha. I used Barbour's (1993) data to examine the number of sites (plot samples) eastern and New England cottontails could occupy and maintain similar survival. I selected all sites within 3-m from cover from all 20 habitat patches for New England cottontails and all sites within 22-m from cover for eastern cottontails (see results). At these distances, the survivorship functions of the two species were not different (Chapter I), suggesting that eastern and New England cottontails could use these sites and maintain similar survival. I then tested whether the number of suitable sites (sample plots that met the habitat selection rule for both species) available to New England cottontails differed from the number available to eastern cottontails with t-tests. To examine changes in habitat suitability throughout winter, I measured the number of suitable sites for New England cottontails and eastern cottontails at the beginning and end of winter. I tested for differences in these proportions with t-test as well.
Chapter II, Page 59

Results

New England cottontails

Neither treatment, distance, or diet, accounted for significant variation in weight loss of cottontails (Table 2.1). However, distance accounted for 38% of the variation in GUDs (Table 2.1). New England cottontails avoided the open (risky) feeders and foraged in cover at the expense of food quality (Fig. 2.1); there was no difference in GUDs of the low or high quality food. This suggested that New England cottontails were willing to sacrifice food quality for safety. In this experiment, four (50%) New England cottontails were killed by raptors and canids. The behaviors those that lived vs those that died differed in the amount of food they consumed. Those that lived through the experiment consumed almost three times more food per day than those that were killed by predators (lived $X = 146$ mls vs died $X = 50.5$, df = 4, $t = 3.149$, $P = 0.017$), suggesting that either predators selected rabbits that were in poorer condition, or rabbits in poor physical condition took greater risks than rabbits in good condition. Tracks left in the snow by predators, indicated that predation events occurred in the open.

Eastern cottontails

Again, treatment effects did not account for variation in weight change of eastern cottontails over the four week experiment (Table 2.2). However, in contrast to New England cottontails, eastern cottontail GUDs were affected
Table 2.1. Experiment 1: Variables that explain the variation in weight loss and give-up-densities (GUDs) among New England cottontails.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Relative weight change</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>diet</td>
<td>0.007</td>
<td>1</td>
<td>3.96</td>
<td>0.0612</td>
</tr>
<tr>
<td>distance</td>
<td>0.006</td>
<td>4</td>
<td>0.90</td>
<td>0.4843</td>
</tr>
<tr>
<td>diet*distance</td>
<td>0.004</td>
<td>4</td>
<td>0.50</td>
<td>0.7393</td>
</tr>
<tr>
<td>period</td>
<td>0.0002</td>
<td>2</td>
<td>0.05</td>
<td>0.9483</td>
</tr>
<tr>
<td>error</td>
<td>0.0357</td>
<td>19</td>
<td>1.82</td>
<td>0.2364</td>
</tr>
<tr>
<td><strong>GUD</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>diet</td>
<td>680.483</td>
<td>1</td>
<td>0.28</td>
<td>0.6021</td>
</tr>
<tr>
<td>distance</td>
<td>62741.800</td>
<td>4</td>
<td>6.42</td>
<td>0.0009</td>
</tr>
<tr>
<td>diet*distance</td>
<td>1571.993</td>
<td>4</td>
<td>0.16</td>
<td>0.9563</td>
</tr>
<tr>
<td>period</td>
<td>5855.663</td>
<td>3</td>
<td>0.80</td>
<td>&gt;0.500</td>
</tr>
<tr>
<td>error</td>
<td>66006.071</td>
<td>27</td>
<td>6.48</td>
<td>0.0155</td>
</tr>
</tbody>
</table>

*aType III SS for unbalanced designs.
Fig. 2.1. Mean give-up-densities (+/- 1 standard error) for New England and eastern cottontails, and both species simultaneously.
Table 2.2. Experiment 2: Variables that explain the variation in give-up densities (GUDs) and weight change among eastern cottontails.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GUD</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>diet</td>
<td>1</td>
<td>10174.42</td>
<td>10.73</td>
<td>0.0024</td>
</tr>
<tr>
<td>distance</td>
<td>4</td>
<td>3270.984</td>
<td>0.86</td>
<td>0.4961</td>
</tr>
<tr>
<td>distance*diet&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Error</td>
<td>34</td>
<td>32225.341</td>
<td>3.62</td>
<td>0.0014</td>
</tr>
<tr>
<td><strong>Relative weight change</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>diet</td>
<td>1</td>
<td>0.001</td>
<td>0.59</td>
<td>0.4489</td>
</tr>
<tr>
<td>distance</td>
<td>4</td>
<td>0.009</td>
<td>1.21</td>
<td>0.3237</td>
</tr>
<tr>
<td>distance*diet&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>period</td>
<td>3</td>
<td>0.07</td>
<td>12.47</td>
<td>0.0001</td>
</tr>
<tr>
<td>error</td>
<td>34</td>
<td>0.064</td>
<td>0.2</td>
<td>1.000</td>
</tr>
</tbody>
</table>

<sup>a</sup>Type III sum of squares for unbalanced designs.

<sup>b</sup>Not enough observations to test for differences.
more by diet than by distance. Diet explained 16% of the variation in GUDs. Eastern cottontails ate 25% more of the high quality diet than the low quality diet when it was available in cover. In addition, there were no differences in GUDs among the feeders in the open (Fig. 2.1), suggesting that predation risk does not increase with distance from cover. In this experiment, no animals were killed by predators.

**Both species simultaneously**

Again, as in the previous two trials, relative weight change by New England and eastern cottontails was not influenced by distance between food patch and cover, or diet. However, the pattern of weight change was common among this, and the previous two series. Animals lost weight in the first and third periods and gained weight in the second and final period. In this experiment, period was the only variable that explained a significant portion of the variation in weight change (Table 2.3).

There was no difference in the mean consumption of food by eastern or New England cottontails (Table 2.3). However, GUDs among feeders did differ between the species (Fig. 2.1), because 74% of New England cottontail intake was from the feeder within cover. GUDs of eastern cottontails, on the other hand, did not differ among feeders (Fig. 2.1). There was a significant species by distance interaction (Table 2.3) because New England cottontails foraged more than three times more than eastern cottontails at the cover
Table 2.3. Experiment 3: Variables that explain variation in give-up-densities (GUDs), and weight change, among New England and eastern cottontails simultaneously.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GUD</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>species</td>
<td>1</td>
<td>176.334</td>
<td>0.16</td>
<td>0.6914</td>
</tr>
<tr>
<td>species*diet</td>
<td>2</td>
<td>15470.857</td>
<td>6.98</td>
<td>0.0019</td>
</tr>
<tr>
<td>species*distance</td>
<td>8</td>
<td>86772.971</td>
<td>9.79</td>
<td>0.0001</td>
</tr>
<tr>
<td>period^c</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>error</td>
<td>57</td>
<td>63128</td>
<td>1.29</td>
<td>0.2188</td>
</tr>
<tr>
<td><strong>Relative Weight change</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>species</td>
<td>1</td>
<td>0.005</td>
<td>1.47</td>
<td>0.2957</td>
</tr>
<tr>
<td>species*diet</td>
<td>2</td>
<td>0.004</td>
<td>0.66</td>
<td>0.5188</td>
</tr>
<tr>
<td>species*distance</td>
<td>2</td>
<td>0.014</td>
<td>0.54</td>
<td>0.8239</td>
</tr>
<tr>
<td>period^c</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>error</td>
<td>57</td>
<td>0.189</td>
<td>0.39</td>
<td>0.9992</td>
</tr>
</tbody>
</table>

^a Type III sum of squares for unbalanced designs.

