# THE EFFECTS OF PREY DISTRIBUTION AND ABUNDANCE ON EASTERN COYOTE LIFE HISTORY AND PREDATION ON WHITE-TAILED DEER

A Thesis Submitted to the College of Graduate Studies and Research

in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in the Department of Biology University of Saskatchewan Saskatoon

By

Brent Ronald Patterson Autumn 1999

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### ABSTRACT

For most medium to large sized carnivores, the distribution and abundance of food resources represent key factors influencing their spatial dynamics and social structure. In that context, I studied the social organization, space-use, and foraging ecology of eastern coyotes (*Canis latrans*) in two areas of Nova Scotia, Canada, from 1992 to 1997. Breeding pairs formed the nucleus of coyote social groups and generally traveled with 1-3 other coyotes during winter. Mean winter traveling group size (2.5) was similar for packs utilizing white-tailed deer (*Odocoileus virginianus*) or snowshoe hare (*Lepus americanus*) as a primary winter food item. Thus, increased use of large prey (deer) was insufficient to explain group formation and cohesion of coyotes.

Home-range sizes decreased significantly with white-tailed deer and snowshoe hare densities but were not influenced by coyote traveling group size. Mid-winter coyote densities ranged from 4.3 to 13.9 coyotes /100 km<sup>2</sup>, and changed markedly during the course of the study due to changes in territory size, habitat saturation, and the abundance of transient coyotes. Coyotes used the same territories during winter and summer, and from year to year. During winter, coyotes used areas of high deer density in proportion to their availability but used areas containing few or no deer proportionately more than expected. Similarly, a greater proportion of deer kills was observed in areas of low deer density relative to areas with high deer densities (P = 0.001), likely owing to the increased vulnerability of deer.

ii

Territoriality appeared to prevent coyotes from concentrating in deer wintering areas and kept the coyote: deer ratio relatively low.

Based on the analysis of 2,443 scats, deer and hare were the dominant food items. Other important food items included small mammals, and fruits during late summer. During winter, coyotes killed 76-86% of the deer they consumed. Most deer killed by coyotes were not malnourished. The consumption of deer fawns during June and July exceeded that of hares in all areas, despite high hare densities in some areas. In areas where they were readily available, coyotes fed predominantly on hares during winter, and 53% percent of the variation in winter killing rates of deer was explained by hare density (P = 0.005). Groups of coyotes initiated proportionately more chases than single coyotes (P = 0.04). Groups of  $\geq 4$  coyotes had higher chase success than smaller groups (P = 0.038). Snow depth also had a significant influence on chase success (P = 0.012). The mean distance of deer kills to recent clear-cuts was significantly shorter than expected in an area where deer yard during winter (P = 0.05) but not in an area where deer did not aggregate during winter (P =0.37).

Overall, high use of deer appeared to have been associated with increased vulnerability due to winter severity or, in the case of young fawns, inability to escape. During mild winters, I suspect that coyotes are forced to focus their hunting efforts on prey other than deer, regardless of density, due to low

iii

vulnerability of deer. When severe winter conditions occur, coyotes switch to feeding mainly on deer.

Coyotes exhibited a Type I numerical response to the total biomass of deer and hares available (P = 0.08). Deer killing rates were negatively with hare density (P = 0.005). Survival of fawns during summer was positively correlated with hare density, further suggesting that high hare densities buffered predation on deer. However, the total response of coyotes to changes in deer and hare density indicated that the presence of hare as an alternate prey increased predation rates on deer by supporting higher coyote densities.

Year-long predation rates on deer were estimated at 25.0 and 13.6% in the Queens county study area during 1992-93 and 1996-97, respectively, and at 9.0% in the Cape Breton study area (1995 - 97). Coyote predation was less significant than hunting (legal and illegal) as a limiting factor for deer.

A model based on the total response of coyotes to changes in deer and hare abundance predicted that deer populations would stabilize at a density of 3.4 - 4.2/ km<sup>2</sup> and would ultimately be regulated by food competition rather than predation. Extirpation was a possible outcome for deer at densities of 0.2 - 0.6 deer/ km<sup>2</sup>, depending on hare densities and deer recruitment, but was considered unlikely to happen because of rapid restrictions of hunting at low deer densities.

Mean urinary urea nitrogen (U): creatinine (C) ratios in territorial coyotes were correlated positively with hare density

iv

(P = 0.004), but negatively with deer density (P = 0.01). Coyote group size did not have a significant influence on the mean U:C ratios (P = 0.21). Coyotes utilizing hares as a primary food source maintained consistently high U:C ratios throughout the winter whereas those using proportionally more deer as a primary food source exhibited lower and more variable U : C ratios. Winter densities of deer and hares were inversely related (P = 0.025) further suggesting that U:C was primarily a function of hare density.

# ACKNOWLEDGEMENTS

Financial and logistical support for this study was provided by Parks Canada, the Nova Scotia Department of Natural Resources (NSDNR), and Forestry Canada under the Cooperation Agreement for Forestry Development. The University of Saskatchewan also supported me during the write-up phase of this project. I thank Mark Elderkin and Tony Duke of NSDNR for securing the initial funding for this project and for providing logistic support thereafter. My primary field assistant, Lawrence Benjamin, gave much more to the project than he was compensated for. Early in the study Bevan Lock and Hughie Broders designed the initial data entry protocols and put an end to the rapidly accumulating piles of paper. I thank the McLean family for letting us place our field camp on their beautiful farm in Cape Breton. Once settled in, they, the Richards, and the Mackenzies provided great friendship and made us feel welcome.

Many other people contributed to the various aspects of this project, including but not limited to: D. Anderson, D. Banks, S. Bondrup-Neilsen, G. Boros, M. Boudreau, D. Brannen, H. Broders, V. Bushell, R. Charlton, G. Corbett, S. Crouse, C. Cushing, C. Doliver, C. Drysdale, T. Fitzgerald, C. Frail, G. Fraser, B. Gilbert, C. Gjerdrum, S. Hawkes, K. Huskins, D. Jewers, A. Kennedy, R. Lawson, B. Lock, K. Lock, B. MacDonald, C. MacDonald, P. MacDonald, J. Mahoney, J. McKnight, M. McLeod, J. Mills, I. Morrison, S. Morrison, E. Muntz, M. O'Brien, G. Parsons, V. Power, M. Pulsifer, D. Richards, M. Robinson, D. Shaw, M. Silver, G. Tatlock, S. Uhlman, J. Wentzel, and R. Williams.

The staff of the Air Services division of NSDNR provided expert assistance with the aerial surveys and tracking flights. Art Crowell, Loydd Duncanson, and Donnie Good assisted with the coyote trapping. I thank Mike O'Brien and Barry Sabean of the

٧i

NSDNR, Wildlife Division, for providing data from the provincial coyote-tracking program. The urinalysis was conducted at Efamol Research Inc., Kentville N.S., under the supervision of Kevin Gall and Ken Jenkins. I am grateful for their contribution.

I am indebted to Dr. François Messier for providing focus and academic support to this research, and for giving me the opportunity to pursue my Ph.D. My colleagues at the University of Saskatchewan: Kim Brown, Steve Ferguson, Damien Joly, Serge Larivière, Phil McLoughlin, and Jim Rettie reviewed most of the manuscripts comprising this thesis and provided a stimulating work environment as well as great friendship. I thank my advisory committee, Drs. Peter Flood, Larry Fowke, Dick Neal, Malcolm Ramsay, and the late Jan Smith for providing guidance and support along the way.

I reserve my greatest appreciation for my wife Lauren and parents Ron and Carlene. Their patience, love and support got me through some hectic times. Seeing this project through to completion was fun, but not always easy. I could not have done it without those mentioned above. Thanks to all!

B.R.P 12 June, 1999

# TABLE OF CONTENTS

PERM	ISSION TO USE i
ACKN	OWLEDGEMENTSvi
LIST	OF TABLES xii
LIST	OF FIGURES xiv
1.	GENERAL INTRODUCTION 1
	The influence of food resources on the population dynamics of carnivores 1
	Other influences on social organization and food habits of predators 2
	Predation and ungulate population dynamics 3
	Historical perspective 4
	Objectives 6
2.	SOCIAL ORGANIZATION AND SPACE-USE OF EASTERN COYOTES IN RELATION TO PREY DISTRIBUTION AND ABUNDANCE
	Introduction 8
	Group formation and cohesion8
	Study areas 11
	Methods 15
	Deer and hare distribution and abundance
	Social organization and group dynamics
	Coyote mortality and reproductive success
	Dispersal
	Group formation and cohesion
	Coyote densities
	Spatial distribution and territoriality
	Influence of prey density and group size on territory size
	Territory stability and extra-territorial excursions 23
	Coyote-deer spatial relationships
	<b>Results</b>
	Deer and hare distribution and abundance
	Social organization and group dynamics
	Coyote mortality and reproductive success
	Dispersal
	Group formation and cohesion
	Coyote densities

Spatial distribution and territoriality	• • • • • • • • •	37
Influence of prey density on territory size	• • • • • • • • •	37
Territory stability and extra-territorial excursion	ons	37
Coyote-deer spatial relationships	• • • • • • • • •	42
Discussion	• • • • • • • • •	42
Impact of human exploitation on coyote social organiz	ation	47
Coyote dispersal and group formation		49
Group cohesiveness	• • • • • • • • •	51
Coyote densities	• • • • • • • • •	52
Spatial distribution and territoriality		54
Coyote-deer spatial relationships	• • • • • • • • •	55
Territoriality and extra-territorial excursions		55
3. PREY SWITCHING AND THE FEEDING HABITS OF EASTERN COYOTES RELATION TO SNOWSHOE HARE AND WHITE-TAILED DEER DENSITIES	IN S	59
Introduction	••••	59
Methods	• • • • • • • • •	62
Scat analysis	• • • • • • • • •	62
Coyote functional response and evidence for prey swit	ching	65
Results	••••	68
Food habits	• • • • • • • • •	68
Coyote functional response and evidence for prey swit	ching	72
Discussion		80
Features of the functional response to changes in dee abundance	er and ha	are 81
Fruits as a potential buffer food		84
The role of prey switching in the diet of the eastern	coyote	84
4. FACTORS INFLUENCING KILLING RATES OF WHITE-TAILED DEER BY	eastern	~ ~
		36
	• • • • • • • • •	30
	• • • • • • • • •	89
Effect of deer and have abundance on killing rates.	• • • • • • • • •	89
Effects of group size and show depth on killing rates	)	90
vulnerability to predation	•••••	on 91
Effects of forest harvesting on deer vulnerability to predation	) coyo	ote 93
Changes in killing rates over winter	••••	93
Results	••••	94
Effect of deer and hare abundance on deer killing rat	:es	94

	Effects of coyote social group size and snow depth on chase success
	Effects of deer distribution and abundance on vulnerability to predation
	Effects of forest harvesting on deer vulnerability to predation
	Changes in killing rates over winter
	<b>Discussion</b> 104
	Effects of coyote social group size on chase success 105
	Effects of deer distribution and abundance on vulnerability to predation
	Effects of forest harvesting on deer vulnerability to coyote predation
	Changes in killing rates over winter
	Management implications 110
5.	COYOTE PREDATION ON WHITE-TAILED DEER IN A MULTI-PREY SYSTEM IN NOVA SCOTIA
	Introduction 112
	Coyote predation on white-tailed deer
	Methods 117
	Estimation of coyote densities
	Coyote food habits 118
	Age, sex, and condition of deer killed by coyotes
	Year-long predation rates and population balances
	Consumption rates 119
	Scavenging by coyotes
	Validating the estimation of deer consumption rates 124
	Modeling coyote predation in relation to deer and hare abundance
	Coyote functional response
	Coyote numerical response128
	Predation rates on deer as a function of deer and hare densities
	<b>Results</b>
	Coyote densities 130
	Age, sex, and condition of deer killed by coyotes 130
	Scavenging by coyotes 133
	Year-long predation rates and population balances
	Consumption rates
	Validating deer consumption rates

Modeling coyote predation in relation to deer and hare abundance
Coyote functional response
Coyote numerical response
Predation rates on deer as a function of deer and hare densities
Discussion
Age, sex, and condition of deer killed by coyotes 149
Year-long predation rates and population balances 150
Predation on fawns150
Coyote functional response
Coyote numerical response
Total response and coyote predation on deer
6. WINTER NUTRITIONAL CONDITION OF EASTERN COYOTES IN RELATION TO PREY DENSITY
Introduction 160
Methods
Collection and processing of urine samples
Statistical analyses 164
<b>Results</b>
Comparison of samples collected along trails vs. kill sites 165
Seasonal and geographic differences in U:C
The influence of deer and hare abundance on U:C
Discussion
Seasonal trends in U : C 173
Urinalysis as an indicator of nutritional condition in carnivores 174
7. CONCLUSIONS AND GENERAL DISCUSSION 176
Main conclusions 176
General discussion 179
Influence of deer and hare abundance on predation of deer. 183
Influences of predation by eastern coyotes on deer population dynamics 185
8. LITERATURE CITED 188

# LIST OF TABLES

Table 2.1. Summary data for family groups of coyotes in the Cape Breton Highlands (CBH), Cape Breton Lowlands (CBL), and Queens County (QC) study areas. Information was included only for those annual territories that were adequately defined and for which deer and hare density data were available	27
Table 2.2. Number and distribution of deer tracks observed along road and trail networks in the Queens County (QC) and Cape Breton (CB) study areas, winters 1996-1997	29
Table 2.3. Seasonal survival rates of coyotes in the Cape Breton (CB) and Queens County (QC, not including coyotes residing in Kejimkujik National Park) study areas, September 1992 to March 1997. The standard deviation and number of telemetry days of data for each social class of coyotes are given in parenthesis	33
Table 2.4. Dispersal patterns of juvenile coyotes in the CapeBreton and Queens County study areas, Nova Scotia, September1992 to March 1997.	35
Table 2.5. Mid-winter density estimates, and relatedinformation, for coyotes in the Queens County (QC) and CapeBreton (CB) study areas, Nova Scotia.	38
Table 2.6. The frequency of excursions (movements >3 km from an established territory) by territorial coyotes in the Queens County (QC), Cape Breton Lowlands (CBL), and Highlands (CBH) study areas, Nova Scotia, 1994-1997. The number of coyote-seasons of telemetry data for each season was calculated by dividing the total number of radio-contact days for all group living coyotes in each study area by the number of days in each season.	44
Table 2.7. Spatial distribution of coyotes in the Cape Breton Lowlands (CBL) and Cape Breton Highlands (CBH) study areas, and Eden deer wintering area (DWA), Nova Scotia, during winter vs. expected distribution assuming coyotes used all deer density classes within their territories equally	48
<pre>Table 3.1. Comparative food habits of coyotes using scat analysis in the Queens County and Cape Breton study areas. Q1= Queens County study area, July 1992- December 1994; Q2 = Queens area, January 1995- March 1997; CBH = Highlands area of Cape Breton study area, January 1995- March 1997; CBL = Lowlands area of Cape Breton study area, January 1995- March County study 1997</pre>	69
Table 3.2. Relative winter density estimates (± SE), and estimated number of deer and hare consumed per coyote, within 9 territories located in the Queens County (QC) and Cape Breton (CB) study areas, Nova Scotia, winters 1996- 1997(no.	70
of sample plots in parentheses}	73

Table 3.3. Relative summer density estimates (density ± SE), and estimated number of deer and hare consumed per coyote, within 6 coyote territories located in the Queens County and Cape Breton study areas, Nova Scotia, June- July 1996 (no. of sample plots in parentheses)	74
Table 4.1. Winter killing rates of deer (deer/ 100 days) by coyotes in the Queens County (QC) and Cape Breton Lowland (CBL) and Cape Breton Highland (CBH) study areas, 1995-97.	
Table 4.2. Coyote social group sizes involved in chases and kills of white-tailed deer during winter in Nova Scotia, 1989- 1997.	97
Table 5.1. Derivation of the density (deer /100 km2) of fawn and adult white-tailed deer on 1 June (post-natal density) in the Queens County (QC) and Cape Breton (CB) study areas.	. 120
Table 5.2. Age, and mortality distribution of 102 deer consumed by coyotes in the Queens County (1992-1997) and Cape Breton (1994-1997) study areas, Nova Scotia.	. 132
Table 5.3. Estimation of the number of deer killed by coyotes (animals /100km2), based on scat analysis and estimates of coyote densities, in the Queens County study area, June 1993 - May 1994, and June 1995 - May 1997, and the Cape Breton study area (CB), June 1995 - May 1997	1376
Table 5.4. Estimated mortality factors (expressed as percentages of the population on 1 June) for white-tailed deer in the Queens County (QC) study area, June 1992 to May 1993, June-May 1995 - 1997; and the Cape Breton study area (CB), June 1995 to May 1997.	138
Table 5.5.Comparison of coyote predation rates on deerestimated using radio-collared deer, coyote scat analysis, andwinter snowtracking of radio-collared coyotes.	. 140
Table 6.1. Urea nitrogen: creatinine ratios (±SE) and relative deer and hare densities (± SE, No. of sample plots in parentheses, data from Chapters two and three) for 552 urine soaked snow samples collected while snowtracking radio- collared coyotes belonging to eight territorial packs in Nova Scotia, January - March, 1996-1997.	166

# LIST OF FIGURES

Fig. 2.1 Queens County (QC) and Cape Breton (CB) study areas in Nova Scotia, Canada	. 14
Fig. 2.2 Winter distribution of white-tailed deer in the Cape Breton study area, Nova Scotia, as determined by aerial and ground surveys, January to March, 1996-1997. Density classes were based on the following criteria: Absent = no sign of deer tracks, Low = one or more scattered tracks, but no trails, Medium = several tracks, with at least one definite trail, High = extensive trail network evident	.26
Fig. 2.3. The relative abundance of (a) white-tailed deer (estimated by pellet group counts) and (b) snowshoe hare (abundance rankings as estimated by fur harvesters) in the Queens County and Cape Breton study areas, 1990-1997	30
Fig. 2.4. Spatial distribution of radio-collared coyotes in the Queens County Study Area, Nova Scotia, September 1992 to March 1997.	39
Fig. 2.5. Spatial distribution of radio-collared coyotes in the Cape Breton Study Area, Nova Scotia, March 1994 - 1997	40
Fig. 2.6. Space-use patterns of breeding adult male AM8, in the Cape Breton study area, Nova Scotia, September 1994 to March 1997.	43
Fig. 2.7. Depiction of the 9 extraterritorial excursions made by territorial coyotes in the Queens County study area, Nova Scotia. Dates of excursions were as follows: a - 1 Oct 96, b - 30 Aug 96, c - 23 Aug 96, d - 6 Jan 95, e - 30 Aug 95, f - 10 Nov 94, g - 1 Oct 95, h - 16 Feb 96, i - 13 Feb 96. Excursions are presented as the minimum straight-line distances.	45
Fig. 2.8. Depiction of the 14 extraterritorial excursions made by territorial coyotes in the Cape Breton study area, Nova Scotia. Dates of excursions were as follows: a - 18 Mar 97, b - 20 Mar 97, c - 10 Jan 96, d - 12 Feb 97, e - 29 Nov 96, f - 29 Jan 97, g - 2 Mar 97, h - 26 Sept 94, i 21 Mar 97, j - 8-10 Mar 97, k - 13-14 Mar 97, 1 - 17 Mar 96, m - 22-23 Mar 96, and n - 1 May 96. Excursions are presented as the minimum straight-line distances.	46
Fig. 3.1. Number of white-tailed deer consumed per coyote within 9 territories during winter (December to March) in relation to the relative density of (a) snowshoe hare and (b) white-tailed	
deer	75

Fig. 3.2. Average number of snowshoe hare consumed per coyote within (a) 9 territories during winter (December- March), and (b) June-July in relation to the relative density of snowshoe hare
Fig. 3.3. Prey selectivity index (elA2/e2A1, where el and e2 are the numbers of white-tailed deer and snowshoe hare eaten from a population of A1 and A2 available) in relation to their relative abundance of snowshoe hare and white-tailed deer (A1/A2), (a) winters (December through March) and (b) June- July, 1996 and 1997. The dashed lines (slope = 0, y intercept = 1) indicate the expected trends, if coyotes fed non- selectively on deer and hare
Fig. 4.1. The influence of snowshoe hare density on per capita killing rates of white-tailed deer by coyotes in Nova Scotia, December through March of 1995 - 1997. Table 4.1 summarizes the original data for each family group of coyotes
Fig. 4.2. The relative winter (December through March) densities of white-tailed deer and locations of 39 deer killed by coyotes in the Cape Breton study area, Nova Scotia, winters 1996-1997
Fig. 4.3. The influence of coyote group size on the mean distance (± SE) of successful and unsuccessful chases of white-tailed deer in Nova Scotia, during winter (December to March), 1989-1997 102
Fig. 4.4. The number of deer kills observed by month from December through March in Nova Scotia relative to the intensity of field sampling each month, winters 1989-1997 103
Fig. 5.1. Population trends of white-tailed deer in Nova Scotia, 1983 - 1997. Deer densities were estimated using pellet group counts conducted along 440 $\pm$ 3 (SE) transect lines distributed randomly throughout the province (Patton 1991). I assumed a defection rate of 16 pellet groups/ day and an average date of leaf fall of 1 November
Fig. 5.2. The prevalence of winter malnutrition (as indexed by <25% femur marrow fat) among fawn and adult (>1 yr) white- tailed deer, in Nova Scotia, 1983 - 1997, as assessed from road-killed deer examined from February - April each year 126
Fig. 5.3. Percent femur marrow fat of adult (>1 year) and fawn deer killed by coyotes in the Queens County and Cape Breton study areas, winters 1994 - 1997, in relation to road-killed deer
Fig. 5.4. The number of deer killed • coyote <sup>-1</sup> • 100 days <sup>-1</sup> as a function of the relative densities of white-tailed deer and snowshoe hare in the Queens County and Cape Breton study areas, winters 1995 - 1997. The multiprey functional response was estimated using the multi-prey disc equation (Charnov 1973, Hilborn and Sinclair 1979)

- Fig. 5.7. Changes in the coyote predation rate (as calculated from the total response) with deer and hare density. The solid line represents deer population growth without coyote predation and the shaded area represents the effects of changing deer recruitment ±5%. Low, mcderate, and high hare densities represent densities of -15, 30, and 45 hares/ km2, as estimated by pellet counts. K represents the density at which net deer population growth (in the absence of coyote predation) is 0. The stable equilibrium condition induced by coyote predation is represented by (S), whereas (U) represents an unstable equilibrium.
- Fig. 5.8. The proportional effects of the functional and numerical responses on the predation rate of coyotes preying on white-tailed deer in a system where deer and snowshoe hare represent the dominant prey available to coyotes. See Messier (1994) for details on the calculations. Proportional effects were calculated assuming moderate (~30 /km2) hare densities. ... 148
- Fig. 6.1. Mean monthly urea : creatinine ratios (±SE) for 552 urine soaked snow samples collected in the Queens County (QC), Cape Breton Highland (CBH), and Cape Breton Lowland (CBL) study areas, Nova Scotia, January to March, 1996-1997. ..... 169

#### 1. GENERAL INTRODUCTION

# The influence of food resources on the population dynamics of carnivores

For most medium to large sized carnivores, the distribution and abundance of food resources represent the most important factors influencing their spatial dynamics and social structure (Kruuk 1966, Bekoff and Wells 1980, Messier 1985). As such, much attention has been devoted to understanding the relationships between prey dispersion and social organization and food habits of predators. Differences in pair bonding, foraging group size and behaviour, juvenile survival, and the timing of dispersal have been correlated with the type and availability of food (Todd and Keith 1983, Moehlman 1987, Desy and Batzli 1989, Gese et al. 1996).