^b F obtained from mean square (main effect)/individual(main effects)

^c Not enough observations to test for contribution to model.
feeder but had higher GUDs at all other feeders. Although there was no statistical difference in the amount of food eaten by either species, New England cottontails ate 12% more food than easterns, and the biggest difference was in their consumption of poor quality food ($t = -4.66$, $df = 11.1$, $P = 0.0007$ for unequal variance).

**Survivorship**

For the duration of these three experiments, a total of eight New England and five eastern cottontails were killed by predators. Survivorship curves for New England and eastern cottontails did not differ ($\text{Log rank} = 0.15$, $df = 1$, $P = 0.6952$). However, in other experiments, where I removed food from cover and placed food patches 3 to 22-m from cover, New England cottontails had lower survivorship functions than eastern cottontails (Chapter I).

**Implications to Habitat Use**

To maintain similar mortality rates in heterogeneous patches, New England cottontails would be limited to an average of 32% of the patches, whereas eastern cottontails could utilize 99% of the patches ($t = -19.665$, $df = 19$, $P < 0.0001$). As snow accumulated on the ground in winter, the availability of both food and cover changed. New England cottontails had less habitat available than eastern cottontails at the beginning ($X = 34\%$ vs $X = 100\%$ of the patches, $t = 10.949$, $df = 2$, $P = 0.0041$) and end ($X = 17\%$ vs $X = 96\%$ of the patches, $t = 9.165$, $df = 2$, $P = 0.0058$) of winter, respectively.
England cottontails also lost more suitable habitat than easterns between the beginning and end of winter. Eastern cottontails lost < 4% ($t = 1.808, df = 2, P = 0.1061$) of suitable habitat with snow accumulation, whereas New England cottontails lost 50% ($t = 2.982, df = 2, P = 0.0482$). The conclusion by Barbour and Litvaitis (1993) that large patches of habitat contain proportionately more suitable habitat for cottontails is confirmed by this investigation ($t = -3.580, df = 7, P = 0.00449$). New England cottontails could occupy 76% more sites on large than on small patches of habitat. Although the loss of suitable habitat during winters with substantial snow accumulation will occur similarly among patches, large patches will have more suitable sites than small patches.

New England cottontails could utilize 34 ha and eastern cottontails could utilize 103.5 ha of the 104.4 ha area sampled in Barbour and Litvaitis (1993) and maintain similar mortality rates. Therefore, in landscapes where eastern and New England cottontails coexist, eastern cottontails would have greater than three times more suitable habitat than New England cottontails.

**Discussion**

Results of these experiments demonstrated that New England cottontails can maintain survival not different from eastern cottontails, by minimizing their use of food patches away from cover. New England cottontail consumption of
the low and high quality diet was not different, suggesting they trade off energy gain for safety, and thus their currency for weighing these conflicting options is predation risk. Although diet did not cause a significant decrease in body mass, I suggest that a 30% reduction in quality for a one-week period does not cause enough physiological stress to force rabbits to forage in patches with higher risk. In other experiments (Chapter I), I found that New England cottontails switched from safe to risky patches only after food quality in cover was reduced by 60%. Eastern cottontails, on the other hand, seem to use a different currency for making foraging decisions. They consumed 25% more of the higher quality diet than the low, and their GUDs did not differ among the feeders with varying predation risk.

In none of the experiments, did distance or diet explain a significant proportion of the variation in weight change. The pattern of weight change, however, was the same among all experiments, though not statistically different in all comparisons. Rabbits lost weight in weeks 1 and 3, whereas in weeks 2 and 4, they gained weight. This pattern did not coincide with consumption means among periods (i.e., rank order of consumption means differed from the rank order of weight change), nor was it an effect of a treatment by treatment-week effect. Because weight change was small (always < 6% [+/-] of the animal’s initial body weight and often within 3%), it may have been a random effect of differences in gut fill. In addition, rabbits
were given a one week period of acclimation to the pen prior to experiments to learn where food patches were located. Nearly all animals lost weight during this period. Also, prior to the first experiments of the year, 1 rabbit was placed in each enclosure with no feeders to remove ambient forage in the cover habitat. Therefore, I do not think that this pattern of weight change reflects an experimental artifact other than timing of weighing rabbits.

This study supports the results of Barbour and Litvaitis (1993) and suggests that the New England cottontail is a cover-obligate. The eastern cottontail, on the other, hand seems to have a more generalized foraging strategy, and thus a larger realized niche. Incidental observations of free-ranging individuals of both species support this. Eastern cottontails can be seen in mowed grassy areas whereas New England cottontails were never observed in completely open habitat, although their tracks suggest they will cross openings.

Several scenarios may explain the present coexistence of these two species. First, and most parsimonious, is that the two species are not competing for habitat. New England cottontails use the more densely vegetated patches whereas, eastern cottontails occupy the unused or underutilized habitat in the landscape, and use cover for refuge only. However, in Connecticut, New England cottontails fell from comprising 100% of the population of cottontails in the late 1800s to only 16% by 1970.
In addition, Eabry (1968) re-sampled 28 sites that had previously contained only New England cottontails and found that 10 of these sites contained only eastern cottontails. Eabry (1968) could not analyze whether stand characteristics at these sites had changed between the two investigations, although he reported that impressions of hunters were that the canopy was more developed and the understory had thinned. Based on his (Eabry 1968) and observations by others (Chapman and Morgan 1973, Jackson 1973), it is also likely that habitat surrounding these patches changed as well.

One possible explanation of patterns of New England and eastern cottontail coexistence is the classical fugitive coexistence scenario (Hutchinson 1951, Skellam 1951, Levins and Culver 1971, Horn and MacArthur 1971, Slatkin 1974, Hanski and Ranta 1983, Hanski 1983, and Nee and May 1991). In this case, there exist asymmetries in the competitive and colonization abilities of both species. The superior competitor is the inferior colonizer and the superior colonizer seeks refuge in patches that do not contain the superior competitor, hence fugitive competition. This scenario, however, is not likely to explain the coexistence of New England and eastern cottontails. For example, Probert and Litvaitis (1996) found that
neither eastern nor New England cottontails were able to dominate the other, nor was either species able to dominate access to food or cover.

The most likely explanation is that current distributions of eastern and New England cottontails only illustrate a "snapshot" in evolutionary time, and eastern cottontails are in the process of monopolizing human-altered landscapes where agriculture and development replace forested and regenerating stands. Support for this comes from southern New England where eastern cottontails have usurped New England cottontails from the habitat historically occupied by New England cottontails exclusively. Eabry (1968) concluded that old-field patches surrounded by mature forested stands may support only New England cottontails whereas old field patches surrounded by mowed field or golf courses would support eastern cottontails only. The distribution of eastern and New England cottontails in southern New England may be more a function of matrix habitat surrounding a patch, than characteristics of the patch. Thus, as landscapes become more fragmented with human-altered habitats, New England cottontails will experience greater predation risk, limiting their use of habitat or inflicting greater mortality. The under- or unused habitat will become vacant, allowing eastern cottontails to occupy these patches (Fig. 2.2).

This still does not explain why there are "islands" of New England cottontails in landscapes dominated by eastern cottontails. New England
Fig. 2.2. Changes in cottontail distribution with increasing habitat fragmentation in the landscape.
cottontails can likely maintain occupancy of patches against eastern
cottontail intrusion (Probert and Litvaitis 1995), but their occupancy is
limited by succession. As the patch succeeds, the canopy closes, the
understory declines, and cottontails lose winter food and cover. However, if
there were habitats that succeeded very slowly, due to poorly drained,
droughty, or infertile soils, then New Englands would have a longer window
of occupancy. Eabry (1968) found New England cottontails predominating
over eastern cottontails in shrub-dominated wetlands, hardwood swamps,
and hardwood, spruce, and hemlock stands with laurel understories. In fact,
the only captures of eastern cottontails in these cover types was when the
trap was located within 16-m of a field edge (Eabry 1968). These cover types,
due to their poor soils for tree growth have may prolonged the shrub-stage of
succession and allowed New England cottontails refuge from eastern
cottontails in human-altered landscapes.

New England cottontails were endemic to the northeast and thus
evolved in a landscape dominated by forest (Jackson 1973). Perhaps the New
England cottontail existed in low densities before European colonization of
North America in shrub-dominated wetlands, forest canopy gaps, river
corridors, and regenerating forest stands (Litvaitis 1993). Populations
increased after farm abandonment in the 1800s, and likely returned to their
original size (Litvaitis 1993). Now, however, populations are likely declining
below their pre-Columbian densities due to dramatic changes in the landscape.

To maintain New England cottontails, the focus on habitat management is not enough. Nugent (1968) suggested that traditional means of enhancing cottontail habitat (e.g. openings, and food plots) in areas where eastern and New England cottontails coexist are probably more beneficial to eastern, than New England cottontails. In southern New England, preservation of New England cottontail refuge (shrub swamps, hardwood swamps, and other slow maturing cover types) will be crucial to maintaining New England cottontails. However, in New Hampshire, both species occupy very similar habitats (Probert and Litvaitis 1995) but in different landscapes that are separated by weak geographic barriers.

Perhaps maintaining a species like the New England cottontail that is strongly affected by both heterogeneity within habitat and heterogeneity within the landscape is the most difficult of all. Habitat management can be accomplished by state wildlife agencies and through landowner education, but landscapes are shared by numerous owners and towns with varying goals for development. Although we can not curtail development within landscapes, we need to manage development to minimize the fragmentation of contiguous forest, and maintain an adequate number of early successional habitat patches to support stable metapopulations (Litvaitis and Villafuerte
Early successional habitat management can be accomplished by maintaining large patches on short rotations to maintain large blocks of suitable habitat within a stand (Litvaitis and Villafuerte 1997).

My results suggest that New England cottontails can occupy only a small (32%) percentage of their habitat in winter and maintain mortality rates not different from eastern cottontails. Eastern cottontails, on the other hand, can utilize 99% of the habitat. Although New England cottontails can forage further than 3-m from cover, they do so with greater predation costs than easterns (Chapter I). Review of previous studies of the distribution of eastern and New England cottontails suggests that conservation of the New England cottontail will require habitat protection, but perhaps more importantly management of human land uses in landscapes occupied by both species.
LITERATURE CITED


Nugent, R.F. (1968) Utilization of fall and winter habitat by the cottontail rabbits of Northwestern Connecticut. MS Thesis, University of
Connecticut, Storrs.


CHAPTER III

DIFFERENCES IN THE EYE SIZE AND PREDATOR DETECTION DISTANCE OF NEW ENGLAND (SYLVILAGUS TRANSITIONALIS) AND EASTERN (S. FLORIDANUS) COTTONTAILS

Introduction

Much research in community ecology has focused on mechanisms that explain species coexistence. In his review of competition, Schoener (1980) suggested that competition, predation, and variable environments are likely the most important mechanisms affecting community membership. Among the basic tenants of competition theory, it has been suggested that if species coexist in nature, they do so by having differences in their use of resources (Schoener 1980). Thus, sympatric species should use different habitats, different foods, or partition resources by time (Schoener 1974). Where behavioral shifts in habitat or food use are perhaps quick to occur, physical character displacements are likely much more expensive over evolutionary time.

New England (Sylvilagus transitionalis) and eastern (S. floridanus) cottontails use similar, early successional habitats where they coexist (Eabry 1967, Probert and Litvaitis 1995). During the past three decades, populations of S. transitionalis have declined, while populations of S.
floridanus have expanded (Chapman and Stauffer 1981). S. transitionalis is endemic to the northeastern United States and S. floridanus was introduced in the 1930s-1960s (Johnston 1972). The decline of S. transitionalis and the simultaneous increase in S. floridanus suggests a competitive mechanism (Fay and Chandler 1955, Reynolds 1975); however, Litvaitis (1993) suggested that S. transitionalis have declined with the loss of early successional habitat. How then could S. floridanus prevail where S. transitionalis can not?

S. floridanus is the most wide-ranging of its genus, and has a large realized niche (Chapter I), whereas S. transitionalis has a very restricted range within the northeastern United States, and smaller realized niche (Barbour and Litvaitis 1993, Chapter I). Therefore, the range of adaptations to habitat, predation, and other environmental factors is likely greater among S. floridanus than among S. transitionalis. Because S. floridanus occupies a greater range of habitats than S. transitionalis, it is likely more polymorphic than S. transitionalis.

Previously, I studied the foraging strategies of S. transitionalis and S. floridanus to understand how each species balances the risk of predation with the risk of starvation (Chapter I). I chose foraging strategies, because in winter, the fitness of S. transitionalis is largely dependent upon maintaining a balanced energy budget and avoiding predators. Barbour and Litvaitis
(1993) demonstrated that *S. transitionalis* on resource-limited patches of habitat used sites further from cover, used poorer quality food, and had lower body weights, and survival rates than *S. transitionalis* on large patches of habitat. This research suggested that perhaps, when resources are limited and predation risk is high, the marginal cost of predation is equal to or lower than the foraging costs in or near cover, because foragers can not maintain a balanced energy budget on the poor food quality in cover.