Among canids, there is a general trend from solitary foraging to obligatory cooperative hunting with increasing body size (Moehlman 1987). For example, wolves (*Canis lupus*) are primarily cooperative hunters of ungulates (Mech 1966, 1970, Peterson 1977) whereas the closely related coyote (*Canis latrans*) is behaviorally plastic and demonstrates large regional and seasonal differences in food habits and social organization (see Harrison 1992a, Parker 1995, and Patterson 1995 for a review).

The relative importance of various factors in influencing group formation and cohesion in coyotes continues to spark considerable debate (Bowen 1981, Messier and Barrette 1982, Gese et al. 1988, Brundige 1993). Bowen (1981) concluded that group foraging in coyotes increased foraging efficiency when utilizing large prey without sacrificing the advantage of smaller body size in exploiting small prey. However, Messier and Barrette (1982) argued that if the primary cause of group formation was to allow access to large prey and increase foraging efficiency, per capita consumption rates should increase with group size; an occurrence that remains to be documented (Schmidt and Mech 1997; but see also Brundige 1993). It remains unclear whether group formation is a direct response to larger prey size (Bowen 1981) or if large prey merely facilitates cohesion of groups formed for other reasons (Messier and Barrette 1982, Andelt 1985).

# Other influences on social organization and food habits of predators

In addition to food, population density (Rausch 1967, Zimen 1976, Andelt 1985) and human exploitation (Rausch 1967, Bowen 1981, Andelt 1985) can also influence the social organization of a predator species. Potential benefits of larger groups in enhancing the survival of young have been discussed (Zimen 1976, Bekoff and Wells 1980, Rodman 1981, Schmidt and Mech 1997) but the resulting effects of intraspecific competition on group members are rarely considered.

In addition to a variable social organization, coyotes also exhibit great regional and seasonal variation in diet (Litvaitis and Shaw 1981, McCracken 1982, 1984, Bowyer et al. 1983, Parker 1986, Andelt et al. 1987, Toweill and Anthony 1988, Patterson et al. 1998). Differences in coyote food habits have been related to differences in prey abundance (Todd et al. 1981, Knowlton and

Stoddart 1992, O'Donoghue et al. 1998), social organization (Harrison and Harrison 1984, Gese et al. 1988), successional changes in habitat (Wells and Bekoff 1982, Andelt et al. 1987), and seasonal changes in the relative vulnerability of prey (Parker and Maxwell 1989, Gese and Grothe 1995).

## Predation and ungulate population dynamics

Predation is an important factor influencing the population dynamics of many animal species (Todd and Keith 1983, Messier et al. 1986, Erlinge 1987, Potvin et al. 1988, Messier 1994, Krebs et al. 1995). However, the role of predation in creating prolonged prey suppression (i.e., regulation at low density as opposed to simple limitation) is an issue of considerable debate (Erlinge et al. 1984, Kid and Lewis 1987, Boutin 1992, Sinclair and Pech 1996, Messier 1991, 1994). Skogland (1991) reviewed "recent" predator-ungulate studies and concluded that although several cases of limitation by predators were evident, evidence for regulation was elusive.

To determine if predation is regulating prey densities, the researcher should quantify the total response of predators to changing densities of the prey (Messier 1994, 1995, Seip 1992). The total response of the predator represents the product of the functional and numerical responses (Seip 1992). The functional response describes how the number of prey consumed per predator varies with prey density, whereas the numerical response describes changes in predator density as a function of prey density (Solomon 1949, Holling 1959, Messier 1995). The major types of functional and numerical responses have been reviewed by May (1981), Pech et al. (1992), and Messier (1994, 1995). However, predation can only be regulatory if the proportion of the prey population killed increases with prey density and exceeds the net productivity of the prey population (Sinclair and Pech 1996, O'Donoghue et al. 1998). Depensatory predation occurs when the percentage of prey killed is inversely related to prey density (Potvin et al. 1988, Messier 1995, Sinclair et al. 1998).

Although clear functional responses have been demonstrated in several predator-prey systems (Todd et al. 1981, Pech et al. 1992, Messier 1984, O'Donoghue et al. 1998), optimal foraging theory (Pyke et al. 1977, Pyke 1984) suggests that foraging behaviour should maximize the function of all benefits (anything that increases an animal's fitness) to costs (e.g., predation risk, energy expenditure, time) (Abrams 1982). Further, some species may actually reduce their vulnerability to predation by aggregating (Nelson and Mech 1981, Messier and Barrette 1985). Therefore predator responses often reflect more than simple prey availability.

#### Historical perspective

Coyotes colonized Nova Scotia during the early 1980s (Moore and Parker 1992). Throughout most of the Northeast, coyotes must contend with lower prey diversity and abundance relative to their western counterparts (Harrison 1992a; Parker 1995; Patterson 1995, Patterson et al. 1998). As a result, two prey species, the

white-tailed deer (*Odocoileus virginianus*) and the snowshoe hare (*Lepus americanus*) have become the staple prey of the eastern coyote (Messier et al. 1986, Parker 1986, Patterson et al. 1998). Larger body size (Larivière and Crête 1993, Parker 1995) and a greater tendency to hunt in extended family groups during winter (Messier and Barrette 1982, Brundige 1993) have been related to the high use of deer by eastern coyotes relative to their western counterparts (Messier et al. 1986, Brundige 1993, Larivière and Crête 1993). Wolves are not present east of the Saint Lawrence River and some researchers have suggested that coyotes have replaced wolves as a significant predator of white-tailed deer in northeastern North America (Mathews and Porter 1992, Brundige 1993, Ballard et al. 1999).

In Nova Scotia, and many other regions of the Northeast, deer densities increased rapidly during the mid 1980s, apparently due to a series of mild winters (Patton 1991, Parker 1995). Despite an effort to curb the increase via liberal hunting regulations, deer in Nova Scotia had presumably exceeded K carrying capacity and were in poor physical condition by winter 1987 at which time a substantial decline in density began (Patton 1991). Coyotes were still becoming established throughout the province at this time, and although coyote predation was unable to prevent the peak in deer density, it may have accelerated and prolonged the subsequent decline (Patton 1991, Parker 1995, Patterson 1995).

### Objectives

Overall, my objective was to determine the spatial distribution, and the social and predatory behaviour of eastern coyotes in relation to the local abundance of white-tailed deer and snowshoe hares. This work begins with a description of coyote space use and social organization in relation to deer and hare densities based on the analysis of telemetry data from marked coyotes and territory-specific deer and hare density estimates. Special emphasis was placed on determining the effects of the aggregation of white-tailed deer in a winter yard on territoriality and group cohesion by coyotes. I then used scat analysis to explore coyote food habits and test the hypothesis that coyotes would switch from deer to hares as hare density increased, as predicted by the Alternate Prey Hypothesis (Keith 1974; Angelstam et al. 1984).

Data from winter snow tracking was then used to examine the influence of deer and hare density, coyote group size, and snow depth on the killing rates of deer by coyotes. Emphasis was placed on determining if deer reduced their vulnerability to predation by aggregating in winter yards.

I then used data on coyote densities and feeding habits to estimate regional predation rates on deer. I estimated the functional and numerical responses of coyotes to changing densities of deer and hares, and developed a predictive model of coyote predation on deer in forested areas where deer and hares are the primary prey of coyotes. Finally, I used urinalysis to

determine if differences in the densities of deer and/ or hares resulted in measurable differences in coyote nutritional condition during winter.

# 2. SOCIAL ORGANIZATION AND SPACE-USE OF EASTERN COYOTES IN RELATION TO PREY DISTRIBUTION AND ABUNDANCE

## INTRODUCTION

Natural selection has lead to wide variation in social and spatial systems (Burt 1943, Bekoff and Wells 1980, MacDonald 1983, Harrison 1992a). For most medium to large sized carnivores, the distribution and abundance of food resources represent important factors influencing spatial dynamics and social structure (Kruuk 1966, Bekoff and Wells 1980, Messier 1985). The social structure of the eastern coyote (Canis latrans) appears to revolve around resident adult pairs and their offspring (Messier and Barrette 1982, Harrison 1992a). These family groups maintain non-overlapping and contiguous home-ranges of 30-50 km<sup>2</sup>, approximately 100-200% larger than their western counterparts (Messier and Barrette 1982, Caturano 1983, Harrison 1992a). Solitary transient coyotes may live on large areas encompassing parts of several different coyote territories and do not breed unless a vacant territory can be found (Messier and Barrette 1982). Winter packs of coyotes are typically comprised of three or four animals, although packs of five and six coyotes have been documented in Nova Scotia (Sabean 1993a).

#### Group formation and cohesion

Factors influencing group formation and cohesion in coyotes continue to spark considerable debate (Bowen 1981, Messier and Barrette 1982, Gese et al. 1988, Brundige 1993). Bowen (1981) concluded that group foraging in coyotes increased foraging efficiency when utilizing large prey without sacrificing the advantage of smaller body size in exploiting small prey. Messier and Barrette (1982) argued that if the primary cause of group formation was to allow access to large prey and increase foraging efficiency, per capita consumption rates should increase with group size (see also Brundige 1993). Additionally, larger groups may be able to utilize large prey carcasses more efficiently by minimizing losses to other scavengers (Bekoff and Wells 1980). Hence, it remains unclear whether group formation is a direct response to larger prey size (Bowen 1981) or if large prey merely facilitates cohesion of groups formed for other reasons (Messier and Barrette 1982, Andelt 1985). If groups are formed primarily to exploit large prey, we should observe smaller, less cohesive groups among coyotes using smaller prey as a primary food source.

Two prey species, white-tailed deer and snowshoe hare are the staple food items of forest-living coyotes in north-eastern North America (Messier et al. 1986, Parker and Maxwell 1989, Parker 1995, Chapter 3). In many areas of the Northeast, deer show a clear tendency to concentrate in traditional wintering areas (Verme 1973, Potvin et al. 1981, Messier and Barrette 1985, Nelson 1995). Because of this behaviour during winter, some coyote territories may have access to large concentrations of deer, while others contain few or no deer. Trespassing into neighboring territories may be expected under such circumstances. However, the size and shape of the territories of coyotes living

in a forested landscape in southeastern Québec remained unchanged despite the presence of a large deer wintering area (Messier and Barrette 1982).

In a deer-wolf system in southern Québec, there was no seasonal variation in size and location of territories for 13 of 17 pack years (Potvin 1988). However, packs in contact with large deer wintering areas generally used that portion of their territory more intensively during winter. Approximately 50% of radio-collared wolves in Algonquin Park, Ontario, undertook seasonal migrations of up to 62 km to a deer wintering area outside of the Park (Forbes and Theberge 1995). A similar phenomenon was observed in Québec by Messier (1985).

The potential effects of different densities of deer and hare on the social and feeding ecology of coyotes in the northeast remain largely unknown. Similarly, there is no consensus as to how prey abundance influences coyote territoriality (Messier and Barrette 1982, Bekoff and Wells 1986, Gese et al. 1988, Mills and Knowlton 1991). Mills and Knowlton (1991) showed that home-ranges were significantly larger on one study site, and a higher incidence of transient coyotes occurred on the other site, during a time of prey scarcity. In Alberta, Canada, coyote home-range sizes were shown to vary directly with group size (Bowen 1982).

This study was designed with the following objectives:

- To determine if the distribution and abundance of whitetailed deer and snowshoe hare can create differences in coyote space-use patterns.
- To investigate the factor(s) responsible for group formation and cohesion by coyotes in the Northeast.

Specifically, I tested the following predictions:

- Annual territory sizes and the occurrence of extraterritorial excursions among eastern coyotes will be negatively correlated with prey density.
- Coyote densities, the incidence of delayed dispersal, and reproductive success will be positively correlated with prey density.
- 3. Coyotes having access to white-tailed deer within their territories during winter will use areas containing concentrations of deer disproportionately more than areas containing few or no deer.
- Territoriality will limit the convergence of coyote family groups on deer wintering areas during winter.
- 5. Winter traveling group size and cohesiveness will be greater for coyotes using deer as a primary food source as opposed to coyotes having access to few or no deer during winter.

## STUDY AREAS

The study was conducted in two distinct areas of Nova Scotia (Fig. 2.1). The Queens County study area (QC) was located in central southwestern Nova Scotia (44° 20'N, 65° 15'W). The study area included the eastern half of Kejimkujik National Park (~200

 $km^2$ ) and approximately 300  $km^2$  of mostly forested land directly to the east of the park. This area was characterized by flat undulating terrain with poor drainage, resulting in many lakes and ponds. Elevation ranged from 100 to 175 m.

The vegetation was characterized by spruce (*Picea spp.*), balsam fir (*Abies balsamea*), hemlock (*Tsuga canadensis*), and heath cover types growing on the flat land between drumlins and eskers, with hardwood and pine (*Pinus spp.*) stands occupying the well drained knolls and ridges. Agricultural fields were concentrated near the few main roads atop drumlins.

The climate of this region was characterized by warm summers typified by 1700 annual degree-days >5°C, and cool winters averaging -5°C in January, with moderate snow fall (Dzikowski et al. 1984). This area does not generally receive accumulations of snow in winter >20 cm and therefore local deer do not typically aggregate in winter yards (MacDonald 1996; Lock 1997).

The Cape Breton study area (CB) was located on Cape Breton Island (45° 45'N, 61° 15'W) and straddled two natural history theme regions (Simmons et al. 1984). The Creignish Mountains represented the Avalon upland (Cape Breton Highlands, CBH) section of the study area, whereas the River Denys Basin represented the Carboniferous lowlands section (Cape Breton Lowlands, CBL).

The Cape Breton study area was centered around the  $24-km^2$ Eden deer wintering area, which typically contained ~200 deer from January through to March. The northern section of the study

area reaches a height of >300 m and slopes sharply at its southern fringe. The mid and upper slopes are mainly undisturbed tolerant hardwood forest of yellow birch (*Betula lutea*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandefolia*), whereas the upland surface is covered with naturally occurring and second growth coniferous stands. Repeated disturbances of the lowland forest have resulted in softwood and intolerant cover types predominating, interspersed with agricultural fields and recent clear cuts. The lowland area slopes gently to the south, with an average elevation of <100 m.

The climate in the Cape Breton area is generally more moist, with approximately the same annual degree days >5°C (1600), as the QC study area (Dzikowski et al. 1984). The higher elevations, lower slopes, and abutting lowland fringe in the northern section of the study area receive 250-300 cm of snow annually, whereas the lowland areas receive 200-250 cm of snow annually (Gates 1975). Similarly, median duration of snow cover varies from 140 days on higher elevations to 130 days on lower elevations (Gates 1975). This contrasts with a median duration of snow cover of only 59 days in the QC area.



Fig. 2.1 Queens County (QC) and Cape Breton (CB) study areas in Nova Scotia, Canada.

#### METHODS

## Deer and hare distribution and abundance

The relative abundance of white-tailed deer was determined within each study area using pellet group counts conducted along approximately 30 1000\*2 m systematic line transects during April and May of each year of study (Neff 1968). Although the use of pellet group counts as an index of deer numbers has been criticized (Fuller 1991, 1992), pellet group counts in Nova Scotia were closely related to the autumn harvest in 1983-1992  $(r^2 = 0.87, P = 0.001, B.R.$  Patterson, unpubl. data).

Regional trends in hare density were estimated using subjective fur harvester abundance rankings (Sabean 1990) obtained from licensed fur harvesters during winters (December to March), from 1990 through 1997. Hare abundance rankings were highly correlated with provincial hare harvest ( $r^2 = 0.83$ , P =0.004, B.R. Patterson, unpubl. data), suggesting a close relationship with actual density.

During spring 1996 and 1997, relative hare density was also estimated using pellet counts within 1-m radius circular plots placed every 100 m along the deer pellet transect lines. Deer and hare density estimates within individual coyote territories were obtained for both study areas during the spring of 1996 and 1997. During those years, each coyote territory contained an average of  $8.5 \pm 0.9$  (SE) transect lines.

Because of limited deer pellet count data in 1992 and 1993, I used provincial pellet count data collected from the region surrounding each study area (Nova Scotia Department of Natural Resources, unpubl. data). These regional areas were climatically and vegetatively similar to the actual study areas. Deer pellet count data were transformed to actual density estimates. I assumed a daily defecation rate of 16 pellet groups  $\cdot$  day<sup>-1</sup>  $\cdot$ deer<sup>-1</sup> and an average date of leaf-fall of 1 November. Although the use of pellet counts to estimate hare densities must be approached with caution (Eaton 1993), for purposes of comparison I used the empirical relationship: hares/ha = (0.061)  $\cdot$  (No. pellets/  $m^2$ ) to estimate the relative density of hares in each territory (Krebs et al. 1987, Eaton 1993). I estimated the density of hares within territories during summer 1996 by averaging the density estimates obtained during the winters 1996 and 1997.

I used the raw pellet group data to estimate the relative summer density of deer in territories within CBH. Because ~60% of the deer wintering in the Eden deer wintering area were seasonal migrants from other areas (MacDonald 1996), I multiplied the winter deer density estimates for the Eden territory by 0.4 to estimate summer densities of deer. All density values are reported ± one standard error (SE). Relative deer and hare pellet densities between study areas and coyote territories were compared using the Kruskal-Wallis one-way ANOVA (Sokal and Rohlf 1995). Significant differences between mean ranks were determined using a non-parametric Tukey-type comparison (Sokal and Rohlf 1995).

While conducting the deer pellet group counts, I tallied all pellet groups deposited after leaf fall (assumed to be 1 November). Considering that most deer in CBH migrated to wintering grounds in CBL by early January (MacDonald 1996), the pellet counts likely overestimated the number of deer actually wintering in CBH between January and March, when the bulk of winter fieldwork was conducted. To provide further information on the relative winter distribution and abundance of deer in CBH and CBL and to define the limits of the Eden deer wintering area, an aerial survey was conducted in mid-February, 1997.

The survey was flown using a Hughes 500 helicopter, in conjunction with the Air Services Division of the NSDNR. The survey crew consisted of one navigator (in the front seat) and two spotters (in the back seat). The study area was divided into a series of north-south grid lines spaced 500 m apart. Grid lines were flown at an altitude of approximately 100 m and an air speed of 60 knots. The navigator asked the spotters for a relative deer abundance score every 500 m based on the following criteria: zero = no sign of deer tracks, one = one or more scattered tracks, but no trails, two = several tracks, with at least one definite trail, three = extensive trail network evident. Based on these data, I generated a density map delineating zones containing similar densities of deer within the CB study area (Fig. 2.2). This information was supplemented with observations made during many (>15) less formal aerial surveys conducted over both study areas during January to March, 1995-1997.

To provide further information on the distribution of both deer and coyotes I conducted ground surveys along a trail network passing through all spring-autumn coyote territories in each study area following fresh snowfalls from December to March, 1996-1997. Each route was approximately 100 km long but the entire routes were rarely completed. All coyote and deer tracks encountered were recorded following the methods of Messier and Barrette (1982). Deer tracks were tallied as belonging to groups of one, two, three, or 4+ deer. Tracks in the 4+ category were assigned a value of five when tallying the total number of tracks observed in each area.

#### Social organization and group dynamics

Fifty-one coyotes representing 14 different family groups were radio-collared and monitored during this study (methodology in Patterson et al. 1999). I classified coyotes as breeding residents, resident associates, juveniles (young of the year), and transients (Messier and Barrette 1982, Person and Hirth 1991, Patterson et al. 1999).

Coyotes were monitored primarily from the ground using handheld antennas and ground-based triangulation (White and Garrott 1990). When coyotes could not be located from the ground, they were relocated from a Hughes 500 helicopter. Most radio-collared coyotes were relocated >5 times/ week from December to March, but <twice/ week from May to November. Overall, telemetry sampling
intensity targeted  $\geq 60$  independent locations from  $\geq 1$  member of each breeding group during both the winter (December to March) and summer (April to October) periods.

# Coyote mortality and reproductive success

I used the software program MICROMORT (Heisey and Fuller 1985) to determine cause-specific mortality and survival rates. I separated the year into two periods; October to April (coinciding with various hunting and trapping seasons) and May to September. The number of radio-days of contact was tallied for each interval and all deaths were recorded. Collared covotes were censored from this analysis following the loss of radiocontact. However, because 94% (n = 32) of all documented mortalities of radio-collared coyotes were human related, I included collared coyotes who had previously been censored but were subsequently recovered at the time of death. Thus, my estimates of human related mortality are maximal. Because no hunting or trapping was allowed within Kejimkujik National Park, survival rate estimates for the QC area included only coyotes residing outside of the Park. I estimated cause-specific mortality and survival rates separately for juvenile, resident adult (included resident associates), and transient (>1 year old) coyotes.

I could not reliably assess coyote recruitment. However, I assumed a family had reproduced if: 1) one or more pups were observed or captured during summer, or 2) breeding adults

exhibited restricted movements and fidelity towards den and/ or resting sites during early summer.

# Dispersal

I considered a covote to have dispersed when it moved >3 km beyond the boundaries of its natal home range and did not return (Harrison 1992b). I defined the date of dispersal as the midpoint between the date of last location in the natal home range and the date when dispersal was first confirmed. I calculated the daily probability of dispersal by modifying Heisey and Fuller's (1985) survival model for dispersal rates (as per Clark et al. 1989, Harrison 1992b). I used the software program MICROMORT (Heisey and Fuller 1985) to calculate the variance associated with each residency rate estimate (where the residency rate = 1 - (dispersal rate)). I compared cumulative residency rates using Z-tests (Heisey and Fuller 1985, Harrison 1992b). I considered three periods of dispersal (after Harrison 1992b): autumn of first year (September to December), winter of first year (January to April), and delayed (>1 year of age). I compared the timing of dispersal by using a contingency table to test if period of departure was independent of study area after calculating expected frequencies of dispersal based on number of coyote-years of telemetry data for each study area.

#### Group formation and cohesion

I determined foraging group sizes by locating the daily resting areas of family groups by radio-telemetry and then investigating these areas on foot or by air. I attempted to do this daily from December through March, 1995-1997, for two to five coyote family groups in each study area. I assessed the effect of primary food source (deer or snowshoe hare) on both mean pack size (the maximum number of socially interacting coyotes within a group, including those members temporally disassociated from the group) and daily traveling group sizes, using one tailed t-tests. I assessed the influence of prey type on group cohesiveness (decrease in traveling group size over the course of the winter) by comparing the mean traveling group sizes observed during the first 10 days of snow-tracking each winter with mean traveling group sizes during the last 10 days of snowtracking for each family group during the same winter. I used a one-tailed 2-test to compare the group cohesiveness between groups using deer or hares as a primary food source in winter.

#### Coyote densities

I estimated coyote densities in each study area by dividing the total number of coyotes known to be present by the total area of the territories of family groups (as per Messier 1985). I determined the ratio of solitary coyotes to territorial family groups from winter track observations. Messier and Barrette (1982) noted that coyote family groups in their study area were actually 1.5 times larger than indicated by track surveys alone due to temporary disassociation of group members. I employed their correction factor to determine the ratios of single, paired and groups of coyotes from actual track counts.

### Spatial distribution and territoriality

Territory size estimates were based on the 95% minimum convex polygon method (MCP; White and Garrott 1990). For comparative purposes, I also calculated home-range sizes using the adaptive (Gauss) kernel method of Worton (1989). In essence, this method gives the probability distribution for the animal being in any part of its home-range at any given time. Independence between successive observations is an implicit assumption with statistical home-range analyses such as the kernel estimator (White and Garrott 1990). Thus, I used only location points separated by a minimum time interval of six hours in the analysis (Harrison and Gilbert 1985, Gese et al. 1990). I used the software program TRACKER (Camponotus AB 1994) for all home-range analyses. I specified a grid spacing of 200 m, a density coefficient of variation of 0.15, and a 30% margin for the kernel analyses. With respect to the calculation of territory size and boundaries, I pooled relocations from all radio-tracked members of a family group. I tested the adequacy of my sample sizes for each estimate using the observation-area curve approach (Bowen 1982, Messier and Barrette 1982).

Influence of prey density and group size on territory size

In most forested areas of northeastern North America, the snowshoe hare and white-tailed deer are the primary prey of coyotes (Parker 1986, Messier et al. 1986, Chapter 3). I calculated an index of prey availability (kg • coyote<sup>-1</sup> • territory<sup>-1</sup>) by multiplying the estimated deer and hare numbers in each territory by the average masses of each, and then dividing this value by the average coyote traveling group size observed during winter in each territory. I determined correlations between annual territory size and prey densities, pack size, and average traveling group size during winter using Spearman's rank correlation (Sokal and Rohlf 1995).

# Territory stability and extra-territorial excursions

I estimated spring - autumn (April to November) and winter (December to March) territory sizes independently. I documented any seasonal shifts in coyote space-use by overlaying the winter relocations of collared coyotes and their group members on a map of the spring- autumn locations. I considered relocations >3 km from established territory boundaries to be excursions and omitted them from the home-range analyses. Coyotes may have been involved in excursions of <3 km but I could not objectively discard these locations because the territorial boundaries themselves were somewhat arbitrary (i.e., determined by the home range analysis). The frequency of excursions was compared between study areas and seasons using *G*-tests (Sokal and Rohlf 1995), using the number of coyote-years of telemetry data to calculate expected frequencies.

## Coyote-deer spatial relationships

Inferences into the spatial relations of radio-collared coyotes and deer in the CB study area were made by comparing the proportion of independent coyote relocations in each deer density

class (zero to three, with zero = no tracks evident, one = some tracks but no trails evident, two = tracks and some trails evident, three = extensive track and trail networks evident, Fig. 2.2) to that expected if coyote movements were uniform within i) each coyote territory, and ii) all territories pooled, using a Chi-square analysis. I considered the CBH and CBL areas to be distinct for both this analysis, and the analysis of excursions, because I felt that the marked differences in winter prey distribution could influence coyote movements.

#### RESULTS

### Deer and hare distribution and abundance

Both deer and hare densities were consistently higher throughout the CB study area than in QC (Tukey test, Q > 3.85, P < 0.001, Tables 2.1, 2.2, Fig. 2.3). Deer densities declined in both study areas between 1992 and 1995 and appeared to have stabilized or increased slightly between 1995 and 1997 (Fig. 2.3a). Abundance rankings suggested that the relative hare density in CB had almost tripled from 1992 through 1997 (Fig. 2.3b). Although hare numbers in QC had also increased significantly during this period ( $r^2 = 0.65$ , P = 0.02), they did so at a considerably slower rate (Fig. 2.3b).

Within the CB study area, hare pellet densities during the winters of 1996 and 1997 were significantly higher in the CBH area (Tukey test, Q = 20.05, P < 0.001, Table 2.1) compared with the CBL area. From May to November, deer appeared to be evenly distributed throughout all study areas. However, there was a

pronounced difference in deer density between CBH and CBL during winter (Tukey test, Q = 12.35, P < 0.001, Table 2.1). In early winter, most deer migrated from the CBH area to wintering grounds in CBL (Fig. 2.2, MacDonald 1996). Because most deer that migrated would have deposited pellets in CBH during November and December, the differences in deer densities among territories from January through March were even more pronounced than indicated by the pellet counts (Fig. 2.2).

During the aerial survey, other tracking flights, and ground tracking, I intensively scanned the CBH area for the presence of deer. During January through March 1996 and 1997, I estimated there were  $\leq 8$  deer remaining in a 40-km<sup>2</sup> area centered on the River Denys Mountain territory (estimated density  $\leq 0.2/km^2$ ). Similarly, I estimated that there were no more than 25 deer within a 40-km<sup>2</sup> area centered on the Skye mountain territory (estimated density  $\leq 0.6/km^2$ ). Overall, I estimated that there were approximately 60 to 80 deer wintering within the 375 km<sup>2</sup> of Highland area surveyed (estimated density 0.16-0.21 deer/km<sup>2</sup>). These deer were not distributed evenly, but were concentrated in small pockets (Fig. 2.2). I adjusted the deer pellet group estimates for the CBH area based on the results of these surveys (Tables 2.1, 2.2).

Overall, the CBH area had high hare densities with only a few scattered pockets of deer during winter. In contrast, the CBL area contained moderate hare densities and relatively high deer densities year round. The QC study area had considerably



Fig. 2.2 Winter distribution of white-tailed deer in the Cape Breton study area, Nova Scotia, as determined by aerial and ground surveys, January to March, 1996-1997. Density classes were based on the following criteria: Absent = no sign of deer tracks, Low = one or more scattered tracks, but no trails, Medium = several tracks, with at least one definite trail, High = extensive trail network evident.

	Study	- x pack	x trav.	100%	95+	95+	Hare	Deer	Prey Eq./	No.
Territory	area	size	group size <sup>1</sup>	MCP	MCP	АК'	pell./m 4	/ km - 1	coyote	reloc,
Keji 97	QC	2	1.9	82.9	61.4	99.5	31.7	1.5	28.5	80
Tupper Lake 97	QC	3	2.3	101.9	95.6	93	29,6	1,6	26.0	110
Tupper lake 96	QC	4	2.7	84,8	74.8	105.3	33.5	2.4	31.6	176
Devonshire 96	QC	4	2.4	57,8	46.5	66	21.0	2,4	36,7	124
Maple Brook 96	CBL	3	2.2	60,8	50,3	55,9	17.8	3.37	63,9	195
Eden 95	CBL	3	2.1	39.2	35	56,3	17.9	4.7	70.4	60
Eden 96	CBL	5	2.5	56,1	50,9	69.4	22.1	9,8	121.7	152
Eden 97	СВЬ	5	2.6	21.3	17.9	23	7.3	9,2	114.9	96
Iona 97	CBL	3	2,5	35,7	29,3	42.1	13.4	1,8	37.3	130
Roseburn 96	Свн	2	1,8	41	34,7	50.5	16,1	0.6	52.9	82
Skye Mt. 96	CBH	4	2.8	51,8	48	58,6	18.7	0,6"	57.7	88
Skye Mt. 97	CBH	5	3,3	64.7	58,5	66,2	21.1	0.6"	31.9	98
RDM 97	СВН	5	3,1	26,7	22.1	30,8	9.8	0,2"	53.0	90

Table 2.1, Summary data for family groups of coyotes in the Cape Breton Highlands (CBH), Cape Breton Lowlands (CBL), and Queens County (QC) study areas. Information was included only for those annual territories that were adequately defined and for which deer and hare density data were available.

<sup>1</sup> Pack size refers the maximum number of socially interacting coyotes within a group, including those members temporally disassociated from the group. Mean traveling group size was based on group sizes observed during snow-tracking.

? MCP refers to the 95% minimum convex polygon method of hume range delineation.

'AK refers to the adaptive kernel method (Worton 1989) of home range delineation.

<sup>4</sup> Based on pellet surveys (Parterson et al.199H).

over-wintering deer in the CB Highlands area. Rates presented here are based on actial and ground surveys and better January, when the bulk of winter field work began. Therefore, pellet counts generally overestimated the density of <sup>6</sup>Although I counted all dear pellets deposited after 1 November, must deer had migrated from the CBH area by early " Prey equivalents per coyote was calculated as the ky of deer and have combined per coyote per territory. represent the actual winter density of deer in this area (Fatlerson et al.1998).

	No. surveys	total km	No. deer	No. deer
Area	completed	surveyed	tracks/100 km	trails/ 100 km
Queens	13	736	81	3.2
CB lowlands	3	228	118	5.3
CB highlands	2	91	8	0

Table 2.2. Number and distribution of deer tracks observed along road and trail networks in the Queens County (QC) and Cape Breton (CB) study areas, winters 1996-1997.

<sup>1</sup>I defined a deer trail as any trail having been traveled by  $\geq 4$  deer.



Fig. 2.3. The relative abundance of (a) white-tailed deer (estimated by pellet group counts) and (b) snowshoe hare (abundance rankings as estimated by fur harvesters) in the Queens County and Cape Breton study areas, 1990-1997.

lower, and more uniform, densities of both deer and hare year round (Figs. 2.3 a, b).

The distribution of deer tracks and trails observed during the track surveys was consistent with the trends indicated by the pellet group surveys (Tables 2.1, 2.2). I adjusted the deer pellet group estimates for the CBH area based on the results of aerial and ground surveys (Tables 2.1, 2.2).

# Social organization and group dynamics

I captured 54 coyotes during this study (51 were radiocollared; one juvenile female was not radio-collared and released, and one adult male and one juvenile female were shot in the traps before I arrived). The 31 coyotes captured in QC consisted of nine breeding adults, 15 juveniles, one non-breeding associate ("helper"), and six transients. The 23 coyotes captured in CB consisted of nine breeding adults, 11 juveniles, one non-breeding associate (later became breeding male), and two transients. The proportion of transients in the two samples was not significantly different (G = 0.50, df = 3, P = 0.92). I obtained >3500 relocations from 51 coyotes representing 14 different family groups and 12 transient or dispersing coyotes.

# Coyote mortality and reproductive success

I recorded 32 mortalities of radio-collared coyotes. Sixteen were killed in snares or foot-hold traps, 10 were shot, three were hit by cars, one was killed by other coyotes, one died of infection resulting from a porcupine quill puncture, and the cause of the final death was unknown. Eighty-eight percent of

mortalities occurred between October and April. Annual survival rates of juvenile, transient (all ages) and territorial adults averaged 52, 19, and 71%, respectively in the CB study area (Table 2.3). Corresponding values for the QC area were 36, 57, and 62%, respectively (Table 2.3). In the CB study area, breeding resident coyotes had significantly higher annual survival rates than transients (Z = 2.70, P = 0.01). Annual survival rates of transient coyotes in QC may have been higher than for transients in CB (Z = -1.66, P = 0.10). There were no other significant differences in survival rates among coyotes from different study areas or social statuses.

Overall, packs in the CB study area successfully reared pups in 83% of attempts (n = 12) vs. 78% of attempts in the QC area (n = 18, Z = -0.13, P = 0.90). Both failed cases in the CB study area were caused by the death (human related) of the breeding female during gestation. In at least two of the four failed cases documented in the QC area, coyote movements during May suggested den attendance but by mid-summer the coyotes were moving extensively without pups.

# Dispersal

Forty-eight percent of juvenile coyotes in the QC area dispersed during their first autumn compared with only 19% in CB (Z = -1.25, P > 0.20, Table 2.4). Seventy-nine and 86% of juvenile coyotes in the QC and CB areas, respectively, had dispersed by the end of the first winter (Z = 0.47, P > 0.20,Table 2.4). I observed two instances of delayed (>1 year)

Table 2.3 Seasonal survival rates of coyotes in the Cape Breton (CB) and Queens County (QC, not including coyotes residing in Kejimkujik National Park) study areas, September 1992 to March 1997. The standard error and number of telemetry days of data for each social class of coyotes are given in parenthesis.

			Study A	rea		
					ŐC:	
		CB				
	May-Sent	OctApril	Annual	May-Sept .	oet April	Annual
Social status	Hay acres					15021 11 0126 0
Juvani les	1.0 (0.20, 119)	0,52 (0.20, 983)	0.52 (0.20, 1102)	1,00 (0, 65)	0. 16 (0. 14, 1414)	
			1121 21 21 2	0 83 10.16. 802)	0.69 (0.15, 1/04)	0.57 (0.16, 2506)
Transients	1.0 (0, 849)	0,19 (0,16, 515)				
Territorial						
	(112 00 01 60 0	0.76 0.10, 3121	(8615, 11, 0, 11, 0, 148)	0.95 (0.05, 304)	0,65 (0.100, 4005)	0.62 (0.10, 2054)
adults						

dispersal in the QC area and one in CB. All three coyotes that exhibited delayed dispersal maintained an association with the breeding pair and appeared to assist in pup rearing. Two of these coyotes remained in their natal territories until 1.5 years of age, while the third coyote remained until the second summer following its birth (>2 year old). Dispersal distances of coyotes averaged 53  $\pm$  12 (SE) km (n = 11) in the CB study area vs. 40  $\pm$  10 km (n = 6) in the QC area. These distances were not significantly different (t = 0.76, df = 15, P = 0.46).

# Group formation and cohesion

The breeding pair formed the nucleus of coyote social groups. Breeding pair members were seldom located apart except during the pup-rearing season when they presumably took turns foraging away from the den or resting sites (Harrison and Gilbert 1985, Patterson et al. 1999). I documented winter pack size for 22 family groups containing one or more radio-collared individuals (two groups of two coyotes, seven groups of three, eight groups of four, and five groups of five).

In cases where the breeding pair traveled alone during winter (n = 2), reproductive failure was evident during the previous summer. Thus, at least one juvenile generally remained with the breeding pair during winter. Packs ( $\geq$ 3 individuals) contained members other than the breeding pair and young of the year in at least three cases. In two cases an unknown individual joined newly formed pairs, and in the remaining instance an

No.     No.     No.     Interval     Linterval     Linterval <thlinterval< th="">     Li</thlinterval<>									св		
No.     Interval     Cumulative     No.       Royotes     coyotes     coyote     Ho.     dispersal				6				No.		Interval	r'neulattve
Coyotes     Coyote     Ho.     dispersal dispersal dispersal     Coyotes     Coyote     Ho.       eriod     monitored <sup>1</sup> days <sup>4</sup> dispersals rate <sup>1</sup> tate <sup>1</sup> tate <sup>1</sup> munitored <sup>1</sup> days     10     567     1     0.19     0.19       Sept 15 pec.     14     925     5     0.48     0.48     10     567     1     0.19     0.19       16 pec April     11     536     4     0.59     0.79     H     410     7     0.85       2     55     2     1.0     1     1     229     1     1.0		No.	No.		Interval	Cumulative			;		disperised
coyotes         coyotes         coyotes         coyotes         coyotes         coyotes         coyotes         coyotes         tate'         tate' <thtate'< th="">         tate'         <thtate'< th=""> <thtate'< th="">         tate'<td></td><td></td><td></td><td></td><td>dispersal</td><td>dispersal</td><td>coyot es</td><td>e toyou</td><td></td><td></td><td></td></thtate'<></thtate'<></thtate'<>					dispersal	dispersal	coyot es	e toyou			
eriod     monitored' days' dispersals rate     late     late       iept15 Dec.     14     925     5     0.48     0.48     10     567     1     0.19     0.19       iept15 Dec.     14     925     5     0.48     0.48     10     7     0.83     0.84       iept15 Dec.     11     536     4     0.59     0.79     H     410     7     0.85       ib DecApril     11     536     2     1.0     1     229     1     1.0		coyotes	coyote			-	month or ed'	days	futs tads to	اطلبأ	1416
app 15 Dec.     14     925     5     0.48     0.48     10     567     1     0.13       dept 15 Dec.     14     925     5     0.48     0.48     0.48     0.48       dept 15 Dec.     14     925     5     0.48     0.48     0.48       dept 15 Dec.     11     536     4     0.59     0.79     H     410     7     0.86       16 Dec April 11     536     4     0.59     0.79     H     410     7     0.86       2     555     2     1.0     1     229     1     1.0	bar i od	monitored <sup>1</sup>	days'	dispersals	rate'	1 41 6				01.0	515
ispt15 Dec.     14     925     5     0.40     0.66       ispt15 Dec.     11     536     4     0.59     0.79     H     410     7     0.43     0.66       16 Dec.     April     11     536     4     0.59     0.79     H     410     7     1.0       16 Dec.     April     11     536     4     0.59     0.79     H     410     7     1.0       16 Dec.     April     11     536     2     1.0     1     229     1     1.0       2     555     2     1.0     1     229     1     1.0	20110				01 0	0.48	10	567	_		
1.0 Le Dec April 11 536 4 0.59 0.79 H 410 7 1.0 1.0 229 1 1.0 229 1 1.0 229 1 1.0 229 1 1.0 229 1 1.0 229 1 1.0 229 1 1.0 229 1 1.0 1 2200 1 1.0 1 2200 1 1.0 1 2200 1 1.0 1 2000 1 1.0 1 1.0 1 1.0 1 1.0 1 1.0 1 1.0 1 1 2000 1 1.0 1.0	tent 15 Dec.	14	925	5	0.40				-	2 H 0	0.86
16 Dec April 11 5.46 1 1.0 1 2.29 1 1.0 2 555 2 1.0 1					0.59	61.0	¥	410			
2 555 2 1.0 1	16 Dec April	11	975	-				956	_		0.1
		2	555	й		1.0	_				

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Dispersal patterns of juvenile coyotes in the Cape Breton and Queens County study areas, Nova Scotia, September 1992 to March 1997. Table 2.4.

Because the final interval is open ended (I considered any dispensal occurring after one yr. to he delayed dispensal) "The cumulative rate considers the total number of coyotes that dispersed by the end of each successive interval. <sup>1</sup>Calculated using the Heisey and Fuller (1985) survival model as modified for dispersal by Clark et al. (1989). <sup>2</sup>Calculated as the total number of days that individual coyotes were monitored during the interval. 'Includes only those coyotes that survived long enough to disperse during each interval. all coyotes dispersed by the end of this interval.

unknown individual accompanied the breeding pair for several weeks during winter despite reproductive failure being evident during the previous summer.

Mean winter traveling group size was similar for packs utilizing deer as a primary winter food source (2.5  $\pm$  0.3 (SD), n = 8) vs. that of groups utilizing primarily snowshoe hare (2.5  $\pm$  0.6, n = 7, Mann Whitney  $U_{9,7} = 26.0$ , P = 0.82). Overall, mean group size declined by an average of 10% over the course of the winter for packs using deer as a primary food source vs. 5% for packs using hares as the primary food source (Z = -0.58, P =0.56).

# Coyote densities

Estimated mid-winter coyote densities ranged from 4.3 to 13.9 coyotes /100 km<sup>2</sup>, and changed markedly during the course of the study (Table 2.5). Although confidence intervals for these estimates can not be computed, a qualitative comparison seems justified because similar methods were employed to obtain all density estimates. Differences in density estimates resulted from changes in territory size, habitat saturation (the proportion of the total landscape in each study area occupied by coyote territories), group size, and the ratio of solitary to group living coyotes (Table 2.5). Estimated densities declined >50% in the QC area from winter 1993 through 1997. I estimated density in CB during 1996 and 1997 only but recorded a substantial increase (88%) due to the formation of two new territories and an apparent increase in fecundity and juvenile survival of resident coyotes.

# Spatial distribution and territoriality

Coyote family-group members shared common home-ranges and based on the presence of non-overlapping, adjacent home-ranges, coyotes in both study areas were territorial (Figs. 2.4, 2.5). Twenty-four annual territories (14 in QC, 10 in CB) were adequately defined during this study.

#### Influence of prey density on territory size

Mean annual territory sizes (95% MCP) were significantly larger in QC (51.2 ± 4.4 (SE) km<sup>2</sup>) relative to CB (36.5 ± 3.7 km<sup>2</sup>,  $U_{14,10} = 86.5$ , P = 0.03, Table 2.1). Both 95% ( $r_s = -0.62$ , P =0.03) and 100% MCP ( $r_s = -0.71$ , P = 0.009), and the 95% adaptive kernel ( $r_s = -0.61$ , P = 0.03) home-range sizes decreased significantly with prey density, but not winter pack size or traveling group size ( $r_s < 0.19$ , P > 0.54) (Table 2.1). The size of the areas used during winter was significantly larger than the areas used during summer (46.5 ± 6.7 (SE) km<sup>2</sup> vs. 34.6 ± 7.0 km<sup>2</sup>, t = 5.4, P = 0.002, n = 7 adequately defined summer-winter ranges).

# Territory stability and extra-territorial excursions

Territories were generally very stable with most territories maintaining the same approximate boundaries (and surviving breeding pair members) for the duration of monitoring. At least two territories in QC remained stable from autumn 1992

Stu	ıdy Area∕	group	solitary	x terr. <sup>2</sup>	Hab. <sup>3</sup>		No. terr./	Winter
per	iod	size	coyotes	size	sat.	Fec.	100 km <sup>2</sup>	density
QC	1993-94	4.0	3.0	60	0.8	5.1	1.33	9.3
QC	1996	3.5	3.0	58	0.6	5.0	1.03	6.7
QC	1997	2.8	1.5	75	0.75	4.9	1.0	4.3
СВ	1996	3.5	2.3	56	0.7	5.5	1.26	7.4
СВ	1997	4.5	3.0	43	0.8	6.1	1.85	13.9

x winter No.