In outdoor enclosures, I studied how *S. floridanus* and *S. transitionalis* trade-off predation risk and the need to forage (Chapter I & II). I found that *S. transitionalis* consumed more food in cover than *S. floridanus* even when food quality in cover was 40% less than food in the open. *S. floridanus* avoided food patches with 40% reduction in quality and foraged at patches with higher quality food but higher risk. As a result, *S. transitionalis* lost ~10% of their body mass in experiments whereas *S. floridanus* gained or maintained weight. In addition, *S. floridanus* had higher survivorship than *S. transitionalis* (Chapter I), despite their use of more risky patches. Because physical condition alone does not explain why *S. transitionalis* had lower survivorship, I hypothesized that perhaps they may not be adapted to foraging in the open, where predation risk was higher.

Litvaitis et al. (1992) developed a discriminant model to differentiate *S. transitionalis* from *S. floridanus* using pelage characteristics, right hind
foot, and right ear length. However, I observed that *S. transitionalis* had smaller eyes that appeared to be flush with the fur around the eye and cheek. *S. floridanus*, on the other hand, had larger, more "bulging" eyes. This characteristic difference was so pronounced that I used it to differentiate the two species.

*S. transitionalis* is associated with dense understory vegetation (Barbour and Litvaitis 1993, Chapter I), and mammals, specifically canids, are their most common predators (Brown and Litvaitis 1994, Barbour and Litvaitis 1995). In these habitats, crypsis is likely the best method of predator avoidance, because the density of shrubs obscures their outline (personal observation). In open habitats, especially in winter, crypsis may not be an effective means of predator avoidance, and the ability to detect a predator before attack is initiated may be a better anti-predator tactic. Large eyes in *S. floridanus* may be an adaptation to predation in open habitats where they frequently forage (Chapter I & II). The smaller eyes in *S. transitionalis* are more likely an adaptation to moving through dense brush where the probability of eye injury may increase with eye protrusion outside of the orbit, or perhaps larger, more exposed eyes are more expensive to maintain in northern climates.

To help explain why *S. floridanus* had higher survivorship than *S. transitionalis* when foraging in open habitats, I hypothesized that the larger
eyes of *S. floridanus* would enable it to detect an approaching predator from a further distance, and thus be able to exploit more open habitats than *S. transitionalis*.

**Methods**

**Eye Size**

I captured six *S. transitionalis* and five *S. floridanus* to measure the "bulginess" of their eyes. I captured cottontails in box traps and took photographic slides of their head from a position facing their nose and parallel with their body. The photographer used a 35-mm camera mounted on a tripod two meters from the nose of the animal. Slides were shot indoors with a flash, with ektachrome 200 ASA at f-8 and f-11. Animals were lightly anesthetized with 0.05 mL/kg xylazine, and held, in hand by an assistant. I attempted to use a rabbit restraint box but I could not control the rabbit's head position. A metric ruler was used for scale, held directly under the chin of rabbits.

After processing, slides were projected onto a grid (3-mm² squares) and both eyes of each animal, as well as 10-cm of the ruler were traced onto the grid. I measured the area of the eye by counting the number of entire squares, and estimated the area filled by partial squares within the outline tracing of the eye. I determined a correction factor by comparing the projected 10-cm with 10-cm on a metric ruler. For example, if 10-cm on the
ruler was 27-cm long on the projected image, the correction factor for the area
of eyes was 2.7. I then multiplied the number of squares by 3-mm (grid size)
and divided by the correction factor of projection.

**Predator Detection Ability**

Five *S. floridanus* and four *S. transitionalis* were used to determine
the distances that individuals detected an approaching avian predator. Prior
to this experiment animals had been used in another experiment (Chapter I,
Titration) where they lived in outdoor enclosures (5.7 x 45.7-m) for 3 months.
However, immediately preceding this experiment, animals were housed in
individual cages (0.9 x 0.8 x 0.6-m) in a covered outdoor animal facility.
Cottontails were taken from the animal housing facility and set out at the
experiment site in individual cages at 1400-h on the day of the trial.
Experiments were conducted in March, 1997, when no snow covered the
ground. Each trial began 30-min before sunset.

To determine the responses of cottontails to an approaching raptor, I
flew a model of a great-horned owl (41 x 103-cm) towards a cottontail housed
in a box trap. A raptor was used in this experiment because owls were the
primary predators in previous experiments (Chapter I & II). The model
raptor was a commercial great-horned owl decoy with black painted plywood
wings (103 x 24-cm). The model was attached to a pulley, and suspended
from a 0.3-cm wire (Fig. 3.1). A short string was attached to the pulley to
Fig. 3.1. Experimental set-up to examine the predator-detection distances of

*S. transitionalis* and *S. floridanus*.  

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
facilitate getting the owl back to its starting position after a trial. I initiated the flight of the raptor model from a small building 30-m away from cottontails. The flight of the model began at a height of 5-m and ended 30-cm above and 1-m in front of the cage containing the subject. Two different flight paths were used in order to conduct 2 trials per night on two different subjects, without having to move animals between trials. I randomly selected the order and flight path for each species.

A video camera recorded the cottontail's behavior from a distance of seven meters away. A remote microphone with a 10-m extension cord recorded the observers' instructions. One observer announced where the owl was located along its flight path in 1-m increments, the other observer had a hand held video camera recording the location of the raptor model on tape.

I determined that the cottontail had detected the approaching raptor when it changed behavior or position. Small movements, such as tightening body posture, ducking head, or flinching ears, were typical responses to the raptor model. Although there are many other responses to predators (e.g., increased heart rate, vasoconstriction to internal organs, and vasodilation to extremities), these are difficult to monitor. I also recorded the distance between the rabbit and the predator model at which the animal attempted to flee. To standardize the orientation of subjects in this experiment, only trials where animals were facing the approaching model were used. I used a t-test
for unequal variance to test the hypothesis *S. floridanus* and *S. transitionalis* can detect predators from the same distance.

**Results**

*S. floridanus* have more eye exposed outside of the orbit and eyelid (t = 2.31, df = 9, P = 0.023, Fig. 3.2), and have eyes more widely spaced (t = 3.16, df = 6, P = 0.01) than *S. transitionalis*, suggesting that *S. floridanus* may have greater cyclopean field of view, which may increase their ability to detect approaching predators. *S. floridanus* also detected the approaching raptor model sooner than *S. transitionalis* (t = 2.99, df = 6, P = 0.0124, Fig. 3.2). However, distance at which rabbit attempted to flee did not differ between the two species (*S. floridanus* $X = 3.6$, *S. transitionalis* $X = 3.2$, $t = 0.89$, df = 8, $P = 0.199$).