Table 2.5. Mid-winter density estimates, and related information, for coyotes in the Queens County (QC) and Cape Breton (CB) study areas, Nova Scotia.

<sup>1</sup> Based on the ratio of solitary to group living coyotes observed during winter track surveys. The ratio was adjusted using the correction factor presented by Messier and Barrette (1982) to account for temporary disassociation of group members.

<sup>1</sup> Territory size estimates were based on the composite 95% MCP home ranges of all radio-collared group members.

<sup>1</sup> Habitat saturation was estimated as the proportion of the total landscape in each study area occupied by coyote territories.

<sup>4</sup> Fecundity was measured as the number of placental scars/ pregnant female, data in Brannen (1997).



Fig. 2.4. Spatial distribution of radio-collared coyotes in the Queens County Study Area, Nova Scotia, September 1992 to March 1997.



Fig. 2.5. Spatial distribution of radio-collared coyotes in the Cape Breton Study Area, Nova Scotia, March 1994 - 1997.

through to the completion of the study in March 1997. I monitored coyotes in QC for 25 "territory years" (five calendar years) and noted one permanent (Fig. 2.4) and one short-term territory shift. In the first instance, the Tupper Lake pack shifted its activities to an adjacent area to the northwest of the former territory boundaries during February 1996. This group maintained the new territory until the end of this study. I noted several deer kills by this group in the new area in March 1996, thus the move may have been related to prey availability.

In the second case, the breeding female and pups from the Peskowesk pack were located in the Grassy Lake (adjacent) territory for all of 10 relocations obtained from late August through early October 1995. I was unable to determine any association with members of the Grassy Lake pack, and the Peskowesk group returned to their native territory by mid-October, 1995. Thus, this movement may be considered an extended excursion.

In the CB study area, I monitored coyotes for 22 "territory years" (Three calendar years) and did not record any shifts in the area used by breeding groups. However, in early January 1996, I noted that the breeding male from the Eden pack (AM8) was injured and limping (cause undetermined). By mid-February, the limp was very pronounced and this coyote was rarely located within the boundaries of his former territory (Fig. 2.5). By early May, this coyote had established a new territory (Iona territory, Figs. 2.5, 2.6), apparently with a new mate, to the

northwest of the range of the Eden Pack. Throughout this time, the territory of the Eden pack remained stable and the Eden group successfully reared a litter of pups during the summer of 1996.

The incidence of extra-territorial excursions was not uniform among study areas (G = 13.3, df = 2, P = 0.001). The frequency of excursions was highest in the CBH area and lowest in the CBL area (Table 2.6, Figs. 2.7, 2.8). In QC and CBL, excursions appeared to occur more frequently during summer, but the differences in seasonal frequency were not significant (CBL; G = 0.48, df = 1, P = 0.49; QC; G = 1.1, df = 1, P = 0.29; Table 2.6). Excursions occurred more frequently during winter in CBH (G = 7.5, df = 1, P = 0.006, Table 2.6). Excursions were generally <10 km and rarely lasted more than three days (Figs. 2.7, 2.8).

# Coyote-deer spatial relationships

Overall, coyotes did not use areas of higher deer density any more than would be expected if they used all areas within their territories equally (Table 2.7). Coyotes in the CBL area (excluding the Eden territory that was composed primarily of the Eden deer wintering area) used areas classified as containing few or no deer proportionately more than expected ( $\chi^2 = 10.4$ , P =0.02; Table 2.7).

#### DISCUSSION

Harrison (1992a, 1992b) stated that the relative distribution, abundance, and vulnerability of various prey items



Fig. 2.6. Space-use patterns of breeding adult male AM8, in the Cape Breton study area, Nova Scotia, September 1994 to March 1997.

Table 2.6. The frequency of excursions (movements >3 km from an established territory) by territorial coyotes in the Queens County (QC), Cape Breton Lowlands (CBL), and Highlands (CBH) study areas, Nova Scotia, 1994-1997. The number of coyote-seasons of telemetry data for each season was calculated by dividing the total number of radio-contact days for all group living coyotes in each study area by the number of days in each season.

	May-November		December-Apr	il	Annual		
Study	No. coyote-	No.	No. coyote	No.	No. coyate	No.	
Area	seasons	Excur.	seasons	Excur.	seasons	Excur.	
QC	23.5	7	31.1	5	27.3	12	
CBL	9.6	2	10.9	1	10.2	3	
СВН	5.6	L	6.3	10	5.9	11	



Fig. 2.7. Depiction of the 9 extraterritorial excursions made by territorial coyotes in the Queens County study area, Nova Scotia. Dates of excursions were as follows: a, 1 Oct 96; b, 30 Aug 96; c, 23 Aug 96; d, 6 Jan 95; e, 30 Aug 95; f, 10 Nov 94; g, 1 Oct 95; h, 16 Feb 96; i, 13 Feb 96. Excursions are presented as the minimum straight-line distances.



Fig. 2.8. Depiction of the 14 extraterritorial excursions made by territorial coyotes in the Cape Breton study area, Nova Scotia. Dates of excursions were as follows: a, 18 Mar 97; b, 20 Mar 97; c, 10 Jan 96; d, 12 Feb 97; e, 29 Nov 96; f, 29 Jan 97; g, 2 Mar 97; h, 26 Sept 94; i, 21 Mar 97; j, 8-10 Mar 97; k, 13-14 Mar 97; l, 17 Mar 96; m, 22-23 Mar 96; and n, 1 May 96. Excursions are presented as the minimum straightline distances. probably represent the dominant forces influencing the social system of coyotes in a particular ecosystem. My results are consistent with this view as territory size, autumn dispersal rates, and population densities were influenced by prey abundance.

Impact of human exploitation on coyote social organization

Survival rates documented during this study were similar to those reported for coyotes in many areas within the historic range of coyotes (see Parker 1995 for a review). As documented in this study, human related activities generally account for the majority of coyote mortality (Pyrah 1984, Windberg et al. 1985, Gese et al. 1989), but in areas where coyotes are lightly exploited, natural mortality can be elevated resulting in survival rates similar to those documented during this study (Windberg 1995). These apparent density-dependent changes in natural mortality suggest that human exploitation of coyotes may be largely compensatory. Higher mortality among juvenile and transient coyotes has also been reported elsewhere (Bekoff and Wells 1986, Gese et al. 1989, Harrison 1992b) and is likely caused by movements into less familiar, "low security" habitats (Pyrah 1984).

Although a substantial proportion of breeding adults was killed every year during the study (Table 2.3), the remaining breeding pair member typically remated within a few weeks (as evidenced by track observations, howling, or subsequent captures). I documented only two instances were human

Table 2.7. Spatial distribution of coyotes in the Cape Breton Lowlands (CBL) and Cape Breton Highlands (CBH) study areas, and Eden deer wintering area (DWA), Nova Scotia, during winter vs. expected distribution assuming coyotes used all deer density classes within their territories equally. Deer density classes were determined by aerial and ground surveys. 0 = no tracks evident, 1 = some tracks but no trails evident, 2 = tracks and some trails evident, 3 = extensive track and trail networks evident (Chapter 3).

	No. locations										
Class:	0		1		2		3				
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	x	P	
Eden DWA	0	0	78	67	67	76	51	52	2.9	0.41	
CBL	94	73	83	104	22	24	2	0	10.4	0.02	
СВН	121	130	27	22	11	7	0	0	4.1	0.26	
Total	215	203	188	193	100	107	53	52	1.3	0.73	

exploitation prevented pup-rearing during 30 "pack reproductive seasons". Brundige (1993) estimated that sustained harvests of 55% would be required to cause significant declines in the population growth rate of eastern coyotes. Although survival among juvenile and transient adult covotes was low (0.19-0.52), survival rates of breeding adult coyotes monitored during this study were considerably higher (0.62 - 0.71; Table 2.3). Most human related mortality occurred near a road or trail, thus remote areas and/ or reserves likely serve as "sources", providing a continued influx of coyotes into areas receiving heavy harvest pressure (Lidicker 1962, Gese et al. 1989). It is unlikely that widespread harvest of covotes in Nova Scotia could ever be sufficient to effect significant declines in coyote numbers. However, given the influence of prey density on coyote numbers, intense harvests during years when coyote numbers are already declining may be effective in reducing coyote numbers.

# Coyote dispersal and group formation

Relative to the CB study area, autumn dispersal rates were higher in QC (48 vs. 19% of radio-collared juvenile coyotes in the QC and CB areas, respectively) where prey densities were considerably lower (Tables 2.1, 2.2). Low prey densities may reduce the occurrence of delayed dispersal (and subsequent pack formation) by eastern coyotes, as suggested by Harrison (1992b). Mean distance of dispersal by juvenile coyotes in Maine (102 km) was considerably larger than the mean distances I observed. This may be due in part to the fact that many of the coyotes monitored

during this study were killed shortly after beginning their dispersal. It is also possible that territory vacancy was lower during the Maine study.

No radio-collared coyotes dispersed between 15 December and 31 January, similar to findings of Harrison (1992b) and Bowen (1982) for coyotes in Maine and Alberta, respectively. Thus, excepting cases where reproductive failure was evident, most family groups had the opportunity to travel in packs during winter. I could not measure the number of pups born in each specific territory, but fecundity of coyotes on Cape Breton Island and southwestern Nova Scotia (representative of QC) averaged 6.1  $\pm$  3.1 (SD), and 4.9  $\pm$  3.0 pups/ female, respectively, during this study (Brannen 1997). Accounting for autumn dispersal rates and juvenile survival through early winter, I estimated that approximately 1.9 and 4.0 pups/ territory should have been available to travel with the breeding pair in early winter in the QC and CB study areas, respectively. However, not all juveniles remaining in their natal territory associate with their parents during winter (Messier and Barrette 1982), and I could not account for juvenile mortality during early summer. Thus, the small group sizes I observed during winter were expected.

Human exploitation strongly contributed to the decrement of pack size in some cases but I could not monitor human related mortality of non-collared coyotes in all groups. I was aware of cases where at least three members were removed from individual

packs during autumn and winter within both study areas. Group dynamics may have been different in Kejimkujik National Park, where human exploitation did not affect coyotes. During the winters of 1993 and 1994, the average traveling group size among three packs within Kejimkujik National Park actually increased an average of 32% from December through March. The only instances of breeding pairs traveling alone throughout the winter resulted from reproductive failure. Thus, I believe that group living during winter is typical of eastern coyotes.

In at least two of the four failed cases of reproduction in the QC area, coyote movements during May suggested den attendance, but by mid-summer the coyotes were moving extensively without pups. I suspect that in these cases the entire litters were lost, likely owing to malnutrition. In the Keji territory, old age of the breeding female (AF1) may also have contributed to low reproductive success. This coyote was estimated to be five or six years old when captured in September 1992. She successfully reared litters during 1992-1994, but not during 1995 or 1996.

#### Group cohesiveness

The occurrence and cohesiveness of coyote packs during winter was independent of prey size, suggesting that cooperative foraging was not the primary factor influencing group cohesion. Although groups of coyotes examined during this study relied on deer as a food source (Chapter 3), and group living coyotes killed deer at a higher rate than pairs or solitary coyotes (Chapter 4), I believe that this was an effect rather than a cause: i.e. groups formed for other reasons and were making use of the most appropriate prey size to maintain cohesion (Messier and Barrette 1982, Andelt 1985).

Group formation resulting from delayed dispersal offers benefits to both the breeding pair and the remaining juvenile coyotes. Juveniles are safer within their natal territories (as evidenced by higher mortality of dispersing and transient coyotes relative to residents), and likely learn hunting techniques from their parents (Andelt 1985, Schmidt and Mech 1997). Parents improve their genetic fitness in at least two respects. First, by allowing juveniles to remain in their territories to learn and mature, they improve the chances of the juveniles surviving and establishing their own territories when they do disperse (Andelt 1985). Increased food competition due to larger group sizes may be offset by greater efficiency at killing deer (Messier et al. 1986, Parker and Maxwell 1989, Brundige 1993). Secondly, juveniles which delay dispersal beyond one year may increase the survival of subsequent litters by providing additional food during a season when food is scarce and the movements of nursing females are limited (Harrison and Gilbert 1985, Brundige 1993, Patterson et al. 1999).

# Coyote densities

Few researchers have estimated densities of eastern coyotes. However, it is generally accepted that they are considerably lower than in many areas within the historic range

of coyotes (Harrison 1992a, Parker 1995). I documented considerable changes in coyote numbers during the study. In the southwest Yukon, coyote abundance increased 600% in three years in response to increasing hare numbers (O'Donoghue et al. 1997). The subsequent decline in coyote abundance following the crash in hare numbers was equally rapid and severe and coyote numbers tracked hare numbers with a delay of one year (O'Donoghue et al. 1997). Coyote numbers were also closely linked to changes in snowshoe hare abundance in Alberta (Todd and Keith 1983).

I suggest that prey abundance and human harvest were the primary factors affecting coyote densities during this study. In QC, coyote numbers continued to decline following a crash in deer numbers during the late 1980s and early 1990s. Hare numbers in QC changed little during this time (Chapter 3). Two consecutive severe winters (1993 and 1994) probably sustained relatively high coyote numbers despite low prey abundance by increasing deer vulnerability (Patterson 1994, Patterson et al. 1998). Low prey abundance, mild winters (low deer vulnerability), and increased coyote harvests in southwestern Nova Scotia (data in Brannen 1997) probably all contributed to recent declines in coyote numbers in this area. In the CB study area, rapidly increasing hare numbers (Chapter 3), and to a lesser degree reduced coyote harvests (data in Brannen 1997), appear to be responsible for the recent increase in coyote numbers.

A demographic analysis of 1,191 coyotes harvested in Nova Scotia during the 1996-97 season (Brannen 1997) provides further

support for the trends in coyote density I observed. Assuming that all (or at least an equal proportion across the province) territorial, breeding females were impregnated, there was a higher proportion of non-breeding coyotes in Cape Breton vs. southwestern Nova Scotia (Brannen 1997). Given the higher density of breeding territories in the CB area, this would suggest that CB had not only a higher density of breeding coyotes, but also a disproportionately higher density of nonbreeding coyotes. Given the relatively high number of solitary coyote tracks observed during winter 1997 (Table 2.5), juvenile survival may also have increased with prey abundance.

Because a given landscape can only support a finite number of breeding territories, territoriality generally results in a Type II numerical response among territorial predators (Messier 1994). In CB, there appeared to be little room for additional breeding territories following winter 1997. Snowshoe hare numbers were likely near peak levels during this winter and may have declined in subsequent years (Nova Scotia Department of Natural Resources, unpubl. data). Thus, coyote densities observed during winter 1997 in CB were likely near maximal for eastern coyotes in Nova Scotia.

# Spatial distribution and territoriality

Coyotes used a smaller portion of their territories during summer, despite the fact that summer is generally considered to be the most food-restricted time of year for coyotes (Messier and Barrette 1982, Poulle et al. 1995). Restrictions imposed by
immobile pups probably limit the distance parents forage from the den or resting sites during pup-rearing (Harrison and Gilbert 1985). Despite the smaller home-range sizes exhibited during summer, daily distances traveled by breeding males during pup rearing were greater than those traveled by coyotes at other times of the year (Patterson et al. 1999) suggesting a more intensive use of the home range during summer.

### Coyote-deer spatial relationships

Coyotes did not use areas containing higher densities of deer proportionately more than expected. In CBL, coyotes actually used areas of low deer density proportionately more than expected. This may be related to the higher vulnerability of deer to predation in low-density areas (Messier and Barrette 1985, Patterson 1999). Messier and Barrette (1985) reported reduced coyote predation on deer within core wintering areas as opposed to deer outside or at the periphery of wintering areas. They attributed this reduction to increased deer mobility due to a well-established network of trails within deer wintering areas, and to the fact that concentrations of deer facilitate earlier detection of predators. Nelson and Mech (1986) also reported that the vulnerability of deer to predation increased with increasing snow depths.

#### Territoriality and extra-territorial excursions

It was difficult to assess the motivating factors for excursions, but in CB coyotes generally traveled to areas where

deer were available (Figs. 2.2, 2.7), often trespassing into neighboring territories. Coyotes in CBH had access to the highest hare densities observed during this study (Table 2.1), and appeared to be the least food restricted of all coyotes observed during this study (Chapter 6). Surprisingly, they exhibited the highest frequency of excursions during winter. Analysis of coyote feeding habits suggested that coyotes in CBH preferred deer to hares despite high hare abundance (Chapter 3). Snowshoe hares are relatively low in fat compared to white-tailed deer (Litviatis and Mautz 1980). Thus, the high incidence of excursions by coyotes in CBH during late winter may have been related to the seeking of a higher quality (more fat) diet during pregnancy by breeding female coyotes.

Alternatively, the relatively high rate of excursions during winter in CBH may have resulted from a reduction in territorial behavior due to abundant food resources. Given the relatively low density of coyotes in much of northeastern North America, the chance of an intruder encountering a resident coyote within its territory is relatively low. Therefore, to maintain a high risk of injury for the intruder and enforce obedience to territorial markers such as scent marks, coyotes must demonstrate a high degree of aggressiveness during encounters with conspecifics (Messier and Barrette 1982).

A radio-collared adult female coyote in the QC study area was killed by an unmarked group of coyotes within her territory in January 1996. Further, I observed coyotes investigating the carcasses of three non-collared coyotes in CB during snowtracking. Although the cause of death of these coyotes was unknown, the low incidence of natural mortality suggests that death due to inter-pack strife was likely. Okoniewski (1982) documented a resident pack killing a solitary adult male in the Adirondack Mountains of New York. The short duration of excursions probably reflected the risk of both aggressive encounters while trespassing, and of losing a territory to other coyotes while absent. The relatively low incidence and short duration of excursions suggests that territorial behaviour prevents coyotes from concentrating in deer wintering areas and helps keep the coyote: deer ratio relatively low.

I believe that territoriality and group formation by eastern coyotes serve to enhance the genetic fitness of the breeding pair by improving the survival of immobile pups during summer, and of juveniles prior to dispersal. Thus, the maintenance of an exclusive territory should be most critical during the pup rearing period. I am not aware of any cases of non-territorial eastern coyotes raising pups. However, Messier and Barrette (1982) reported that solitary coyotes in Québec had good fat reserves and appeared to be as healthy as group living coyotes. The reason that solitary coyotes (transients) do not attempt to maintain territories is probably because they are not necessary for non-breeding coyotes (as opposed to the idea that they simply can not defend a territory against pairs or groups), as suggested by Messier and Barrette (1982). Although, the size and distribution of food resources may strengthen the tendencies towards a given social system, I believe that increased reproductive fitness, and inclusive fitness for non-dispersing juveniles, represent the ultimate factors influencing group formation and cohesion among eastern coyotes.

# 3. PREY SWITCHING AND THE FEEDING HABITS OF EASTERN COYOTES IN RELATION TO SNOWSHOE HARE AND WHITE-TAILED DEER DENSITIES

# INTRODUCTION

Successful exploitation of a fluctuating food base requires plasticity with regards to foraging behavior, space use patterns, and even social organization of the predator (Bergerud 1983, Peek 1986). Throughout North America, the coyote exhibits such plasticity (Parker 1995). The ability of the coyote to respond to changing prey availability (Clark 1972, Parker 1986, Todd and Keith 1983) has been implicated, along with landscape changes, in its recent and successful expansion throughout northeastern North America (Moore and Parker 1992, Samson and Crête 1997).

Throughout most of the Northeast, the coyote must contend with lower prey diversity and abundance relative to their western counterparts (Harrison 1992a, Parker 1995, Patterson 1995). As a result, two prey species, the white-tailed deer and the snowshoe hare have become the staple prey of the eastern coyote (Messier et al. 1986, Parker 1986, Patterson 1994, 1995). Larger body size (Larivière and Crête 1993, Parker 1995) and a greater tendency to hunt in extended family groups during winter (Messier and Barrette 1982, Harrison 1992a) have both been related to the high use of white-tailed deer by eastern coyotes (Messier et al. 1986, Harrison 1992a, Larivière and Crête 1993).

In northern New Brunswick, Parker (1986) found that snowshoe hare was the most important prey species of coyotes,

with hare remains varying seasonally from 50 to 80% occurrence in scats. Alternatively, several studies conducted in the Northeast (Messier et al. 1986, Brundige 1993, Poulle et al. 1993, Patterson 1995) have reported ≥80% occurrence of white-tailed deer in covote scats collected during winter. The occurrence of deer in coyote scats is typically at its lowest in the autumn (10-30 % depending on locality). Raspberries (Rubus spp.), blueberries (Vaccinium spp.), and other vegetation are also important food items, where available, during their respective seasons (Harrison and Harrison 1984, Parker 1986, Samson and Crête 1997). Harrison and Harrison (1984) and Knowlton and Stoddart (1992) suggested that when readily available, fruits could act as buffer species and thereby reduce predation on deer during summer. Conversely, Samson and Crête (1997) suggested that the high use of fruits by coyotes during summer in the Gaspe Peninsula, Québec, was due to the scarcity of mammalian prey.

The functional response of a predator describes how the number of a particular prey species eaten per predator changes with prey density (Holling 1959). A Type III functional response occurs where the number of prey eaten per predator increases slowly at low prey densities, rapidly at intermediate prey densities, and then levels off at high prey densities, producing an S shaped curve. Often, this S shaped curve is attributed to prey switching (Murdoch 1969, Akre and Johnson 1979), whereby the focus of a predator is switched from one prey type to another only after the "new" prey species increases beyond some threshold

density. Prey switching may have a potentially stabilizing effect on prey populations because the proportion of the "new" prey type taken by predators increases with prey abundance (Murdoch 1969, Hughes and Croy 1993).

The alternate prey hypothesis (Keith 1974, Angelstam et al. 1984) describes a shift in predation pressure on various prey species, whereby predators switch to alternate prey when numbers of their primary prey are low. In Alberta, snowshoe hare biomass in the diet of coyotes changed from 0 to 77% between 1964 and 1975, largely as a result of changing hare density  $(r^2 = 0.94;$ Todd et al. 1981). In northern New Brunswick, coyotes switched from feeding primarily on hares during early winter to deer in February and March, despite no apparent decrease in hare abundance (Parker and Maxwell 1989). An increase in deer vulnerability resulting from dense snow cover was cited as a principal cause of this switch (see also Messier and Barrette 1985). Parker (1986) suggested that in years of hare scarcity, coyote productivity would decline and predation upon white-tailed deer would increase, especially upon young fawns in early summer and within deer vards in mid and late winter.