**Discussion**

Habitat selection can promote coexistence of competing optimal foragers (Rosensweig 1981, 1985), and behavioral or morphological adaptations can help to facilitate differential resource use (Murray and Boutin 1991). For example, Murray and Boutin (1991) found that coyotes (*Canis latrans*) had higher foot loading than sympatric lynx (*Lynx canadensis*), but foraged on the same prey. Thus, coyotes foraged in sites where snow was packed or shallow, at lower elevations, and tended to ambush prey, which minimized their disadvantage in winter.
Fig. 3.2. Predator-detection distance and eye size of S. transitionalis and S. floridanus.
S. floridanus and S. transitionalis select similar habitat in New England (Earbry 1968, Probert and Litvaitis 1995), but their use of microhabitat differs when food patches vary in quality and predation risk (Chapter I). S. transitionalis avoids open microhabitat when food is available in cover, whereas S. floridanus avoids food patches in cover when there is a quality differential between food patches in the open and cover (Chapter I). Fitness consequences of these strategies differ as well. S. floridanus maintains weight by foraging on high quality food in open microhabitats, whereas S. transitionalis loses weight from foraging on lower quality food in cover, and suffers higher predation costs than S. floridanus (Chapter I).

In these experiments, we tested whether vision in cottontails could help explain the microhabitat and associated survival differences between these sympatric lagomorphs. We initially attempted to quantify the visual acuity of both species (sensu Porciatti et al. 1989a, 1989b), but were not able to anesthetize animals with a drug that did not affect the methods to determine visual acuity (D. Smith and W. Hodos, unpubl. data).

My comparisons of eye bulginess and predator detection distance suggest that S. floridanus could have better predator detection abilities than S. transitionalis. Although eye bulginess is not a direct measure of visual field, Martin (1986, 1994) has shown that birds with similar eye placement have extensive cyclopean visual fields. Both woodcock (Scolopax rusticola),
and mallards (Anas platyrhynchos) have nearly 360° cyclopean vision and eye placement similar to cottontails (i.e., on the sides of the head). Martin (1994) illustrated an inverse relationship between binocular retinal visual field and cyclopean field width with 8 species of birds. Binocular retinal visual field decreases with increasing cyclopean field width, which is a function of eye position on the cranium. Raptors have the smallest cyclopean field and the largest binocular retinal field whereas herons, starlings, and pigeons fall between raptors and mallards which have the largest cyclopean field and smallest binocular field. Martin (1994) suggested that binocular retinal field is correlated with the use of vision in foraging, where raptors and herons, pigeons and starlings require binocular vision for foraging, whereas woodcock and mallards can use their bills as sensory instruments. Although understanding of the form and function of visual fields is often complex (Martin 1995), especially for mammals (Hughes 1977), I suggest that cottontail visual fields are a trade-off between precisely directed foraging and predator detection. Eye location in the cranium of the rabbit suggests the importance of predation and increased eye bulginess may increase cyclopean visual field.

My findings on eye size and predator detection distance are supported by the life history of these two species. S. transitionalis are cover-obligates (Barbour and Litvaitis 1993), and evolved in forested landscapes in northern
latitudes (Litvaitis 1993), whereas *S. floridanus* has the largest range of its genus, and exploits a wide range of habitat types. Large eyes may be an adaptation that enables *S. floridanus* to forage in risky patches, where predators approach from all directions. However, this adaptation may be an expense if the forager is limited to dense cover. Eyes that protrude from the protection of the cranium may be prone to injury in dense brush, and may even be an added energetic expense. *S. transitionalis* tends to avoid foraging in the open (Chapter I, II), and does not appear to have the adaptations to do so. However, as landscapes become fragmented by human development, predation risk increases, and availability of resources decreases. The generalist, *S. floridanus* will be more adapted to these landscapes, whereas *S. transitionalis* will likely be limited to more dense patches of early successional habitat.
LITERATURE CITED


CHAPTER IV

A DATA LOGGING SYSTEM USING OPTICAL SENSING TECHNIQUES TO DESCRIBE FORAGING OF COTTONTAIL RABBITS

Introduction

Recently, ecologists have looked to behavioral studies to explain mechanisms causing demographic patterns, dispersal, habitat use, and other responses to habitat fragmentation (Lima and Zollner 1996, Yahner and Mahan 1997). For example, Lima and Zollner (1996) encouraged investigation of the type of information available to animals as they move through the environment and how this information is used to select foraging sites, breeding habitat, etc.

In this paper I describe the techniques I used to investigate the currency New England (Sylvilagus transitionalis) and eastern (S. floridanus) cottontails use to evaluate costs and benefits of food patches that vary in predation risk. Previous work (Barbour and Litvaitis 1993) suggested that New England cottontails weigh the costs of predation with the potential energetic gains of foraging at a particular site. In this study I also examined the foraging strategies of eastern cottontails because their populations are stable or increasing in the region whereas populations of New England cottontails are declining. I compared the foraging strategies of these two
lagomorphs in enclosures where I could manipulate the predation costs and energy content of food.

Optimal foraging theory states that foragers will maximize their fitness (survival, # of young produced) when evaluating food items and food patches. Typical approaches have been to measure what food items should be included in a forager's diet (Hanson and Green 1989), where to forage (MacArthur and Pianka 1996) and how long to remain in a patch (Charnov 1976). Typically, these models assume that maximizing energy intake maximizes fitness (Stephens and Krebs 1986). However, for prey animals, food patches may vary in predation risk, and the forager must trade-off rich patches with high risk for poorer patches with low risk in order to minimize predation risk (Lima and Dill 1990). Thus, maximizing fitness is a trade-off between energy maximization and predation risk minimization.

There are several components to foraging that may be affected by predation risk. For example, the amount of food eaten in risky patches versus safe patches, the amount of time foraging in a patch, time handling food (i.e., chewing), and time vigilant (scanning for predators). Foragers can minimize searching for food items while at risk by selecting the more abundant food items in risky habitats, minimize handling time by carrying food items back to safety, or minimize their time vigilant, all of which would minimize their time at risk. Alternatively, foragers may dedicate more time
Fig. 4.1. Experimental set-up of enclosures indicating locations of feeders with optical sensors, databus, and data processors.
to vigilance in risky habitats. To determine the optimal behavior, the researcher must know how much time is dedicated to each behavior.

Our objective of this research was to develop a simple system that would remotely monitor the behaviors of foraging cottontails in outdoor enclosures. Specifically I were interested in the time cottontails allocate to each of the above listed behaviors.

**Methods**

Rabbits were randomly assigned to one of eight enclosures. Each enclosure was 46-m x 5-m and contained 40% shrub (refuge) and 60% open (risky) microhabitat (Fig. 4.1.). Though enclosures were surrounded by a 2-m fence and covered with monofilament line (1-m spacing), predators (typically owls) were able to enter the enclosure. Four feeders were placed at 3, 9, 15, and 22-m from the protective cover with the most distant from cover representing the most risk. Several different techniques were considered to detect activity at each feeder. The technique I used was a break-beam circuit utilizing infrared emitter/detector (photo transistor) pairs in each of the feeders. The head of the rabbit breaks the beam, signifying a feeding event. The major precaution using this method was minimizing effects from sunlight. This was accomplished by mounting the photo transistors inside 1- in tubes, inside the feeders.

In order to determine the total time at risk (in the open area), another
sensor was required at the cover/open area border. This also uses an infrared beam, but the driving/sensing circuitry was more elaborate. To obtain the range of the width of the enclosures (5-m), a high gain was required by the photo transistor. This also required a stable biasing point which called for complete shielding of the phototransistor from ambient sunlight. This was accomplished by enclosing the transistors in 4 inch tubes. Further immunity from ambient light was accomplished by modulating the beam at 1 kHz. Detection circuitry for the modulated beam was composed of a 2nd order bandpass filter and an LM567 tone decoder.

A logic zero representing a feeding event or entrance into the open area was transmitted via data bus to an 80c51 microcontroller which recorded the time of day an event occurred and the duration of that event over a 24 hour period. The 80c51 was interfaced with 32K of external SRAM to provide ample storage of feeding events. Typically, sixty to eighty foraging events from each feeder were recorded nightly. Data stored in memory was downloaded serially to a PC as text. The entire system was designed for low power consumption and can be run from a low capacity 12-V deep-cycle marine battery.

Data from the microprocessors contained the time the event occurred, and the elapsed time of the event. The time the event occurred was recorded as the elapsed time since the system was started (e.g., 1.534-h past restarting
the system. To convert event times into time-of-day, I converted the event
time fraction into minutes and seconds and I added the time the system was
started to each of the event times using a C-program.

**Definition of behaviors**

Data from microprocessors were imported into a spreadsheet and the
number of events and elapsed time in feeders were totaled for each feeder
each night. Elapsed time in feeders was considered to be searching behavior
and pauses between events were used to separate events into discrete bouts
of foraging. To characterize handling and vigilance, and differentiate
between pauses within and pauses between bouts, pauses between events
were calculated by adding the elapsed time to the event time and subtracting
the next event time from the end of the first foraging event (e.g., if an event
occurred at 13:00:00 for 6 seconds, and its next feeding event occurred at
13:00:30, then the pause between feeding events is 13:00:30-13:00:06 or 24-
sec.). Relative frequencies of pauses were plotted on semi-log plots to
determine the shape of the distribution of pauses between foraging events
(Machlis 1977). A distribution with different slopes, can be considered
different processes, or different behaviors (Machlis 1977). Direct
observations were then used to define those processes. I considered events
within bouts as those events with pauses with a frequency ≥ 1. All pauses
after the first encountered pause with zero frequency were considered
alternative activities. I then used nonlinear (two-phase) regression to
determine whether the distribution could be described by one or two
regression lines, and the break point between the curves. Nonlinear
regression fits a least squares curve to observations, and estimates the
breakpoint between curves with 95% confidence intervals (Systat 1996).

These analyses revealed that eastern cottontails had shorter handling
time than New England cottontails and the probability of eastern cottontails
returning to foraging after handling food was equal for handling pauses up to
16 seconds (95% CI = 11 to 21 sec., Fig. 4.2). New England cottontails
handled food for up to 32 seconds (95% CI = 26.6 to 38 sec., Fig. 4.2), but the
probability of returning to foraging after handling food declined with time,
and was different from zero (P >0.05). This result suggests that New
England cottontails alternate between vigilance and handling during short
pauses within bouts but eastern cottontails do not. Vigilance and handling
are mutually exclusive in eastern cottontails but not so in New England
cottontails.

**Conclusion**

The data collected from this system allowed me to evaluate the costs of
predation in terms of time spent searching for food, handling food, time
vigilant, sequence of feeder use, duration of time spent at risk while
Fig. 4.2. Log relative frequency distribution of pauses in New England and eastern cottontail foraging described by non-linear (two-phase) regression.
foraging, and timing of foraging. I found that the two species behave
differently in response to predation risk (Chapter I). I also found that at the
most distant feeder, one species minimizes its time at risk, by minimizing its
time vigilant, whereas vigilance in the other species does not differ among
feeders. Further, the order of feeder use was not random and cottontails
typically exploit most of the food in feeders near cover before moving on to a
more distant feeder, but behave differently at the distant feeders. Patterns
in foraging in this study corroborate with information in the literature on
habitat use for both species.
LITERATURE CITED


CHAPTER V

BEHAVIORAL TRADE-OFFS BETWEEN FOOD QUALITY AND PREDATION RISKS: SYNOPSIS OF THE INTERSPECIFIC DIFFERENCES IN FORAGING BETWEEN NEW ENGLAND AND EASTERN COTTONTAILS

In Chapter I, I demonstrated that quitting harvest rates of New England and eastern cottontails are affected by the local patch quality, predation risk at the patch, as well as predation risk and food quality at other available patches. For example, when food quality was the same among food patches, GUDs increased with increasing predation risk for New England cottontails (Sylvilagus transitionalis), but not for eastern cottontails (S. floridanus, Chapter I). Eastern cottontail GUDs increased from cover to 10-m from cover, but GUDs at further feeders were not different (Chapter I). When food quality in and near cover declined by 40%, eastern cottontails shifted their foraging to feeders with the higher food quality and higher risk, whereas New England cottontails sacrificed food quality for safety. It is only when food quality dropped by 60% that New England cottontails accepted the higher predation costs to forage on higher quality food.

Several authors have suggested that the hungry foragers should take greater risks than satiated foragers (Millinski and Heller 1978, Dill and
Fraser 1984, Mangel and Clark 1986, 1988, McNamara and Houston 1986, Magnhagen 1988, Pettersson and Brömark 1993), but I did not have data on the physical condition of foragers to test this prediction. However, Kotler (1997) used cache size of rodents as a surrogate to a state variable in his test of four models. In the context of evaluating my results relative to contemporary issues in foraging theory, I wanted to quantify the effects of distance, state, and food patch size (quantity of food) on the give-up-densities (GUDs) of New England and eastern cottontails. Specifically, I wanted to know whether past experience in a patch and the state of the forager affected the marginal value of patches ranging in predation risk. I used data from my titration experiment (Chapter I) to test three models for each species.

**Model Development**

In an attempt to predict the importance of environmental quality, local patch predation risk, and the state of the forager, I constructed linear models using least squares regression. I selected two variables that described the state of the forager, one that described the risk of predation at the food patch, and one that described the overall availability of food in the environment. I developed models to describe the three environmental conditions in Chapter I: low, medium, and high quality. In the high quality environment, all feeders had 100% commercial rabbit chow. In the medium quality environment, the feeder in cover had 60% rabbit chow, the next nearest
feeder (10 to 13-m from cover) had 70% rabbit chow, and the furthest feeders had 100% rabbit chow. Finally, in the low quality environment, the feeder in cover had 40% rabbit chow, and the other feeders corresponded to the medium quality environment.