Herein, I document changes in coyote feeding habits in relation to the relative densities of white-tailed deer and snowshoe hares in two ecosystems in Nova Scotia from 1992 to 1997. I hypothesized that coyotes would switch from deer to hares as hare density increased, as predicted by the Alternate Prey Hypothesis (Keith 1974, Angelstam et al. 1984).

#### METHODS

Scat analysis

Scats were collected at regular time intervals, generally every two weeks or more often in frequently travelled areas, from July 1992 through March 1997 in the QC study area and from January 1995 through March 1997 in CB. Scats were also collected opportunistically, while snowtracking radio-collared coyotes in both study areas during winter. Based on segment diameter and length (Murie 1954), and associated tracks and scrapes, I discarded any scats that could not be positively identified as being from coyote.

Scats were washed in nylon stockings after being boiled for at least ten minutes to kill any bacteria, parasites, or eggs. The contents of each scat were separated by species, and identified by comparison with a reference collection. Unknown hair samples were identified by macrofeatures and microscopic identification of cuticular scale patterns using the method outlined by Adorjan and Kolenosky (1969). Because of the high possibility for error in small mammals and song birds, these prey species were placed in the general categories of small mammals and birds. The relative volume of each prey item in each scat was estimated to the nearest 5%. Items occurring in trace amounts were assigned a value of 5%. I summed the percent-values to calculate the number of whole scat units associated with each prey item. These frequency data were used in the statistical analyses. I divided the year into five seasons for the analyses

(April-May, June-July, Aug.- 15 Sept., 16 Sept.-Nov., Dec.-March).

Although physical evidence such as hooves, teeth, and spotted fur positively identified the remains of newborn fawns in some summer scats, I did not always distinguish between the hair of fawns and adults using cuticular scale patterns. I therefore attributed 50% of the unclassified deer hair (~40% of summer deer hair was unclassified) in scats from June through August, as belonging to fawns. Because the hair of fawn and adult deer is difficult to distinguish after August, the ratio of fawns: adults consumed by coyotes from September through May was estimated from the proportion of fawns in the total sample of deer killed by coyotes during winter in each study area (as observed during winter snowtracking; see Chapters 4, 5).

Although scat analyses receive widespread use as a means of determining the diet of carnivores, the degree to which the relative frequencies of identifiable remains represent the proportion of prey types eaten is usually unknown (Weaver 1993). Problems relating to incomplete consumption, differential prey digestibility, and the fact that a single prey item may be expressed in several scats have been discussed in the literature (Andelt 1985, Weaver 1993). Weaver (1993) concluded that, based on scat analysis alone, small prey are over represented in biomass and under-represented in numbers, compared with larger prey species. To compensate for this shortcoming, and to allow a more realistic analysis of actual prey consumption, I converted the percent volume of prey items in scats to percent biomass ingested following the methods of Weaver (1993). Fruit percentages were halved after Andelt and Andelt (1984). I subsequently converted this into the relative number of deer and hares consumed using the average weight of both adult and fawn deer, and snowshoe hares, during each time period (adult deer 68 kg - Banfield 1987, fawn deer 3.5 kg at birth - Mathews 1989 and an assumed weight gain of 252g /day from birth through autumn - Brundige 1993, and snowshoe hare 1.4 kg - Litviatis and Mautz 1980). I assumed that adult and fawn deer contain 80% and 90% edible biomass, respectively. Coyotes generally ate snowshoe hares whole (Patterson 1995).

The frequencies of major food items in the diet of coyotes were compared among study areas and periods, using a Chi-square analysis (Sokal and Rohlf 1995). In QC, the collection of scats spanned five years. Preliminary analyses indicated that the diet of coyotes had changed considerably within this area after January 1995 ( $X^2$ =129, P < 0.001, df = 2). Therefore, I divided the scats collected in QC into two distinct periods: July 1992-December 1994 (Q1) and January 1995-March 1997 (Q2).

To examine the relationship between mammalian prey density and fruit consumption, I correlated the percentage of scat volume composed of fruits from August to September, with the relative density of deer and hares in each territory.

Coyote functional response and evidence for prey switching

I calculated the number of adult deer, fawns, and hares eaten per coyote during the December to March and June-July time intervals using the following formula:

$$N_{1} = (T) * (B_{1}) / 100 * (C)$$

$$(K_{1}) * (M_{1})$$
(3.1)

where:  $N_1$  = the number of prey item no. one eaten, T = the number of days in the interval,  $B_1/100$  = the fraction of total biomass consumed specific to prey item no. 1, C = the daily caloric requirement (kcal) of an average coyote,  $K_1$  = the energetic content (kcal/kg) of prey item no. 1,  $M_1$  = the edible biomass (kg) of prey item no. 1. The daily caloric requirement of coyotes was calculated following Pekins (1992) assuming that:

- 1. the average weight of adult coyotes = 16 kg (Sabean
  1993b)
- 2. coyotes spend 45 to 58% of the time active, depending on season (Patterson et al. 1999)
- 3. coyotes travel from 14.3 to 24.8 km/ day, depending on season (Patterson et al. 1999)

The energetic content of fresh deer and hare meat from Litviatis and Mautz (1980) was used in all calculations.

Pearson's partial correlations (Sokal and Rohlf 1995) were used to examine the contributions of the relative densities of deer and hare to the number of each prey consumed per coyote, within each territory during winter. Partial correlations were also used to examine the influence of deer and hare density on deer consumption during June - July, the period when predation on fawns is greatest (Harrison and Harrison 1984). Only territories for which I analyzed >20 scats during each interval were included in this analysis.

I determined the functional response by fitting all significant (P < 0.05) correlations using both linear (representative of a Type I response) and hyperbolic Michaelis-Menton functions (the mathematical equivalent to Holling's (1959) disk equation, representative of a Type II response, Real 1977). The Michaelis-Menton function takes the form y = ax/(b + x), where y is the per capita killing rate, x is prey density, a is the asymptotic killing rate when predators are fully satiated, and b is the prey density at half of the maximum killing rate. A Type III functional response can be described simply by adding an exponent to the variable x (Real 1977). All three types of equations were fitted to the data using a Marquardt-Levenberg algorithm (a least-squares technique, Press et al. 1986). Model fitting was conducted with the software program SPSS 6.1 (SPSS statistical software, SPSS Inc., Chicago, IL.). I used F-tests to assess whether a Type II functional response (reduced model) fit each data set as well as a Type III (full model; Marshal and Boutin 1999). A significant improvement in fit by a Type III functional response relative to a Type II response (see also chapter 5) was considered indicative of prey switching.

Prey switching has also been assessed by comparing the relative use versus availability of alternate prey types

(Greenwood and Elton 1979, Hughes and Croy 1993). Assuming that e<sub>1</sub> and e<sub>2</sub> are the numbers of two prey types eaten from a population of  $A_1$  and  $A_2$  available, the ratio  $e_1A_2/e_2A_1$  should remain constant as  $A_1/A_2$  changes, if prey are consumed nonselectively and in proportion to their abundance (Greenwood and Elton 1979). I calculated the selectivity index  $e_1A_2/e_2A_1$  for territories in which >20 scats were analyzed during the December - March and June-July time intervals. A<sub>1</sub> and e<sub>1</sub> represented the numbers of hares available and eaten, respectively, and  $A_2$  and  $e_1$ represented the number of deer available and eaten, respectively. During winter, all deer were considered, but during June and July, only fawns were taken into consideration. Significant departures of the selectivity index from unity was determined by a Student's t test (Sokal and Rohlf 1995) or the Mann-Whitney rank sum test (Sokal and Rohlf 1995) when the test for normality failed. Values significantly below unity indicated disproportionately high use of deer and values above unity indicated disproportionately high use of hare.

I used Spearman's rank correlation (Greenwood and Elton 1979, Sokal and Rohlf 1995) to determine whether the selectivity index changed as a function of  $A_1/A_2$ . I considered a significant positive correlation between the selectivity index and the hare: deer abundance ratio ( $A_1/A_2$ ) to be indicative of prey switching. Because it should be easier for coyotes to capture hares than deer, I hypothesized that coyotes would respond primarily to changes in hare abundance. Specifically, I hypothesized that relative to the availability of both deer and hare, coyotes would eat proportionately more deer than hares when the hare: deer abundance ratio was low and proportionately more hares than deer (switch to hare) as the ratio increased.

### RESULTS

#### Food habits

I identified the contents of 2,443 coyote scats collected during all months of the year (Table 3.1). Coyotes consumed a minimum of 35 different prey items (18 wild mammals, three reptiles, one amphibian, four birds, domestic livestock, cats and dogs, six species of wild berries, and other vegetation). Diet was most diverse during late summer and most restricted during winter, reflecting seasonal changes in the availability and abundance of common food items (Table 3.1).

Together, deer and hare represented from 66% (Q1) to 81% (CBL) of the total annual scat volume (Table 3.1). Other important food items included small mammals (6.5-12% of the total annual scat volume) and fruits (primarily raspberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), and huckleberries (*Gaylussacia spp.*))during late summer through early autumn (5.6-30% of scat volume). Deer was the single most important food item in Q1 (53% of the total annual scat volume, 63% of the biomass originally consumed), whereas deer and hare each

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Domestic livestock' 6,8 6,0 0.0 4.3

Fruits	0,0	0.0	1.4	0.0	2.2	1,0	05. <b>4</b>	0.5	20	26	5.2	15	14	6.0	4,9	0.0	0.2	1.1	1.7	0,0	9,8	11	.',0	1,6
Misc, items	4.5	2.8	7.5	1.6	8.6	2.8	3.0	5.3	5,6	3.7	0.5	3.2	4.1	2,5	4.4	4.2	1.1	2.6	6.5	2.3	5,9	3.0	4.8	1,0
No, ingested pe	r co	yote	ə <sup>6</sup>																					
Adult deer	0.9	0,9	0.1	0.3	0.5	0,5	0.4	0.5	0.3	0.1	0.2	0.1	1.0	1.0	0,1	Ð. E	2.2	1.5	0,9	),4	4,2	1.0	.'.0	1,1
Fawn deer	0,3	0,3	0,0	0,2	1,1	1.0	0.1	0,9	0.5	0.1	(),6	0.5	0.3	0,3	0.0	0.4	0,6	0.4	0.5	0.9	3,3	3.0	21,8	1, 9
Snowshoe hare	7.7	0.5	32	26	5.5	6.6	11	12	3.7	11	17	14	3.8	10	41	25	6.4	25	48	27	4.2	84	1D	110

<sup>1</sup> Annual values were derived by pooling scats collected throughout the year,

<sup>2</sup> By mid-August it was difficult to distinguish the hair of fawn (<1 yr. of age) and adult deer in scats. Therefore total deer from September through May was apportioned on the basis of the adult: fawn ratio of coyote killed deer examined during winter snow tracking,

<sup>9</sup> Primarily red squirrels (Tamaisciurus hudsonicus), eastern chipmunks (Tamais striatus), meadow voles (Microtus pennsylvanicus), and red backed voles (Cleithryonomys gapperi).

<sup>4</sup> Primarily porcupines (Erithrizon dorsatum, QC only), raccoons (Procyonis lotor), beaver (Castor canadensis), and muskrat (Ondatra zibethicus).

<sup>5</sup> Primarily cows (Bos taurus), goats (Capra hircus), and pigs (Sus scrofa).

<sup>6</sup> Percent volume in scats was converted to percent biomass ingested as described by Weaver (1993). Fruit percentages were halved after Andelt and Andelt (1984). Assumed whole prey weights (kg) were: adult deer (65), fawn deer (9.7, 19.2, 27 for June- July, Aug- Sept 15, and Sept 16- May, respectively ), snowshoe hare (1.2), small rodents (0.05), other wild mammals (6.0), domestic livestock (100). represented 34% of the total annual scat volume (47% and 24% of the total biomass originally consumed) in Q2. This difference was significant ( $X^2 = 129$ , P < 0.001, Table 3.1) indicating that the use of deer declined and hare increased between periods in QC. Although prey densities changed only slightly between Q1 and Q2 (Fig. 2.3), there was much more snow accumulation in QC during the winters of 1993 and 1994 relative to the winters of 1995 to 1997.

In Q1 and Q2, the use of deer was highest from December through May and lowest during late summer (Table 3.1). In CBH and CBL, the use of deer was highest during June and July and lowest during spring and autumn (Table 3.1). The use of hare was relatively consistent throughout the year, except during early summer, when fawns replaced hares in the diet (Table 3.1). The percentage of total scat volume composed of hare was greater than that of deer in both CBH and CBL (56% vs. 23%, and 43% vs. 38%, respectively). However, the biomass of deer actually consumed was greater than that of hares in CBL (52% vs. 31%, Table 3.1). On an annual basis, coyotes consumed from 7.4 (Q1) to 89 (CBH) hares for every deer consumed (Table 3.1).

Fawns composed 23-34% of the total biomass consumed by coyotes during June and July (25.1-37.8% of total scat volume, Table 4.1). The utilization of fawns during summer was highest in Q1 and lowest in CBH (Table 3.1). However, during June and July the consumption of fawns exceeded that of hares in all areas, despite very high hare densities in CBH (Table 3.1).

Based on the average body weight of fawn and adult deer, coyotes consumed 5-6 fawns for every adult deer during June and July (Table 3.1). Insect larvae (the undigested cuticles of maggots) were rarely observed in scats containing the remains of fawns, suggesting that most young fawns were killed rather than scavenged. Fawn consumption declined by >50% in all areas during late summer, when fruits became an important food item (Table 3.1).

The use of fruits in late summer was greatest in QC and least in CBH. Although I could not quantify the relative availability of fruits among study areas, wildberries were common in all areas. In each study area, the use of fruits declined with increasing densities of deer and/ or hare (Table 3.1). However, the volume of fruits in scats collected during late summer was not significantly correlated with relative density of either deer or hares (deer:  $r^2 = 0.10$ , P = 0.31, df = 6; hare:  $r^2$ = 0.44, P = 0.18, df = 6).

## Coyote functional response and evidence for prey switching

The relative numbers of deer and hare consumed per coyote per territory during winter and summer are shown in Tables 3.2 and 3.3. During winter, the relative number of deer consumed per coyote decreased significantly with increasing hare density (Partial correlation, r = -0.73, P = 0.04, df = 6, Fig. 3.1a), but not with deer density (r = 0.58, P = 0.13, df = 6). Although partial correlation analysis revealed that hare density exerted a greater influence on coyote feeding habits during winter than

Pack ID	Study Area	Hare / km² (A <sub>1</sub> )	Hares eaten/ coyote (e <sub>1</sub> )	Deer/ $km^2 (A_2)^1$	Deer eaten/ coyote (e <sub>2</sub> )	$\frac{e_1A_2}{e_2A_1}$	A1/A2
Tupper Lake 96	QC	14.1 ± 1.0 (73)	8.2	2.4 ± 0.8 (7)	2.4	0.6	5.9
Tupper Lake 97	QC	11.4 ± 1.9 (115)	23,5	1.6 ± 0.3 (9)	2.2	1.5	7.1
Eden 96	CBL	17.6 ± 3.5 (163)	20.6	9.8 ± 2.0 (16)	2.6	4.4	1,8
Eden 97	CBL	28.4 ± 6.6 (147)	22.1	9.2 ± 1.9 (11)	2.8	2.0	9.8
Maple Brook 96	CBL	34.4 ± 7.4 (65)	37.5	3.4 ± 1.0 (6)	1.2	2.6	3.1
Iona 97	CBL	34.5 ± 7.4 (64)	37,9	1.8 ± 0.4 (6)	1,9	3.1	0.1
Roseburn 96 <sup>1</sup>	СВН	47.6 ± 8.9 (63)	30,7	0.6	1,6	0.6	34.0
Skye Mt. 97 <sup>1</sup>	Свн	56.9 ± 8.0 (111)	46.3	0.6	1,6	0.3	94.8
River							
Denys Mt. 97 <sup>1</sup>	Свн	65.0 ± 11.4 (77)	71.5	0.2	0.6	0.4	325.1

Table 3.2. Relative winter density estimates (±SE), and estimated number of deer and hare consumed per coyote, within 9 territories located in the Queens County (QC) and Cape Breton (CB) study areas, Nova Scotia, winters 1996-1997(no. of sample plots in parentheses).

<sup>1</sup>Although I counted all deer pellets deposited after 1 November, most deer had migrated from the CBH area by early January, when the bulk of winter field work began. Therefore winter the pellet counts overestimated the density of overwintering deer in CBH. The density estimates presented here are based on aerial and ground surveys and should better represent the actual winter densities of deer. The unadjusted density estimates based on the pellet surveys are : Roseburn 96, 1.4  $\pm$  0.7 (6); Skye Mt. 97, 1.3  $\pm$  0.5 (8); River Denys Mt. 97, 3.0  $\pm$  0.7 (7).

	Stud	/	Hares eaten/		Fawns eaten/	e <sub>1</sub> A <sub>2</sub>	
Pack ID	Area	Hare / $km^2 (A_1)^3$	coyote (e <sub>1</sub> )	Deer/ $km^2 (A_2)^2$	coyote $(e_2)$	e <sub>2</sub> A <sub>1</sub>	A1/A2
Tupper Lake	QC	12.6 ± 1.0 (178)	14.4	2.0 ± 0.3 (16)	6.5	0.4	6,3
Eden <sup>2</sup>	CBL	25.2 ± 1.0 (310)	30.6	3.9 ± 0.8 (27)	3.8	1.4	5.9
Maple Brook	CBL	37.8 ± 7.4 (107)	36.9	3.9 ± 0.7 (10)	5.2	0,7	9.7
Roseburn	СВН	47.6 ± 8.9 (63)	24.0	1.4 ± 0.7 (6)	4.6	0.2	34.0
Skye Mt.	Свн	56.9 ± 8.0 (111)	30.0	1.9 ± 0.4 (15)	3.7	0.2	35.2
River Denys Mt,	СВН	65.0 ± 11.4 (77)	41.5	3.0 ± 0.7 (7)	3.7	0.5	21.7

Table 3.3. Relative summer density estimates (density ± SE), and estimated number of deer and hare consumed per coyote, within 6 coyote territories located in the Queens County and Cape Breton study areas, Nova Scotia, June- July 1996 (no. of sample plots in parentheses).

<sup>1</sup> I estimated the density of deer and hare within territories during summer 1996 by averaging of the density estimates obtained during the winters of 1995- 1996 and 1996- 1997.

<sup>2</sup> Because ~60% of the deer wintering in the Eden deer wintering area were seasonal migrants from other areas, 1 multiplied the winter deer density estimates for the Eden territory by 0.4 to estimate summer densities.





Fig. 3.1. Number of white-tailed deer consumed per coyote within 9 territories during winter (December to March) in relation to the relative density of (a) snowshoe hare and (b) white-tailed deer.

deer density, coyotes did exhibit a positive functional response to increasing deer density (Michaelis-Menton model,  $r^2 = 0.62$ , P = 0.01, Fig. 3.1b). A Type III functional response of the general form described by Real (1977),  $y = bx^c/(a + x^2)$  did not improve the fit (best model,  $r^2 = 0.62$ , df = 8, P = 0.01). The number of hare consumed per coyote during winter increased with increasing hare density (Partial correlation, r = 0.84, P = 0.009, df = 6), but did not change with deer density (r = -0.19, P = 0.65, df = 6). A linear model was the best descriptor of this relationship ( $r^2 = 0.77$ , P = 0.002, Fig. 3.2a).

Partial correlation analysis also revealed that during June and July the number of hares consumed per coyote increased significantly with relative hare abundance (Partial correlation, r = 0.98, P = 0.002, df = 3), with the Michaelis-Menton model providing a significantly better fit ( $r^2 = 0.56$ , P = 0.01, df = 5, Fig. 3.2b), than the linear model ( $r^2 = 0.49$ , P = 0.12, df = 4). The number of fawns consumed per coyote during June and July may have been negatively correlated with relative hare abundance (Partial correlation, r = -0.77, P = 0.13, df = 3), but not with deer density (r = -0.44, P = 0.46). The number of adult deer consumed per coyote during June and July was not significantly correlated with either deer or hare density (P > 0.26).

During winter, the mean value of the selectivity index  $(e_1A_2/e_2A_1)$  was 1.7 ± 0.5 for nine coyote packs, suggesting a disproportionately high use of snowshoe hare; however, this value was not significantly greater than unity (t = 1.52, P = 0.17, df



Fig. 3.2. Average number of snowshoe hares consumed per coyote within a) 9 territories during winter (December-March; 121 days), and b) June-July (61 days) in relation to the relative density of snowshoe hares.

= 8). Contrary to my prediction, the selectivity index decreased significantly as the abundance ratio of hare to deer  $(A_1/A_2)$  increased  $(r_s = -0.72, P = 0.02, df = 9, Table 3.3, Fig. 3.3a).$ 

Thus, although the utilization of hare increased and use of deer decreased significantly with increasing hare density (Figs. 3.1a, 3.2, 3.3), coyotes ate proportionately more deer and fewer hares at high hare densities, and/ or low deer densities, than would be expected if they fed on deer and hare in proportion to their respective abundance. This observation was further supported by the fact that covotes in the CBH territories (n =3), which contained the highest hare and lowest deer densities during winter, ate proportionately more deer than all other groups combined (t = -2.4, P = 0.04, df = 7). Although coyotes ate more deer and fewer hares (relative to the abundance of deer and hare) as the ratio of hare to deer increased, the selectivity index did increase significantly (coyotes ate proportionately fewer deer) with increasing deer density ( $r_s = 0.79$ , P = 0.006, df = 9). Further, there was no correlation between the selectivity index and hare density ( $r_s = -0.48$ , P = 0.17, df = 9, Table 3.2). This indicates that low deer densities, rather than high hare densities, were primarily responsible for the significant negative correlation between the selectivity index and the abundance ratio of hare to deer.

During June and July, the mean value of the selectivity index was  $0.6 \pm 0.2$  (Table 3.3) for six coyote packs, suggesting an overall preference for fawns over hares. However, although





Fig. 3.3. Prey selectivity index  $(e_1A_2/e_2A_1)$ , where  $e_1$  and  $e_2$  are the numbers of white-tailed deer and snowshoe hare eaten from a population of  $A_1$  and  $A_2$  available) in relation to their relative abundance of snowshoe hare and white-tailed deer  $(A_1/A_2)$ , (a) winters (December- March) and (b) June- July, 1996 and 1997. The dashed lines (slope = 0, y intercept = 1) indicate the expected trends, if coyotes fed non-selectively on deer and hare.

the selectivity index was less than unity in five of the six territories (Table 3.3), the mean value was not significantly different than unity (t = -2.36, P = 0.07, Table 3.3). The selectivity index during June and July also decreased as the ratio of snowshoe hare: deer increased ( $r_s = -0.81$ , P = 0.06, df = 6, Table 3.3, Fig. 3.3b).

### DISCUSSION

The eastern coyote has been described as a generalist predator (Messier et al. 1986, Parker 1986, Morton 1988, Brundige 1993, Patterson 1995). Generalist predators have little need to distinguish individual prey species and are expected to feed nonselectively (Cornell 1976). However, the documentation of switching behaviour among several generalist predators does not support this conclusion (Murdoch 1969, Cornell 1976, Akre and Johnson 1979). Deer and hare were the principal food items in this study and there was a pronounced functional response by coyotes to changes in the density of both species. In areas where they were readily available, coyotes fed predominantly on hares and utilization of deer declined as hare density increased. However, I could not identify a traditional switch in prey selection (Murdoch 1969, Akre and Johnson 1979) in relation to the relative abundance of each prey species.

Although use of hare increased and deer decreased with increasing hare densities, the responses were not proportional to the changes in the relative densities of each species (Tables 3.2, 3.3, Fig. 3.3). This was particularly evident at low deer

densities, where even in the presence of high hare densities, coyotes continued to feed disproportionately on deer (Tables 3.2, 3.3, Fig. 3.3). The high use of deer appeared to be facilitated by increased deer vulnerability in deep snow during winter and the inability of fawns to escape during summer. Deer meat contains more fat than snowshoe hare meat (Litviatis and Mautz 1980) and represents a larger package of food when available (Pekins and Mautz 1990). The data supports the conclusion that although coyotes should be considered generalists, they deer rather to hares, when available, presumably because of higher profitability.

# Features of the functional response to changes in deer and hare abundance

A Type I (linear) response to increasing hare densities was observed during winter (Fig. 3.2a). This finding suggests that hare might represent an even greater portion of the diet at higher hare densities than I observed. However, during June and July, a Type II functional response was observed with increasing hare density (Fig. 3.2b), suggesting that hare consumption rates would not increase much further with increasing hare density. While snowtracking, I noticed that although hares were usually consumed completely in the QC area, incomplete consumption (caecum, feet, and head not consumed) was common in CBH. Thus, coyotes in CBH appeared to be satiated during winter. Coyotes continued to feed on a disproportionately higher amount of deer, even during low deer densities. In CBH, hares may have provided the energetic base for coyotes to pursue alternate prey, namely deer. Thus, eastern coyotes may not switch from deer to hares when hare density increases if larger alternate species remain available, as a result of factors other than abundance.

The preceding discussion identifies an important limitation of the use vs. availability model employed to quantify prey selection. Although the model assumes that deer and hare are equally vulnerable and deer exhibit equal vulnerability throughout the year, such is not the case (Messier and Barrette 1985, Parker and Maxwell 1989, Patterson 1994). Differences in social behaviour (Messier and barrette 1982) and learning (MacCracken and Hansen 1987) may also have influenced coyote feeding habits and confounded my analysis.

The response by coyotes to increasing deer density was less pronounced than the response to hare density, probably because deer vulnerability, not just density, was a critical factor determining killing rates on deer (Messier and Barrette 1985, Patterson 1994). Deer consumption in areas where hares were readily available was associated with increased deer vulnerability due to deep snow conditions (Chapter 5). In areas of lower hare abundance, deer represented a significantly larger portion of the diet throughout the year. A significant decrease in deer use between Q1 and Q2 occurred despite only a minor increase in hare numbers. The high use of deer by coyotes in Q1 was due to increased deer vulnerability during two consecutive harsh winters (1993 and 1994) (Patterson 1994, 1995). Winters

are generally mild in this region and deer typically remain distributed throughout the entire area. When deep snow occurs, deer may be particularly vulnerable to predation (Patterson 1994). Between 1995 and 1997, QC experienced relatively mild winters. I suspect that during most winters, coyotes in QC are forced to focus their hunting efforts on hares and/ or other small mammals, despite low hare densities, because of low vulnerability of deer. However, when severe winter conditions do occur, coyotes switch to feeding mainly on deer (Table 3.1). Parker and Maxwell (1989) documented a similar switch related to deer vulnerability in northern New Brunswick.

Although the consumption of hares increased with hare density during June and July (Fig. 3.2b), the consumption of fawns exceeded hares in all areas. In relation to the relative abundance of deer and hare, coyotes fed on a disproportionate number of fawns in five of six territories (Table 3.3). Harrison and Harrison (1984) speculated that it was more energetically efficient for adult coyotes attending pups to kill and transport fawns than other smaller prey items. The relatively low density of deer, and high use of fawns, by coyotes in QC suggests that summer predation may have a substantial limiting effect on deer populations. Further research is needed to quantify the impact of coyote predation on fawns and deer population dynamics in the Northeast.

# Fruits as a potential buffer food

Tremblay et al. (1998) and Samson and Crête (1997) suggested that in forested regions of the Northeast, wildberry consumption increased with decreasing availability of mammalian prev. Although no significant relationship between the density of either deer or hare and the use of fruits was found, low sample sizes may have influenced this result. Wildberries were readily available in all study areas and yet utilization declined sharply in areas with high densities of snowshoe hares (Table 3.1). Andelt and Andelt (1984) reported that fruits were approximately 50% as digestible as most mammalian prey. The nutritional value of wildberries as a food item for coyotes is unclear. However, as wildberries are available in large quantities and contain high amounts of carbohydrates (Robbins 1983), they may be of important caloric value during certain times of the year. Nonetheless, mammalian prey would be nutritionally superior to wildberries and probably represents a preferred food source. As high fruit use appeared to be associated with decreased prey availability, fruits probably did little to buffer predation on deer cr hare.

The role of prey switching in the diet of the eastern coyote

Predation was not proportional to the changes in the relative densities of deer or hare, but I could not demonstrate switching in the traditional sense. However, coyotes did exhibit pronounced functional responses to changes in hare and deer abundance. Differences in the relative and seasonal

vulnerabilities of deer and hare, and the potential influences of learning and social behaviour, appear to have complicated the functional response of coyotes such that they fed disproportionately on deer when deer became increasingly vulnerable. In conclusion, prey switching by eastern coyotes may be influenced by changes in prey diversity, abundance, and vulnerability. In areas where deer and hare are principal prey items, predation on deer may increase sharply with increased snow depths or when hare and/ or deer numbers decline. However, an understanding of the effects of the densities of major prey species on the numerical response of eastern coyotes is essential for an assessment of the effects of coyote predation on whitetailed deer.

# 4. FACTORS INFLUENCING KILLING RATES OF WHITE-TAILED DEER BY EASTERN COYOTES

#### INTRODUCTION

Predation affects the dynamics of many ungulate species (Gasaway et al. 1992, Messier 1994). Most early field studies involving predation focused primarily on describing the extent of predation in a given system (Rudebeck 1950, Erington 1967, Mech and Karns 1977). Until recently, little attention has been given to understanding the underlying processes and relationships in predator-prey systems (Holling 1959, Messier and Crête 1985, Messier 1994, Krebs et al. 1995, Sinclair and Pech 1996). Factors such as predator and prey densities, predator hunting behavior, and the relative availability, distribution, and vulnerability of alternate prey species can all affect predatorprey relationships. The extent and significance of predation for any species can not be fully understood until the major factors affecting predation rates have been identified and their effects quantified.

Social grouping in coyotes allows access to large prey without sacrificing the advantage that smaller body size provides in allowing the efficient use of small prey (Bowen 1981, Brundige 1993). For example, in southeastern Colorado, 71% of the variation in ungulate consumption by coyotes was explained by group size (Gese et al. 1988). All of 17 deer killed by coyotes in northern New Brunswick during winter 1984-85 were killed by groups of ≥3 coyotes (Parker and Maxwell 1989). Messier et al.

(1986) noted a similar trend in southern Québec and commented that predation by solitary coyotes on ungulates other than neonates was rare. Solitary coyotes are generally considered more apt to scavenge large carcasses and kill smaller prey (Bowen 1981, Messier et al. 1986, Gese et al. 1988).

The vulnerability of deer to predation appears to be correlated positively with winter severity and negatively with the use of winter yards (Potvin 1980, Nelson and Mech 1981, Messier and Barrette 1985, Lavigne 1992a, b). Messier and Barrette (1985) reported reduced coyote predation on deer using winter yards as opposed to those outside or at the periphery of yards. They attributed this reduction to increased deer mobility due to a well-established network of trails within winter yards, and to the fact that concentrations of deer facilitate earlier detection of predators. Potvin (1980) and Lavigne (1992a) felt that deer using harvested and/ or budworm damaged yards may have been pre-disposed to coyote predation due to increased snow depth and poorer nutritional status. Snow depth accounted for 51% of the variation in annual predation rates by wolves on white-tailed deer in Minnesota (Nelson and Mech 1986a). In Alberta, wolves increased their predation rates on ungulates and decreased their scavenging activities with increasing snow depths (Huggard 1993). Delgiudice (1998) reported that surplus killing of deer by wolves might be predicted when snow depths exceed 70 cm for four to eight weeks.

Seasonal switches in prey selection by coyotes have been discussed (Parker and Maxwell 1989, Dibello et al. 1990, Chapter 3), but the extent and causation of prey switching by coyotes remain unclear. In Alberta, snowshoe hare biomass in the diet of coyotes changed from 0 to 77% between 1964 and 1975, largely as a result of changing hare density (Todd et al. 1981). Similarly, the use of deer and hare by eastern coyotes was heavily influenced by snowshoe hare density in Nova Scotia (Chapter 3). Group living coyotes in northern New Brunswick switched from hares to deer in late winter despite no apparent change in hare densities (Parker and Maxwell 1989). More data is required to fully assess the effects of alternate prey on killing rates of deer by coyotes.

The objectives of this study were to determine if killing rates of white-tailed deer by coyotes during winter were affected by:

- the relative abundance of white-tailed deer and snowshoe hare
- 2. social group size of coyotes
- 3. deer sinking depth in snow
- 4. the use of wintering areas by deer
- 5. the presence of clear-cut stands, and
- Julian date (to document temporal changes in killing rates)

#### METHODS

I investigated coyote-deer interactions primarily while snow-tracking radio-collared coyotes, monitoring radio-collared deer (MacDonald 1996, Patterson et al., in prep.), and patrolling the study areas from December through March, 1993-1997. Additionally, staff of the Nova Scotia Department of Natural Resources (NSDNR) snow-tracked unmarked coyotes in the counties encompassing each study area during winters 1989-1994. Observers followed the first set of tracks they encountered for distances of up to 15 km ( $\bar{x} = 1.6 \pm 0.07$  km (SE), n = 303) and recorded information on distances traveled, snow conditions, coyote group size, and occurrences of chases, kills, and scavenging (Sabean 1993a).

Dead deer were classified as coyote kills if there was evidence of attack or chase (blood soaked fur and /or snow, bleeding observed around tooth puncture wounds). Predation was excluded as the cause of death when no evidence of pursuit, struggle, or bleeding from wounds was noted. Where possible, a jawbone and femur were collected from any coyote-killed or scavenged deer to provide information on the age structure and physical condition of killed deer (Chapter 5).

# Effects of deer and hare abundance on killing rates.

Unless disturbed, eastern coyotes generally remain in the vicinity of a freshly killed deer for one to three days (Messier and Barrette 1985, Brundige 1993). Therefore, during winters 1996-1997 I determined the daily resting locations of two radio-

collared coyote family groups in each of the QC, CBH and CBL areas, and then investigated these areas on foot to check for evidence of a deer kill. Additionally, one family group in the CBL area was intensively monitored during winter 1995.

Killing rates of deer were calculated from the cumulative tracking periods and the respective number of kills. For each family group, I considered only those tracking sessions in which relocations were separated by <60 hours. I am aware that the carcasses of some fawns may have been completely consumed during this period. However, the minimal snowfall and frequent rains experienced during the winters of 1995-1997 often made snowtracking difficult. The relative contributions of deer and hare abundance, and mean winter travelling group size of covotes on deer killing rates were examined using multiple linear regression (Sokal and Rohlf 1995). Preliminary analysis suggested a non-linear relationship between deer density and kill rate that was best described by a Type II functional response (Holling 1959,  $y = (4.03)x/(1 + 4.03 \bullet 0.35 \star x), r^2 = 0.47, P =$ 0.009, n = 13). Therefore, I used log-transformed data for deer density in the multiple regression model to partially compensate for the non-linear functional response.

Effects of group size and snow depth on killing rates.

When snow conditions permitted, I recorded coyote group sizes, snow depth, actual deer sinking depths (while running), and chase distance associated with each coyote-killed deer. I compared the number of chases initiated by groups of one, two,
three, and 4+ coyotes with the number expected if group size had no influence on chase initiation using G-tests (Sokal and Rohlf 1995). The expected distribution of coyote group sizes associated with chases was taken from the distribution of group sizes documented during snowtracking.

I predicted that chase success would increase with coyote group size and also that chases would be more successful, and shorter, where thick snow conditions inhibited deer movements. I compared the number of successful and unsuccessful chases initiated by groups of one, two, three, and 4+ coyotes using a Gtest (Sokal and Rohlf 1995). Because chase success was dichotomous (either successful or not), I used logistic regression (Sokal and Rohlf 1995) to assess the influence of snow depth on chase success.

The relative influence of snow depth and coyote group sizes on the mean distances of both successful and unsuccessful chases was assessed using multiple linear regression (Sokal and Rohlf 1995). Kendall's partial rank-order correlation ( $T_{xy,z}$ , Siegel and Castellan 1988) was used when violation of the assumption of normality or homogeneity of variance precluded the use of multiple linear regression. I excluded cases where deer were killed on sheer ice (n = 5) from these analyses.

Effects of deer distribution and local abundance on vulnerability to predation.

An important function of forest cover for deer is snow interception, a process that facilitates deer mobility and thus

may increase the chances of deer escaping predators (Nelson and Mech 1981, Messier and Barrette 1985, Lavigne 1992a). Deeper snow conditions may also lead indirectly, via food limitation, to deterioration in body condition that may further predispose deer to predation (Lavigne 1992a, Delgiudice 1998). In the CB study area, deer were not uniformly distributed during winter and tended to concentrate in areas that provided good snow interception (MacDonald 1996, Lock 1997). Aerial and ground track surveys were used to determine the winter distribution of deer in the CB study area and to partition the area into four deer density classes ranging from the absence of tracks to the presence of extensive trail networks (Fig. 4.2, Chapter 2).

Using data on territory-specific deer densities and the proportion of each deer density class within each territory (Chapter 2), I estimated the average densities of deer in the four density classes to be 0.1, 0.75, 4.0, and 10.0 deer /km<sup>2</sup>, respectively. The number of deer occupying each deer density class was then estimated by multiplying the total area of each density class by the respective deer density estimate. I assigned each deer kill to one of the four deer density classes based on location and track observations made in the vicinity of each kill. The proportion of coyote-killed deer occurring within each deer density class was compared to that expected if deer vulnerability to predation was independent of deer density, using a G-test (Sokal and Rohlf 1995). I did not attempt a similar

analysis in the QC area because the winter distribution of deer was relatively uniform (MacDonald 1996, Lock 1997).

Effects of forest harvesting on deer vulnerability to predation.

Theoretically, forest harvesting may affect killing rates of deer by coyotes by removing forest cover for deer (and thus increasing snow depths) and, in the case of recent harvest operations, by causing deer to congregate around a predictable food source (Verme 1965, 1973, Tierson et al. 1985). I compared the distances of deer kills and randomly generated points to recent (<10 year old) clear-cut stands in both study areas using the Mann-Whitney U test (Siegel and Castellan 1988). I generated one random point for each kill used in the analyses. Distances of kills and random points to clear-cuts were determined using the ARC/ INFO Geographic Information System (GIS). In the CB area the number of random points in each deer density class (Fig. 4.2) was proportional to the percentage of the total study area comprised of each class. Because forest harvesting has not occurred in Kejimkujik National Park since the early 1960s, I considered only deer kills occurring outside the park in the QC study area.

## Changes in killing rates over winter.

I investigated the possibility of a change in deer killing rates over winter by comparing the number of deer kills observed per month during winter with the number that would have been expected if deer kills were made in proportion to sampling

intensity, regardless of month, using a Chi-square test. I measured relative sampling intensity by month as the total number of snow-tracking sessions conducted during my intensive telemetry study, and by NSDNR staff during the provincial tracking program (counties encompassing each study area only). Some deer carcasses were discovered opportunistically while patrolling the study areas or monitoring radio-collared deer (MacDonald 1996, Patterson et al., in prep.). I assumed that the intensity of these activities was uniform throughout the winter.

### RESULTS

I collected information on coyote group sizes and coyotedeer interactions from 586 tracking sessions conducted during my intensive telemetry study and 303 sessions conducted by NSDNR staff in the vicinities of the two study areas (186 in CB, 117 in QC, Tables 4.1, 4.2). The observed distribution of coyote group sizes differed significantly between the two data sources ( $\chi^2_3$  = 349, P < 0.001). Because I followed primarily radio-collared pairs and groups during my study, I tracked fewer single coyotes than NSDNR staff did during the provincial tracking program (Table 4.2). I conducted individual analyses with each data source when expected frequencies of coyote group sizes were required. Data were pooled for the analyses of chase distances and success in relation to group size and snow depth.

Effects of deer and hare abundance on deer killing rates.

Relative hare density was the only significant parameter

					Deer	Deer	Hare
	Study	_ x group	Tracking	No.deer	Killing rate	density	pellets/
Pack/Year	Area	size	effort <sup>L</sup>	killed	(/100 da <b>ys</b> )	(/km <sup>2</sup> ±SE)	m <sup>2</sup> (±SE)
Tupper Lake 96	QC	2.7	95	9	9.5	2.3±0.8	2.1±0.4
Tupper Lake 97	QC	2.3	75	3	4.0	1.6±0.3	1.9±0.3
Devonshire 96	QC	2.4	59	4	<b>6.8</b>	2.4±1.0	2.6±0.9
Keji 97	QC	1.9	60	2	3.3	1.5±0.2	1.5±0.4
Eden 95	CBL	2.1	43	3	7.0	4.7±0.9	1.7-
Eden 96	CBL	2.5	43	3	7.0	9.8±2.0	2.9±0.5
Eden 97	CBL	2 <b>.6</b>	72	5	6.9	9.2±1.9	4.7±1.1
Maple Brook 96	CBL	2.2	46	2	3.5	3.4±1.0	5.6±1.1
Iona 97	CBL	1.8	82	3	3.7	1.8±0.4	5.7±1.1
Roseburn 96	СВН	1.8	54	2	3.7	0.6'	7.8±1.5
Skye Mt. 96	CBH	2.8	29	1	2.9	0.8'	12.7±2.0
Skye Mt. 97	CBH	3.3	68	2	2.9	0.6	9.3±1.3
River Denys Mt.	97CBH	3.1	63	1	1.6	0.23	10.7±1.9
<u></u>	QC	2.3	289	18	6.2	2.5±0.3	1.8±0.2
	CBL	2 <b>.2</b>	286	16	5.6	5.5±0.7	4.3±0.4
	CBH	2.8	214	б	2.0	0.3	10.1±0.8

Tabl	e	4.1.	Wi	nter	kil	ling	rat	es	of	deer	(deer	/ 100	days	) by	соуо	tes	in
t	he	Que	ens	Coun	ty	(QC)	and	Ca	pe	Breton	Low1	and	(CBL)	and	Cape	Bre	ton
H	ig	hlan	d (1	CBH)	stud	iy ar	eas,	1	995	-97.							

<sup>1</sup> Calculated as the number of pack contact days included in the analysis. Only one day was counted even if multiple collared pack members were located on a given day.

 $^{2}$  No hare pellet data was available during this winter. This estimate was calculated based on the relative hare harvests in Inverness County (the county containing the CB study area) from 1995 - 1997 relative to pellet counts conducted in the CB area during 1996-1997.

<sup>1</sup> Although I counted all deer pellets deposited after 1 November, most deer had migrated from the CBH area by early January, when the bulk of winter field work began. Therefore pellet counts generally overestimated the density of overwintering deer in the CB Highlands area. The estimates presented here are based on aerial and ground surveys and better represent the actual winter density of deer in these territories. Table 4.2. Coyote social group sizes involved in chases and kills of white-tailed deer during winter in Nova Scotia, 1989-1997.

	Provincial		Intensive			
	snowtracking		study		Combined	
Counte	NO.	No. chases	No.	No. chases	Chase	No. deer
	chaervations (6)	initiated (%)	observations {\$}	initiated (%)	success (% (n))	kills obs. (%)
avre dnoi6	166 (54.8)	14 (36.8)	93 (15.9)	8 (16.3)	40.9 (22)	16 (22.9)
	(0.4E) EUT	13 (34.2)	258 (44.0)	21 (42.9)	32,4 (34)	18 (25.7)
<b>v</b> (	22 (7.3)	4 (10.5)	140 (23.9)	14 (28.6)	27.8 (18)	21 (30.0)
r ¶2	12 (4.0)	7 (18.4)	95 (16.2)	6 (12.2)	61.5 (13)	15 (21.4)

retained by the multiple linear regression model ( $R^2 = 0.53$ , P = 0.005; Fig. 4.1b). Log<sub>10</sub>(deer/ km<sup>2</sup>) ( $r^2$  partial = 0.14, P = 0.23) and winter traveling group size ( $r^2$  partial = 0.04, P = 0.51) had no significant influence on killing rates after controlling for the other explicative variables in the model.

Effects of coyote social group size and snow depth on chase success.

I documented 49 chases of deer by coyotes during the intensive telemetry study and an additional 38 during the provincial tracking program (Table 4.2). Thirty-eight percent of observed chases were successful. Chase initiation documented during the intensive study was similar among group sizes ( $G_1 = 0.96$ , P = 0.81, Table 4.2). Conversely, solitary coyotes initiated fewer chases than expected during the provincial tracking program ( $G_1 = 6.3$ , P = 0.04, Table 4.2). Groups of  $\geq$ 4 coyotes had higher chase success ( $G_3 = 8.4$ , P =0.038, Table 4.2), whereas chase success was similar among smaller groups (Table 4.2). Logistic regression [Logit P = -1.527 + (0.042 \* (snow depth)), Likelihood ratio test statistic = 6.81, P = 0.009] revealed that snow depth (Wald  $\chi^2 = 6.28$ , P = 0.012) had a significant influence on success.