I used a surrogate for a state variable, the total amount of food harvested by the forager the previous day (D-1SUM), in an attempt to predict whether the marginal value of patches changed with the state of the forager. I used the food consumed the day before because I thought that the size of the previous day’s meal might represent the energy budget of the forager. If it did not consume food the day before, I thought the forager might value high energy patches more than if it had foraged the day before. I also selected an environmental variable that described the predation risk at the patch (DIST), and another to describe the total amount of food available in all patches (TOT_AVAI). Volume of food available to cottontails was varied in one experiment (D. Smith, unpubl. data) in an attempt to determine whether cottontails take advantage of patches that have been augmented with additional food (sensu Kotler 1997). However, unlike Kotler (1997), I varied the amount of food available in all feeders every week (40-mL to 80-mL), instead of every day. The last variable I used in the model was the amount of food the forager consumed in the feeder the day before (D-1FEEDR). This variable was used to describe the forager’s experience in the patch, and
determine whether previous experience was related to greater consumption. Correlations among variables were < 0.62, except DIST and D-1FEEDR (r=0.71) in the high quality environment for New England cottontails.

**Model Results**

For both species, the high quality environment model explained the greatest variation in GUDs (New Englands: $r^2 = 0.74$, $F = 181.295$, $P < 0.0001$, easterns: $r^2 = 0.48$, $F = 61.310$, $P < 0.0001$). In both of these models, total availability explained the most variation in GUDs, followed by D-1FEEDR in the New England model, and Distance in the eastern model (Table 5.1 & 5.2). The total amount of food cottontails consumed the day before explained the least variation in GUDs, suggesting that either food consumed the day before is not a good surrogate of state, or the state of the forager does not affect how it forages. In the other models, distance always explained a significant amount of variation in New England cottontail GUDs and was always positive (Table 5.1). However, distance did not explain a significant amount of variation in GUDs among eastern cottontails in the models of lower environmental quality. Although not significantly different from zero (Table 5.2), the distance parameter was negative on these lower quality environment models, reinforcing the results in Chapter I.

Conclusions made in Chapter I are confirmed by these models. Both New England and eastern cottontails balance the risks of predation with the
Table 5.1. Parameter estimate, standard error of estimate, partial correlation, T, and Significance of T, for New England cottontails in environmental conditions ranging in food quality.

<table>
<thead>
<tr>
<th>Variable</th>
<th>B</th>
<th>SE Beta</th>
<th>Part. Corr</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>High quality (100%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>r² = 0.74, P &lt; 0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D-1FEEDR</td>
<td>-0.52</td>
<td>0.057</td>
<td>-0.29</td>
<td>-9.174</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>D-1SUM</td>
<td>0.08</td>
<td>0.030</td>
<td>0.09</td>
<td>2.80</td>
<td>0.0055</td>
</tr>
<tr>
<td>DIST</td>
<td>1.28</td>
<td>0.18</td>
<td>0.23</td>
<td>7.13</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>TOT_AVAIL</td>
<td>0.68</td>
<td>0.07</td>
<td>0.33</td>
<td>10.35</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>constant</td>
<td>-14.42</td>
<td>4.24</td>
<td>-</td>
<td>-3.40</td>
<td>0.0008</td>
</tr>
<tr>
<td><strong>Medium quality (60%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>r² = 0.26, P = 0.0102</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D-1FEEDR</td>
<td>-0.60</td>
<td>0.19</td>
<td>-0.48</td>
<td>-3.06</td>
<td>0.0048</td>
</tr>
<tr>
<td>D-1SUM</td>
<td>0.05</td>
<td>0.12</td>
<td>0.07</td>
<td>0.43</td>
<td>0.6709</td>
</tr>
<tr>
<td>DIST</td>
<td>0.67</td>
<td>0.45</td>
<td>0.23</td>
<td>1.49</td>
<td>0.1468</td>
</tr>
<tr>
<td>constant</td>
<td>53.03</td>
<td>11.60</td>
<td>-</td>
<td>4.57</td>
<td>0.0001</td>
</tr>
<tr>
<td><strong>Low Quality (40%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>r² = 0.55, P &lt; 0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D-1FEEDR</td>
<td>-0.51</td>
<td>0.06</td>
<td>-0.32</td>
<td>-8.93</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>D-1SUM</td>
<td>0.00</td>
<td>0.02</td>
<td>0.00</td>
<td>0.13</td>
<td>0.8953</td>
</tr>
<tr>
<td>DIST</td>
<td>0.84</td>
<td>0.16</td>
<td>0.193</td>
<td>5.42</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>constant</td>
<td>-3.40</td>
<td>5.46</td>
<td>-</td>
<td>-0.62</td>
<td>0.5343</td>
</tr>
</tbody>
</table>
Table 5.2. Parameter estimate, standard error of estimate, partial correlation, T, and Significance of T, for eastern cottontails in environmental conditions ranging in food quality.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>High quality (100%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r^2 = 0.47$, P &lt; 0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D-1FEED R</td>
<td>-0.32</td>
<td>0.07</td>
<td>-0.20</td>
<td>-4.56</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>D-1SUM</td>
<td>0.02</td>
<td>0.03</td>
<td>0.02</td>
<td>0.54</td>
<td>0.5918</td>
</tr>
<tr>
<td>DIST</td>
<td>1.32</td>
<td>0.19</td>
<td>0.31</td>
<td>7.02</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>TOT_AVAI</td>
<td>0.57</td>
<td>0.07</td>
<td>0.347</td>
<td>7.83</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>constant</td>
<td>-10.21</td>
<td>4.83</td>
<td>-</td>
<td>-2.11</td>
<td>0.0355</td>
</tr>
<tr>
<td><strong>Medium quality (60%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r^2 = 0.31$, P = 0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D-1FEED R</td>
<td>-0.39</td>
<td>0.17</td>
<td>-0.31</td>
<td>-2.32</td>
<td>0.0263</td>
</tr>
<tr>
<td>D-1SUM</td>
<td>0.01</td>
<td>0.12</td>
<td>0.02</td>
<td>0.12</td>
<td>0.9050</td>
</tr>
<tr>
<td>DIST</td>
<td>-0.82</td>
<td>0.45</td>
<td>-0.24</td>
<td>-1.83</td>
<td>0.0760</td>
</tr>
<tr>
<td>constant</td>
<td>70.19</td>
<td>.45</td>
<td>-0.24</td>
<td>5.41</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Low quality (40%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r^2 = 0.43$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D-1FEED R</td>
<td>-0.54</td>
<td>0.06</td>
<td>-0.37</td>
<td>-9.06</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>D-1SUM</td>
<td>0.06</td>
<td>0.03</td>
<td>0.10</td>
<td>2.31</td>
<td>0.0214</td>
</tr>
<tr>
<td>DIST</td>
<td>-0.20</td>
<td>0.13</td>
<td>-0.06</td>
<td>-1.5</td>
<td>0.1332</td>
</tr>
<tr>
<td>TOT_AVAI</td>
<td>0.82</td>
<td>0.06</td>
<td>0.53</td>
<td>12.97</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>constant</td>
<td>-5.22</td>
<td>5.06</td>
<td>-</td>
<td>-1.03</td>
<td>0.3028</td>
</tr>
</tbody>
</table>
quality of food at local patches, and as environmental quality declines, foraging costs at safe food patches become greater than the predation costs at higher quality food patches. Based on the results of these models, food harvested in the previous day did not influence how much food the forager will harvest. Further, when more food was available in patches, neither species consumed more food there. When more food was available, GUDs increased suggesting that cottontails may minimize their exposure to risk by minimizing their time foraging. However, in more abundant patches, harvest rates will be greater (Kotler and Brown 1990, Brown 1992, Kotler 1997).