The mean distance of successful chases was 279  $\pm$  82 (SE) m, not significantly different than the mean distance of 314  $\pm$  58 m for unsuccessful chases (Mann-Whitney  $U_{27,52} = 660$ , P = 0.66). The distance of successful chases was independent of group size ( $T_{xy,z} =$ 0.073, P > 0.25, n = 27, Fig. 4.3) whereas snow depth may have had an influence ( $T_{xz,y} = 0.204$ , P = 0.08, n = 27). Conversely, the



Fig. 4.1. The influence of snowshoe hare density on per capita killing rates of white-tailed deer by coyotes in Nova Scotia, December through March, 1995 - 1997. Table 4.1 summarizes the original data for each family group of coyotes.



Fig. 4.2. The relative winter (Dec - Mar) densities of white-tailed deer and locations of 39 deer killed by coyotes in the Cape Breton study area, Nova Scotia, winters 1996-1997.

distance of unsuccessful chases was positively correlated with group size ( $T_{xy,z} = 0.437$ , P = 0.001, n = 52, Fig. 4.3) but not snow depth ( $T_{xz,y} = -0.12$ , P = 0.11, n = 52).

Effects of deer distribution and abundance on vulnerability to predation.

A greater proportion of deer kills in the CB study area was observed in areas of low deer density. Of the 39 deer killed by coyotes in this area, 17.9, 56.4, 15.4, and 10.3% were located in deer density classes zero to three respectively (Fig. 4.2). This differed markedly from the estimated distribution of 9.0, 18.0, 34.6, and 38.3% respectively, of deer in the CB area living within each of the four density classes ( $\chi^2_3 = 47.9$ , P = 0.001).

Effects of forest harvesting on deer vulnerability to coyote predation.

The mean distance of deer kills to recent clear-cuts was significantly shorter than for the corresponding random points in CB (273  $\pm$  53 (SE) m vs. 431  $\pm$  48 m, Mann-Whitney  $U_{39,39}$  = 1155, P = 0.05) but not in QC (732  $\pm$  170 m vs. 910  $\pm$  189 m, Mann-Whitney  $U_{27,27}$ = 313, P = 0.37).

Changes in killing rates over winter.

The number of deer kills observed per month from January through March was not proportional to the intensity of fieldwork conducted each month ( $G_2 = 12.3$ , P = 0.003, Fig. 4.4). The number of kills increased monthly from January through March, although proportionately less fieldwork was conducted during March than



Fig. 4.3. The influence of coyote group size on the mean distance (± SE) of successful and unsuccessful chases of white-tailed deer in Nova Scotia, during winter (December through March), 1989-1997.



Fig. 4.4. The number of deer kills observed by month from January through March in Nova Scotia relative to the intensity of field sampling, winters 1989-1997.

during January or February (Fig. 4.4).

#### DISCUSSION

Snowshoe hare densities largely influenced killing rates of deer by coyotes in Nova Scotia (Fig. 4.1). Similarly, scat analysis suggested significant functional responses by coyotes to changes in both hare and deer abundance (Chapter 3). However, after controlling for the influence of snowshoe hare density, both scat analysis and direct observations of killing rates of deer during winter indicated that coyotes did not exhibit a significant functional response to increasing deer densities (see also the partial correlation analysis in Chapter 3). While snowtracking I noted that coyotes rarely followed deer tracks or trails when encountered. Overall chase success was relatively high (~38%), thus coyotes probably did not pursue deer unless they were reasonably confident of success. I suggest that it was generally difficult for coyotes to kill adult deer unless deer were disadvantaged (i.e. deep snow or sheer ice), thus a lack of a functional response for coyotes preying on deer is not unexpected.

Although vulnerability of deer to predation was influenced by local snow conditions and deer densities, winters 1995-1997 (when the bulk of field work was conducted) were relatively mild (MacDonald 1996, Lock 1997, Patterson et al. 1998). In March 1993, a group of five female deer (three adults and two fawns) in the QC study area were killed by coyotes in a single night after being mired in an open mixed-wood stand following a severe snowstorm (Patterson 1994). Parker and Maxwell (1989) reported a deer killing rate of ~12.8/ 100 days (six deer killed in 47 days of tracking) by a group of three coyotes in an area with abundant snowshoe hare and severe winter conditions in northern New Brunswick. Given the influence of severe winter conditions on killing rates of deer, I suggest that killing rates documented during this study (6.2, 5.6, and 2.8 deer killed • pack<sup>-1</sup> • 100 days<sup>-1</sup> in the QC, CBL, and CBH study areas respectively, Table 4.1) are relatively low for eastern coyotes in predominately forested areas of north-eastern North America.

Effects of coyote social group size on chase success.

Larger (≥4) groups of coyotes were more successful in killing deer (Table 4.2). However, there was little difference in chase success for groups of one to three coyotes, and observations made during snow tracking suggested that in instances where multiple coyotes were involved in a chase, individual coyotes within each group often killed deer unassisted (see Patterson 1994). Single coyotes killed at least 16 deer (22.9% of all kills for which group size could be determined). Previous conclusions that predation on deer by solitary eastern coyotes in winter is insignificant (Messier et al. 1986, Parker and Maxwell 1989, Brundige 1993) may be incorrect. These studies may have underestimated deer killing rates of solitary coyotes because tracking efforts focused primarily on pairs and groups of coyotes.

Although the distance of successful chases was independent of group size, the mean distance of unsuccessful chases increased with

coyote group size (Fig. 4.3). Larger groups were probably more reluctant to give up chase due to a greater expectation of success.

Effects of deer distribution and abundance on vulnerability to predation.

In many areas of low deer density, coyotes fed primarily on snowshoe hares (Chapter 3) yet the few deer living in these areas appear to have been more heavily exploited by coyotes (Fig. 4.2). This is similar to findings from deer-coyote systems in Québec (Messier and Barrette 1985) and New York (Brundige 1993). Although encounters with deer probably occurred less frequently in areas of low deer density, the success of these encounters was higher. This likely occurred because deer were more vulnerable to predation due to impeded movements from deep snow (due to the lack of established trails) and the reduced ability of deer to detect predators at low densities (Messier and Barrette 1985).

Whitlaw et al. (1998) reported that survival of adult deer in winter yards in northern New Brunswick was not higher than for a non-yarding population in southern New Brunswick. They suggested that this finding refuted the hypothesis that yarding behaviour results in increased winter survival for deer. However, given the large differences in winter severity experienced by the two populations (Whitlaw et al. 1998), higher winter survival rates would be expected for the southern population, regardless of yarding behaviour (Verme 1965, Nelson and Mech 1981, Nelson and Mech 1986b). The analyses presented by Messier and Barrette (1985), and in this paper, suggest only that within a given study area yarded deer are

less likely to be killed by coyotes. Neither study suggests that predation rates on yarded deer within a given study area should be lower than for non-yarded deer in other geographic areas.

Further, Whitlaw et al. (1998) did not comment on the exact timing or specific locations of deaths for deer killed by coyotes in their study (in the core yarding area, edge of yard or pocket yard, enroute to summer range etc.). However, an unpublished progress report (H. A. Whitlaw et al. 1994. Survival and mortality of whitetailed deer in managed forests of northern New Brunswick-status report, unpublished. New Brunswick Cooperative Fish and Wildlife Research Unit, Fredericton, New Brunswick, Canada) states that five of seven mortalities attributed to coyote predation during winter 1994 (includes adults and 10 month old fawns) occurred while deer were travelling to their summer ranges. Therefore it is clear that at least some of the killed deer documented by Whitlaw et al. (1998) were not actually killed within the Odell yard. A more appropriate test of the hypothesis of reduced predation on yarded deer would be to compare predation rates of yarding vs. non-yarding deer within the same region or study area (and thus subjected to similar climatic and environmental conditions). Based on existing data (Nelson and Mech 1981, Messier and Barrette 1985, this study), I suggest that the hypothesis of reduced predation for yarded vs. nonyarded deer is sound.

Effects of forest harvesting on deer vulnerability to coyote predation.

The mean distance of deer kills to recent clear-cuts in the CB study area was less than expected. I stratified the distribution of the random points, thus, this result is probably not due to differences in deer abundance near harvested areas. I did not compare the number of kills actually occurring within clear-cuts with the number expected if kills where uniform throughout each study area because the mean distance of successful chases (270 m) was sufficient to allow many deer to enter forested stands before being subdued. I found a significant relationship between the proximity to clear-cuts and deer kills in CB despite the fact that most deer ran away from more open areas when pursued, which reinforces the significance of this relationship. I suggest that relatively deeper snows, and less escape cover, increased the vulnerability of deer to predation in and around clear-cut stands. Generally milder weather, and less reliance on browse in clear-cut stands as a food source (Lock 1997) likely resulted in the lack of a significant relationship between deer kills and the proximity to clear-cuts in OC.

#### Changes in killing rates over winter

An increased proportion of deer in the diet of coyotes from mid to late winter has been previously documented by Huegel and Rongstad (1985), Parker and Maxwell (1989), and Dibello et al. (1990) for coyotes in Wisconsin, northern New Brunswick, and Maine, respectively. This study supports Parker and Maxwell's (1989)

contention that this change occurs despite no perceptible change in the availability of alternate prey. Parker and Maxwell (1989) suggested that increased travel and sociality of coyotes during the breeding season, and greater vulnerability of deer due to winter severity, resulted in the switch from hare to deer as a principal prey item during mid to late winter. Breeding pairs of covotes in Nova Scotia are very stable throughout the winter and family groups are generally largest during early winter, before this change in prey use occurs (Chapter 2). Further, daily movements of coyotes were actually reduced during winter relative to other times of the year (Patterson et al. 1999) and mate seeking did not appear to be a common or time intensive activity for coyotes (Chapter 2, Patterson et al. 1999). My data do not support the theory that increased travel and sociality of coyotes during the breeding season contributed to greater use of deer. However, I do agree with Parker and Maxwell (1989) that increased vulnerability of deer as winter progresses is likely an important contributor.

Coyotes in CBH left areas of very high hare abundance during late winter, apparently in search of deer or agricultural carrion (see Chapter 2). White-tailed deer meat contains more fat than the relatively lean snowshoe hare (Litvaitis and Mautz 1980, Pekins and Mautz 1990), and the energetic requirements of coyotes during winter likely favor consumption of deer rather than hare (Pekins and Mautz 1990). I believe that an innate preference for deer over hare, and increased deer vulnerability (due to a snow impediment and a reduction in body condition) during late winter, contribute to the switch from hare to deer during late winter in many areas.

#### Management implications

The eastern coyote has been implicated as a major contributor to widespread deer declines throughout northeastern North America (Lavigne 1992b, Patterson 1994, Parker 1995, Crête and Lemieux 1996). It appears that over a broad range of deer densities, killing rates of deer by coyotes are influenced primarily by deer vulnerability, coyote social behaviour, and the availability of alternate prey. Although coyotes did not exhibit a significant functional response to different deer densities after controlling for the influence of snowshoe hare, individual deer were less likely to be killed in areas of high deer density (Fig. 4.2). Thus, over the lower range of deer densities (~0-1 deer/ km<sup>2</sup>), deer density may be inversely related to the vulnerability of deer to predation during winter.

Deer managers in the Northeast should consider the limiting effects (sensu Sinclair 1989) of coyote predation when establishing harvest quotas (Lavigne 1992b). Traditionally, management agencies have addressed the limiting effects of predation by considering predator and/ or prey abundance (Theberge 1990). However this study demonstrates that factors such as the relative abundance and vulnerability of alternate prey, winter severity, and coyote social organization also significantly influence predation on deer by coyotes, and thus must be considered. In areas where deer and hare are principal prey items, I suggest that predation on deer may increase sharply with increased snow depths or when hare and/ or deer numbers decline (also see Chapter 3). However, an understanding of the numerical response of coyotes to deer and hare densities is essential for a more complete understanding of the effects of coyote predation on white-tailed deer.

# 5. COYOTE PREDATION ON WHITE-TAILED DEER IN A MULTI-PREY SYSTEM IN NOVA SCOTIA

#### INTRODUCTION

Predation is an important factor influencing the population dynamics of many mammal species (Todd and Keith 1983, Messier et al. 1986, Erlinge 1987, Potvin et al. 1988, Messier 1994, Krebs et al. 1995). However, the role of predation in creating prolonged prey suppression (i.e., regulation as opposed to simple limitation) is an issue of considerable debate (Erlinge et al. 1984, Kid and Lewis 1987, Boutin 1992, Pech et al. 1992, Messier 1991, 1994). Limiting factors refer to any factors that quantifiably affect population growth, whereas regulating factors are limiting factors characterized by density-dependent processes that keep populations within normal density ranges (Murray 1982, Sinclair 1989, Messier 1991). The distinction between limiting and regulating factors has only recently been emphasized in predator-ungulate studies (Sinclair 1989, Messier 1991, Dale et al. 1994).

Skogland (1991) reviewed "recent" predator-ungulate studies and concluded that although several cases of limitation by predators were evident, evidence for regulation was elusive. Much of our current understanding of predator-ungulate dynamics comes from studies of wolf predation on moose (*Alces alces*) (see Boutin 1992, Messier 1994, and Van Ballenberghe and Ballard 1994 for reviews). Boutin (1992) reviewed studies examining the influence of predation on moose population dynamics and concluded that the wide acceptance of predation as a major limiting and/ or regulating factor for moose was premature. Other researchers (Messier and Crête 1985, Messier 1994, Van Ballenberghe and Ballard 1994, Hayes 1995, Joly and Messier 1999) have suggested that there is evidence for predator regulation of moose.

To determine if predation is regulating prey densities, the researcher should quantify the *total response* of predators to changing densities of the prey (Messier 1994, 1995, Seip 1992). The total response of the predator represents the product of the functional and numerical responses (Seip 1992). The functional response describes how the number of prey consumed per predator varies with prey density, whereas the numerical response describes changes in predator density as a function of prey density (Solomon 1949, Holling 1959, Messier 1995).

The major types of functional and numerical responses have been reviewed by May (1981), Pech et al. (1992), and Messier (1994, 1995). However, predation can only be regulatory if the proportion of the prey population killed increases with prey density and exceeds the net productivity of the prey population (Sinclair and Pech 1996, O'Donoghue et al. 1998). Depensatory predation occurs when the percentage of prey killed is inversely related to prey density (Potvin et al. 1988, Messier 1995).

#### Coyote Predation on White-tailed Deer

Coyotes colonized Nova Scotia during the early 1980s (Moore and Parker 1992). In much of the Northeast, coyotes must contend with lower prey diversity and abundance relative to their western counterparts (Harrison 1992a, Parker 1995, Chapter 3). White-tailed

deer and the snowshoe hare are the primary prey species of the eastern coyote (Messier et al. 1986, Parker 1986, Chapter 3). Larger body size (Larivière and Crête 1993, Parker 1995) and a greater tendency to hunt in extended family groups during winter (Messier and Barrette 1982, Brundige 1993) have been related to the high use of deer by eastern coyotes relative to their western counterparts (Messier et al. 1986, Brundige 1993, Larivière and Crête 1993). Wolves are not present east of the Saint Lawrence River and some researchers have suggested that coyotes have replaced wolves as a significant predator of white-tailed deer in northeastern North America (Mathews and Porter 1992, Brundige 1993, Ballard et al. 1999).

In Nova Scotia, and many other regions of the Northeast, deer densities increased rapidly during the mid 1980s (Fig. 5.1), apparently due to a series of mild winters (Patton 1991, Parker 1995). Despite an effort to curb the increase via liberal hunting regulations, deer in Nova Scotia had presumably exceeded K carrying capacity and were in poor physical condition by winter 1987, at which time a substantial decline in density began (Patton 1991). Coyotes were still becoming established throughout the province in 1987, and although coyote predation was unable to prevent the peak in deer density, it probably accelerated the subsequent decline (Patton 1991, Parker 1995, Patterson 1995). In the autumn of 1993, hunting in Nova Scotia was restricted to antlered (males >1 yr) deer only. However, despite mild winter conditions from 1994 through



Fig. 5.1. Population trends of white-tailed deer in Nova Scotia, 1983 - 1997. Deer densities were estimated using pellet group counts conducted along 440  $\pm$  3 (SE) transect lines distributed randomly throughout the province (Patton 1991). I assumed a defection rate of 16 pellet groups/ day and an average date of leaf fall of 1 November.

1998 (MacDonald 1996, Patterson et al. 1998), deer densities did not show a noticeable increase until the winter of 1997 (Fig. 5.1).

Several authors have suggested that coyote predation can be a significant limiting factor for white-tailed deer. In the 212 km<sup>2</sup> Bonaventure deer yard in eastern Québec, coyotes removed an estimated 20% of the pre-wintering deer herd during winter 1992, despite relatively mild winter conditions (Poulle et al. 1993). Messier et al. (1986) concluded that coyote predation may limit deer densities in southern Québec. Coyotes were the largest single cause of mortality for both adult (Whitlaw et al. 1998) and fawn (Ballard et al. 1999) deer in Northern New Brunswick. Patterson (1995) suggested that coyote predation was limiting deer at densities well below K carrying capacity (sensu Caughley 1976) in Kejimkujik National Park, Nova Scotia.

If coyotes primarily remove deer that would have died of other causes in the absence of predation (compensatory mortality), the impact of predation would be minimal regardless of the number of deer removed. However, Lavigne (1992b) determined that 50-70% (depending on age class) of a sample of 863 deer killed by coyotes in Maine were in good physical condition (based on >80% femur marrow fat (FMF)). Further, nearly half of these deer were mature, suggesting that losses to coyotes may be an important, additive, limiting factor. In a deer-wolf system in south-western Québec, wolves preyed mainly on prime-aged deer in periods of deer scarcity but selected fawns and older animals when deer were more abundant (Potvin et al. 1988). In situations like this, predation may have little effect on deer populations when deer densities are high but a major limiting effect when deer densities are low and may be antiregulatory (Potvin et al. 1988).

The purpose of this study was to determine the extent and significance of coyote predation as a limiting factor, and to explore the possibility of predator regulation for white-tailed deer in Nova Scotia. The consumption of deer by territorial coyotes in Nova Scotia was inversely related to the density of snowshoe hares (Chapters 3, 4). Further, deer vulnerability to predation by coyotes may have been inversely related to deer density (Chapters 3, 4, see also Messier and Barrette 1985). I predicted that predation rates on deer would be greatest in areas with low deer and hare abundance and would subsequently decrease as the abundance of deer and/ or hare increased. Consequently, I predicted that predation on deer by coyotes is anti-regulatory, and may lead to local extirpation of deer.

#### METHODS

#### Estimation of coyote densities

I estimated mid-winter coyote densities in each study area by dividing the total number of coyotes observed by the total area occupied by the territories of radio-collared family groups (details in Chapter 2). I calculated densities for other seasons of the year by multiplying the mid-winter density estimates by the survival rates of radio-collared coyotes in each area and the reproductive success of radio-collared breeding pair members (Chapter 2).

#### Coyote Food Habits

Seasonal food habits of coyotes within each study area were determined primarily from scat analysis (Chapter 3) and more directly by back-tracking radio-collared coyotes to kill sites during winter (Chapter 4). I classified a dead deer as a coyote kill if there was positive evidence of attack or chase. Deer killing rates (deer killed • coyote<sup>-1</sup> • 100 days<sup>-1</sup>) were calculated from the cumulative tracking periods and the respective kills (Chapter 4).

# Age, sex, and condition of deer killed by coyotes

I collected a jawbone and femur from any coyote-killed or scavenged deer discovered to provide information on age structure and physical condition. Deer were aged based on tooth wear and development (Severinghaus 1949). Errors in aging resulting from this method are generally only significant in the older age classes (8 yr +, Gilbert and Stolt 1970) which represented less than five percent of deer encountered during this study. I examined whether ages of coyote-killed deer were representative of the local deer populations by comparing the age distribution of road-killed deer with that of deer killed by coyotes using *G*-tests (Sokal and Rohlf 1995). I used femur marrow fat (FMF) as an index of body condition (Neiland 1970). Although Bischoff (1954) and Mech and Delguidice (1985) cautioned that FMF does not always indicate that an ungulate was in good physical condition, Lavigne (1992b: 155) concluded that "FMF levels approximating 80% or higher are closely associated with

substantial reserves (e.g.,  $\geq$ 5 percent total body fat) of other body fat depots that are characteristic of 'good' physical condition." Deer with FMF <25% were classified as malnourished. I compared the numbers of healthy and malnourished fawn and adult deer killed by coyotes with those in the road-killed sample using *G*-tests (Sokal and Rohlf 1995). I used the Bonferroni *Z*-Test for proportions if the *G*-test led to the rejection of the hypothesis of homogeneity of age classes or relative conditions among coyote and road-killed deer (see Neu et al. 1974, Messier and Barrette 1985).

#### Year-long predation rates and population balances

To estimate year-long predation rates I estimated the number of adult (>1 yr old) and fawn deer alive on 1 June in each study area (Table 5.1), and the total number killed by coyotes over the ensuing biological year. With a few exceptions, I followed the methods outlined by Messier and Crête (1985). Predation rates refer to the percent losses of postnatal (immediately following the birth pulse each summer) populations from 1 June of the current year to 31 May of the following year. Although other researchers may choose different values for some assumptions, applying the same assumptions for both study areas during all periods validates my comparison.

## Consumption rates

Total annual consumption of deer by coyotes was estimated by calculating the energy requirements of the coyote populations in each study area and then converting this into deer equivalents. The proportion of both fawn and adult deer in the biomass originally

		Queens County		Cape Breton		
		1993	1995-1996	1995-1996		
(A)	Mid winter density <sup>2</sup>	221	216	350		
(B)	Proportion surviving					
	until June l <sup>2</sup>	0.850	0.937	0.874		
(C)	Density of deer ≥l yr					
	old on June 1	188	2 <b>02</b>	306		
(D)	Density of females >1 yr					
	old on June l <sup>1</sup>	94	91	122		
(E)	Density of females 1 yr					
	old on June l <sup>1</sup>	25	-18	68		
(F)	Number of fawns per					
	dce >1 yr old <sup>4</sup>	1.20	1.55	1.45		
(G)	Number of fawns per					
	female l yr old'	0.20	0.17	0.13		
(H)	Density of fawns,					
	[(D*F)+(E*G)]*0.9 <sup>5</sup>	106	120	167		
(I)	Overall density (C+H)	294	322	473		

Table 5.1. Derivation of the density (deer /100  $\text{km}^2$ ) of fawn and adult white-tailed deer on June 1 (post-natal density) in the Queens County (QC) and Cape Breton (CB) study areas.

<sup>1</sup>Estimated from pellet group inventories (see text).