Differences in the foraging behavior of New England and eastern cottontails seem to be most marked when food quality in and near cover was low. Eastern cottontails sacrificed safety for the higher food quality further from cover, but New England cottontails did not. Survivorship between species differed when New England cottontails could not forage in cover, but was not different when they had access to food in cover. Perhaps eastern cottontails do not accrue the increased predation costs away from cover because they have an anti-predator behavior or morphological adaptation (Chapter III) that enables them to exploit risky patches without paying the costs. In fragmented landscapes, where generalist predators are abundant, New England cottontails may either be limited to protective cover, or suffer higher mortality than eastern cottontails (Chapter II). These patterns in
their behavior may explain the New England cottontail decline and the
eastern cottontail population expansion.

Throughout this text I have shown in a number of different
environmental scenarios, that eastern and New England cottontails titrated
foraging and predation costs. The most striking difference in the foraging
strategies of the two species is that eastern cottontails avoid low quality food
and sacrifice safety, whereas New England cottontails avoid risky feeders,
and sacrifice food quality. These patterns suggested that the foraging costs
or missed opportunity costs are higher for eastern cottontails at low quality
patches than for New England cottontails. In fact, these costs are higher
than predation costs at more distant feeders, as eastern cottontails have
lower quitting harvest rates (GUDs) at risky than low quality patches.

Because these two species are very similar in size and morphology, I assumed
that foraging costs and missed opportunity costs are the same for both
species, but how they are evaluated is different. For eastern cottontails, the
marginal value of low quality patches is low, lower than more distant
patches. If I were to manipulate the state of the forager, by restricting their
consumption prior to experimentation, I would expect their GUDs to be high
at low quality patches and lower at risky, high quality patches. But this
prediction does not describe results I found for New England cottontails.

New England cottontails, on average lost 10% of their body mass in my
experiments (Chapter I), suggesting that even though they should value high quality patches above low quality patches, they do not. New England cottontails consistently fed at patches nearer cover than eastern cottontails, yet suffered more than two times the predation rate (Chapter I).

Unfortunately, I could not measure the body mass of animals on a daily basis, so I could not evaluate whether the marginal value of patches changed with the forager’s state. I attempted to answer this question with the above linear models, but my surrogate state variable had little predictive value. Averaged over long periods, the marginal value of risky patches is probably lower than the marginal value of safe, low quality patches for New England cottontails. However, New Englands may value these high quality patches more than safe ones after they missed a day of foraging due to snowfall, or presence of a predator. When their energy reserves are low, New Englands may try to hedge predation risk and high foraging rates at distant feeders, by partially depleting distant feeders, and making up the balance at safe feeders. Although I could not test this relationship, several authors have found similar results, but came to different conclusions (Lima et al. 1985, Valone and Lima 1987). These authors concluded that foragers were attempting to balance the probability of surviving predation, and the fitness value of net energy gain. However, this explanation requires that the forager’s probability to survive changes significantly during a bout, which is
not likely in my study, considering the short time foragers remained at a patch at one time (6 to 11-min.). Alternatively, I believe that the forager's feeding rate (joules/sec.) alters its valuation of food (Lima and Dill 1990). As foragers feed from high quality, high risk patches (high feeding rate), the marginal value of food there declines and the cost of predation increases. Under this explanation, the probability of surviving predation remains relatively unchanged (Brown 1992b), and harvesting food from risky and safe patches strikes a balance between marginal value of food and the cost of predation (Brown 1992b).

In summary, the state of the forager is an important variable in predicting foraging strategies when patches vary in quality and predation risk. If we assume that foragers maintain a positive energy budget, we would never expect them to accept high risk patches if low risk patches will meet their requirements, and we would not be able to explain the paradoxical results in these chapters.

In one of the most commonly used patch use models, where predation risks vary among patches, foragers minimize predation risk subject to an energy constraint (Gilliam and Fraser 1987, Brown 1992a, Kotler 1997). In this model, foragers must maintain a certain energy intake. Perhaps this constraint could be the daily energy expense of the forager. By assumption, this model does not allow animals to go into a negative energy budget, and
they should never value high risk patches over lower risk patches. But if foragers occasionally miss a meal, and then seek patches with high net energy gains, this model misses perhaps the more important impacts on fitness. In the case of New England cottontails, I believe that this is the most plausible explanation for the high predation rate, yet rare use of distant feeders. Eastern cottontails on the other hand, perhaps could be modeled with a less restrictive cost function than the above model. Minimizing the risk:reward ratio does not adequately describe eastern cottontail foraging. I suggest that the cost function for eastern cottontails should be to maximize energy intake, subject to some minimal threshold of safety.
LITERATURE CITED


List of References, Page 117

Hall, New York.


Lima, S.L. (1987a) Vigilance while feeding and its relation to the risk of
Martin, G.R. 1986. Total panoramic vision in the mallard duck, Anas
(Oncorhynchus gorbuscha) and Chum salmon (O. Keta). Can. J. Fish
Aquat. Sci. 45:592-596.
Mangel, M., and Clark, C.W. (1986) Towards a unified foraging theory.
foraging behavior of sticklebacks (Gasterosteus aculeatus J.). Nature
275:642-644.
Morin, P.J. (1981) Predatory salamanders reverse the outcome of competition
Morin, P.J. (1984) The impact of fish exclusion on the abundance and species
composition of larval odonates: results of short-term experiments in a
Morin, P.J. (1986) Interactions between intraspecific competition and
Morin, P.J. (1987) Salamander predation, prey facilitation, and seasonal
succession in microcrustacean communities. In: Kerfoot W C, Sih A
(eds) Predation: direct and indirect impacts on aquatic communities.
250.
Nugent, R.F. (1968) Utilization of fall and winter habitat by the cottontail
rabbits of Northwestern Connecticut. MS Thesis, University of
Connecticut, Storrs.
Oehler, J.D., Litvaitis, J.A. (1996) The role of spatial scale in understanding
responses of medium-sized carnivores to forest fragmentation. Can J
List of References, Page 121

Zool 74:2070-2079.


browse species of snowshoe hares. J Wildl Manage 41:144-147.