"Estimated from mortality rates of radio collared deer in each study area (see text). No data was available for QC during 1993. The rate presented for 1993 is an estimate of winter mortality based on winter severity experienced during this winter relative to winters for which survival data was available. "Proportion of females and fawns in population during winter were taken from regional road kill data. Sample sizes were as follows: QC 1993 = 65, QC 1995-96 = 165, CB = 136.

"Calculated from mean in utero reproductive rates of road-killed deer examined in the region of each study area during winter. Sample sizes (no. females examined) were as follows: QC 1993 = 40, QC 1995-96 = 96, CB = 58. "The correction factor (0.9) was used to account for perinatal mortality (Verme "The correction factor (0.9) was used to account for perinatal mortality (Verme ingested by coyotes was determined by scat analysis, using the equation of Weaver (1993) to convert percent biomass in scats to percent biomass originally ingested for each prey species (Chapter 3). Energetic requirements of coyotes were estimated using time budget analyses (Pekins 1992). I monitored collared coyotes for continuous 24-hour periods throughout the year to provide more accurate data on the timing and duration of activity periods, and daily distances traveled (Patterson et al. 1999).

I estimated the number of adult deer, fawns, and hares eaten by coyotes/ 100 km<sup>2</sup> during each of five seasonal periods (Apr. -May, June - July, Aug. - 15 Sept., 16 Sept. - Nov., Dec. - Mar.) using equation 3.1. The daily caloric requirement of coyotes was calculated as outlined in chapter 3. with the addition of the following assumptions:

- the average masses of pups = 4.0, 7.5, 9.0 kg during the June-July, Aug- Sept 15, Sept 16- Nov 30 time intervals, respectively (calculated as per Brundige 1993)
- 2) pups are inactive at birth, and their activity increases progressively throughout the summer until autumn, when their activity and movements equals that of adults.
- 20% of the biomass from the carcasses of adult deer was lost to scavenging (see Hayes 1995).

During winter, killing rates of deer (deer killed  $\cdot$  pack<sup>-1</sup>  $\cdot$  100 days <sup>-1</sup>) were estimated directly from the cumulative tracking periods and the respective kills (Chapter 4). Per capita killing rates (deer killed  $\cdot$  coyote<sup>-1</sup>  $\cdot$  100 days <sup>-1</sup>) were estimated by dividing the

number of deer killed • pack<sup>-1</sup> • 100 days <sup>-1</sup> by mean winter traveling group sizes (Chapter 2). For each family group included in this analysis, I considered only those tracking sessions in which none of the relocations were separated by >60 hours. I am aware that the carcasses of some fawns may have been completely consumed during this period. However, the minimal snowfall and frequent rains experienced during the winters of 1995-1997 have necessitated this assumption. The relatively low killing rates observed in this study (Chapter 4) should minimize any appreciable bias resulting from this assumption.

# Scavenging by coyotes

The amount of scavenging of deer by coyotes was determined for each study area based on the examination of 81 deer carcasses fed upon by coyotes during this study for which the cause of death was ascertained (Table 5.2). Seasonal consumption rates of deer were adjusted to represent only those deer killed by coyotes. I could not estimate the proportion of fawns in the summer diet resulting from scavenging and arbitrarily assigned a value of 10% of the biomass of fawn consumed (Verme 1977). Because hairs of fawn and adult deer were difficult to distinguish after August, the ratio of fawns:adults consumed by coyotes from September through May was estimated from the proportion of fawns in the total sample of deer killed by coyotes during winter in each study area (as observed during winter snowtracking).

Validating the estimation of deer consumption rates

Predation rates were calculated independently for each study area (QC, June through May, 1993-94, and 1996-1997) and the CB study area (June 1996 through May 1997). I did not estimate separate predation rates for deer living in the highland and lowland areas of CB due to the seasonal migration of most deer from CBH to CBL during winter (MacDonald 1996, Chapter 2). I assessed the accuracy of deer killing rates calculated from time budget analyses by comparing predicted rates during winter with actual killing rates based on winter tracking of radio-collared coyotes. I also compared predation rates predicted from the above two methods with estimates obtained by monitoring radio-collared deer in each study area (Patterson et al., in prep.). One hundred and twenty-four deer were equipped with radio-collares containing mortality switches. Monitoring schedules for collared deer and specific details of the analysis are detailed in Patterson et al. (in prep.).

I compared predicted predation rates with the rate of increase of deer in Nova Scotia expected if coyotes were absent. The finite rate of increase ( $\lambda$ ) for deer was calculated using data on agespecific fecundity rates calculated from *in utero* reproductive counts from road-killed deer examined on Cape Breton Island and in south-western Nova Scotia (representative of QC), during winters 1994-1997 (n = 200 for QC, 170 for CB). I assumed a baseline neonatal mortality rate of 10% to estimate the number of live births in relation to the number of fetus per doe (Verme 1977). Non-coyote related mortality for fawns <6 months were taken from the recent

study of Ballard et al. (1999) for neonatal fawns in Northern New Brunswick. Mortality factors other than coyote predation for deer >6 months were estimated from radio-telemetry (Patterson et al., in prep.). I averaged the annual predation rates estimated by scat analysis and telemetry to arrive at my final estimates for both fawn and adult deer.

Food competition must depress deer population growth at higher densities (McCullough 1979, Eberhardt 1998). The percentage of road-killed deer examined during winter in Nova Scotia with FMF <25% increased dramatically when the provincial deer population exceeded 100,000 (~2.7/ km<sup>2</sup> province wide, Fig. 5.2). However, the exact relationship between malnutrition and mortality in deer is not clear (see Bischoff 1954, Mech and Delguidice 1985, Lavigne 1992a, b, Torbit et al. 1985). Fecundity rates of deer in Nova Scotia also declined during the boom in deer density during the 1980s (Patton 1985, 1991). I estimated density-dependent changes in  $\lambda$  for deer in Nova Scotia in the absence of coyote predation using the following generalized logistic growth function:

 $\lambda_{d} = [\lambda_{m}^{*}((K - d/K)^{-0.3})] * (1 - M)$ (5.1)

where:  $d = no. \text{ deer} / \text{ km}^2$ ,  $\lambda_d$  is the rate of growth at density d,  $\lambda_m$ is the maximum potential rate of growth in the absence of forage competition, K is carrying capacity for deer in Nova Scotia (assumed to be ~6.0 /km<sup>2</sup>), and M is the baseline mortality rate from all factors other than coyote predation (estimated with radio-telemetry; Patterson et al., in prep.). I assumed that density dependent effects on  $\lambda$  were negligible at densities <2.0 deer/ km<sup>2</sup>.



Fig. 5.2. The prevalence of winter malnutrition (as indexed by <25% femur marrow fat) among fawn and adult (>1 yr) white-tailed deer, in Nova Scotia, 1983 - 1997, as assessed from road-killed deer examined from February through April each year.
### Modeling coyote predation in relation to deer and hare abundance

### Coyote functional response

Although many multi-prey models assume that different prey are taken in proportion to their abundance (Hilborn and Sinclair 1979, Powell 1980, Eberhardt 1998), this assumption may be inappropriate for the coyote-deer-hare systems observed in forested regions of northeastern North America because of differences in the relative vulnerability of deer and hares to predation (Chapters 3, 4). I used the multiprey disc equation (Charnov 1973, Hilborn and Sinclair 1979):

$$E_{d} = \frac{a_{d}N_{d}}{1 + ((a_{d}h_{d}*N_{d}) + (a_{h}h_{h}*N_{h}))}$$
(5.2)

where E is the number of prey eaten per unit time by each predator, N is the abundance of each prey, and a and h are the attack rate and handling time constants as per Holling's (1959) disk equation. The subscripts d and h refer to deer and hare, respectively.

I estimated the number of hares eaten  $\cdot$  coyote<sup>-1</sup>  $\cdot$  100 days<sup>-1</sup> in each territory during winter using equation 3.1. In addition to the 9 territories used to estimate hare consumption in chapter 3, I used data from two more territories. Data from the Devonshire territory was not used in chapter 3 because only 19 scats were analyzed during winter 1996, whereas we had set an *a priori* minimum of 20 for inclusion when publishing chapter 3 (Patterson et al. 1998). Similarly, data from the Eden territory during winter 1995 was not previously used because the hare density estimate presented in Table 4.1 was unavailable.

I obtained estimates for  $h_d$  and  $h_h$  as per Hilborn and Sinclair (1979) as follows:

Based on the calculations detailed in chapter 3, the average adult and juvenile coyote required approximately 1570 and 1260 Kcal/ day, respectively. Assuming that 35 and 1.4 kg of usable biomass were available from each deer and hare, respectively, each coyote would have required approximately 2.9 deer or 83 hare per 100 days. Thus, the corresponding estimates of  $h_d$  and  $h_h$  are 1/2.9 and 1/83, or 0.35 and 0.012, respectively.

Values of  $a_d$  and  $a_h$  were not estimated a priori but were obtained during the model fitting. I fitted each equation to the data using the non-linear regression module of the software program SigmaStat 2.03 (SPSS statistical software, SPSS Inc., Chicago, IL.). Statistical testing of each model was based on the coefficient of multiple determination (Sokal and Rohlf 1995).

### Coyote numerical response

Coyote densities closely track lagomorph abundance in several areas where lagomorphs are the dominant prey item (Todd et al. 1981, Knowlton and Stoddart 1992, O'Donoghue et al. 1997). Studies of wolves and their ungulate prey have also indicated the presence of a strong numerical response (Fuller 1989, Messier 1994, Hayes 1995). In the southwest Yukon, where coyote and hare densities changed markedly from year to year, coyote density was linearly related to hare density from the previous year (O'Donoghue et al. 1997). I estimated the coyote numerical response to the combined biomass of deer and hare by plotting the five coyote density estimates

determined during this study, and a single density estimate presented by Messier (1979) for a coyote-deer-hare system in a forested region in Québec, against the estimated biomass of deer and hare during the previous winter. I assumed that average hare densities encountered during Messier's (1979) study were comparable to moderate densities estimated during this study (~30 hare/ km<sup>2</sup>). I assumed that 35 and 1.4 kg of useable biomass was available to coyotes from each deer and hare, respectively.

Predation rates on deer as a function of deer and hare densities

I calculated the *total response* (deer killed •100 km<sup>-2</sup> •100 days <sup>-i</sup>) of coyotes to changes in deer and hare abundance as the product of the functional and numerical responses. I estimated the number of deer consumed/ 100 days during each of the following seasons: April-May, June-July, Aug.-Sept. 15, Sept. 16-Nov. 30, relative to the number consumed/ 100 days during winter (Dec. - March). Using this calibration, I then calculated the year-long predation rate as:

Year-long predation rate = total response \*  $\sum ((l_1/100) \cdot (k_1/k_w))$  (5.3) where:  $l_1$  = length of each season in days,  $k_1$  = no. deer consumed/ 100 days during each season, and  $k_w$  = no. deer consumed/ 100 days during winter. I investigated the proportional effects of the functional and numerical response on predicted predation rates over the range of observed prey densities following methods detailed by Messier (1994).

### RESULTS

### Coyote densities

Mid-winter coyote densities ranged from 4.3 to 13.9 coyotes/ 100 km<sup>2</sup>, and changed markedly during the course of my study (Chapter 2). Differences in density estimates resulted from changes in territory size, habitat saturation (the proportion of the total landscape in each study area occupied by coyote territories), group size, and the abundance of solitary coyotes (Chapter 2). Coyote densities declined ~50% in the QC area from winter 1993 through 1997. I estimated density in CB during 1996 and 1997 only but my results suggest a substantial (88%) increase, resulting primarily from the formation of two new territories augmented by an apparent increase in fecundity and juvenile survival.

### Age, sex, and condition of deer killed by coyotes

I examined the carcasses of 102 deer consumed by coyotes during winter (Table 5.2). Sixty-nine deer were victims of predation, five died of natural causes (includes two prime aged bucks and one old female that died of malnutrition, and two old females that died of unknown causes), two were killed in coyote snares, two were road-killed, two shot and not recovered during the autumn firearms deer hunting season, and one was shot and abandoned in early winter. The cause of death of remaining 21 deer could not be determined.

Based on a winter sample of local road-killed deer (obtained from the counties containing each study area) examined from January

through March, 1994 - 1997, the age distribution of deer killed by coyotes in CB differed significantly from that of the local deer population (n = 136 road-killed deer, G = 6.74, P = 0.03). Fawns were over-represented among the sample of coyote-killed deer (Z = 2.24, P = 0.02). The age distribution of deer killed by coyotes in QC did not differ significantly from that of local road-killed deer (n = 165 road-killed deer, G = 3.56, P > 0.10). However, considering the 1992-1994 and 1995-1997 periods separately (based on differences in winter severity and coyote feeding behavior - see Chapter 3), fawns were over-represented among the sample of coyotekilled deer examined in QC during 1992-94 (Z = 2.52, P = 0.01) whereas deer  $\geq 8$  yr were over-represented in the sample of coyote killed deer examined in the same area during 1995-97 (Z = 3.11, P = 0.002).

Femur marrow fat reserves of fawn and adult deer killed by coyotes appeared to be as good or better than those of road-killed deer in the vicinity of each study area (G < 5.02, P > 0.08, Fig. 5.3). Only one of the 56 deer killed by coyotes that were assessed had <25% FMF. Seven percent had FMF levels between 26-50%, 25% had between 51-79% and the remaining 66% had FMF levels ≥80% (Fig. 5.3). Most of the deer exhibiting depleted FMF levels were killed in the CBH area, which experienced the greatest snow depths encountered during this study.

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<sup>1</sup>Includes two prime aged bucks and one old female that died of malnutrition, and one old female that died of unknown causes.

<sup>2</sup>Includes two deer killed in coyote snares, two road kills, two wounded during hunting season, and one shot and abandoned after the hunting season.

### Scavenging by coyotes

Overall, 13.5 and 24.4% of deer consumed during winter in the Queens County and Cape Breton study areas, respectively, died of causes other than predation (Table 5.2). Most of the deer scavenged by coyotes, for which the original cause of death could be ascertained, were killed by hunting or trapping related activities during the autumn firearms and winter trapping seasons, or of natural causes during winter. Because these sources of mortality were largely absent from May through September, I assumed that summer scavenging rates were 50% of those observed during winter. Estimates of deer consumption based on the scat analyses were adjusted to account for these estimates of scavenging.

### Year-long predation rates and population balances

### Consumption rates

All coyote packs examined during this study killed deer during winter (Chapter 4). Winter killing rates averaged 2.7, 2.5 and 1.0 deer killed  $\bullet$  coyote<sup>-1</sup>  $\bullet$  100 days <sup>-1</sup> in the QC, CBL, and CBH areas, respectively. Winter severity and the availability of snowshoe hare influenced winter killing rates more than pack size (Chapter 4). The presence of high concentrations of deer in the Eden DWA did not substantially elevate the killing rates of deer by coyotes. Many of the deer killed by the pack living within the Eden DWA were killed in areas peripheral to the actual winter yard (Chapter 4).

Year-long predation rates were estimated at 25.0 and 13.6% of the deer population in QC during 1992-93 and 1996-97, respectively



Fig. 5.3. Percent femur marrow fat of adult (>1 year) and fawn deer killed by coyotes in the Queens County and Cape Breton study areas, winters 1994 - 1997, in relation to road-killed deer.

(Table 5.3). The predation rate was estimated at 9.0% in CB during 1996-97 (Table 5.3). Predation on fawns during summer accounted for a large portion of the total estimates, but predation on adult deer was substantial during 1992-1993 (Table 5.3). Coyote predation was less significant than hunting (legal and illegal combined) as a limiting factor for deer (Table 5.4, Patterson et al., in prep.). However, when the additional impact of predation by bobcats (*Lynx rufus*), black bears (*Ursus americanus*), and lynx (*Lynx canadensis*) was considered, the gap narrowed considerably, particularly in QC (Table 5.4). Losses to malnutrition during winter were minimal in both study areas.

### Validating deer consumption rates

There was some variation in deer killing rates as estimated by radio-telemetry, scat analysis, and winter snowtracking (Table 5.5). Estimates of winter killing rates based on snowtracking were similar to estimates based on scat analysis, suggesting that I probably missed few kills while snowtracking. Annual predation rates based on telemetry (Patterson et al., in prep.) were slightly higher in CB and considerably lower in QC (outside the 95% confidence interval, Table 5.5), relative to estimates based on scat analysis and estimates of coyote densities (Table 5.5). I averaged the rates estimated by scat analysis and telemetry to arrive at my final estimates of annual predation rates on both fawn and adult deer (Table 5.5).

Table 5.4 summarizes the natality-mortality balances for deer

	QC 1993-1994			QC 1995-1997			CB 1995 - 1997		
	Summer	Winter	Annual	Summer	Winter	Annua l	Summer	Winter	Annual
(A) no, adult coyotes									
/100 km <sup>21</sup>	7.7	9.3		4.1	5.5		6.5	10.6	
(B) no. FD <sup>2</sup>									
Adult	112	89.3	201	105	60,3	165	41.7	44.5	86.2
Fawn	37.7	12.4	50.1	34.6	8.3	42,9	28.7	12,6	41.3
(C) Kg consumed /100km <sup>2</sup> <sup>3</sup>									
Adult	1305	978	2283	695	338	1033	404	475	676
Fawn	428	111	539	237	46.6	283.6	291	134	342
{D} no. kills/100km <sup>2 4</sup>									
Adult	25.3	24.2	49.5	15.5	8.4	23.9	8.3	10.3	18,6
Fawn	32.2	4.0	36,2	10.4	1.7	20,1	19,7	4,2	23,9
(E) Year-long predation rate	(%)5								
Adult			20.0			11.0			6,1
Fawn			34.1			16,8			14,4
All ages			25.0			13,6			9.0

Table 5.3. Estimation of the number of deer killed by coyotes (animals /100km<sup>2</sup>), based on scat analysis and estimates of coyote densities, in the Queens County study area, June 1993-May 1994, and June 1995-May 1997, and the Cape Breton study area (CB), June 1995-May 1997.

<sup>1</sup> See Chapter 2.

<sup>2</sup> No. Feeding Days was calculated as (percent volume of deer in the diet during each time interval)\*(number of days),

<sup>3</sup> Calculated as [(Total daily caloric requirements of all coyotes/ 100km<sup>2</sup>)/ 1400 kcal/ kg]\*(B).

<sup>4</sup> Calculated as ((C)\*(proportion of deer consumed that is actually killed - see text)/average weight of both fawn and adult deer during each time interval -see text).

<sup>5</sup> Calculated as the annual estimate from (D)/(deer population estimates outlined in Table 2).

in each study area and period. I had no data on the relative abundance of bobcat, lynx, and black bears among or within either study area. However, based on track and scat observations, and actual sightings of the predators, I believe that both black bears and bobcats were more common in QC than CB (despite higher hare densities in CB). Lynx were restricted primarily to CBH. Coyotes were implicated in 12 of 16 cases of predation on radio-collared deer (>6 months) examined during this study for which the predator could be positively identified (Patterson et al., in prep.). I assumed that predators other than coyotes removed 25 and 50%, respectively, as many adult and fawn (<6 months) deer as coyotes (Table 5.4, see also Linnell et al. 1995).

## Modeling coyote predation in relation to deer and hare abundance Coyote functional response

Coyotes showed strong functional responses to changes in the densities of deer and hares (Figs. 5.4, 5.5). The multiprey disc equation for deer:

deer killed • coyote<sup>1</sup> • 100 km<sup>-2</sup> = 
$$\frac{9.3 * (deer / km^2)}{(1 + (9.3 * 0.35 * deer / km^2) + (3.9 * 0.01 * hare / km^2)}$$
(5.4)

was significant at P = 0.005 ( $r^2 = 0.53$ , n = 13, Fig. 5.4) and suggested that coyotes exhibited a Type II functional response to increasing deer densities. The number of deer killed • coyote<sup>-1</sup> • 100 days<sup>-1</sup> was inversely related to hare density (Fig. 5.4, see also Chapter 4). At intermediate deer densities (1.5 - 3.5 deer/ km<sup>2</sup>), killing rates of deer declined by ~22% as hare densities increased

	QC 92-93	OC 95-97	CB 95-97
Registered harvest			
Males >1 yr old	35 <sup>1</sup>	24.0	18.8
females and fawns	18.0 <sup>1</sup>	0	0
Unregistered harvest			
males >1 yr old	4 <sup>2</sup>	8.0	4.7
females and fawns <sup>1</sup>	4 <sup>2</sup>	13.4	6.7
Winter malnutrition <sup>3</sup>			
Males >1 yr old	4	3	6.4
Females >1 yr old	3	2	2.0
Fawns	5	3	14.8
Coyote predation <sup>4</sup>			
adults	20.0	7.2	7.6
fawns	34.1	16.5	16.4
Other predators <sup>5</sup>			
adults	5.3	1.9	1.9
fawns	17.0	8.3	8.2
Other mortality <sup>6</sup>			
fawns	3	8.2	4.0
adults	2	3.2	4.0
Recruitment (%)	26.6	47.5	44.4
Growth Rate $(\lambda)^{\frac{3}{2}}$	0.56	1.24	1.23
Comments	Continued to decl	ine	Population increasing
	until winter 1996, increasing in 1997		regionally during winters 1996-97

Table 5.4. Estimated mortality factors (expressed as percentages of the population on 1 June) for white-tailed deer in the Queens County (QC) study area, June 1992 to May 1993, June-May 1995 - 1997; and the Cape Breton study area (CB), June 1995 to May 1997.

<sup>1</sup>Harvest rates for this period were calculated based on regional population estimates and registered harvest (NSDNR, unpubl. data). Harvest rates (registered and unregistered) for other periods are based on radio-telemetry data (Patterson et al., in prep.).

<sup>2</sup> Antierless deer were not legally protected during this season thus it was easier for hunters to legally kill a deer. Poaching of both sexes of deer was probably more extensive after autumn 1992 when only antiered deer could be harvested legally. <sup>1</sup>I observed only 1 malnutrition loss during 28,959 telemetry days of monitoring deer in QC from spring 1994 - 1997, however, a higher incidence of malnutrition loss was suspected based on the proportion of road-killed deer with low femur marrow fat (see text). Although winter 1994 was much more severe than subsequent winters I assumed that the high predation rates observed during this winter would have partially compensated for a substantial increase in deaths due to malnutrition.

<sup>4</sup>Estimated rates for adults are based on the average of rates predicted from radiotelemetry and scat analysis. Because limited telemetry data were available for fawns, predation rates on fawns are based on scat analysis.

<sup>5</sup>Four of 16 radio-collared deer killed by predators were killed by either bobcats or lynx so I estimated this predation rate on adult deer as (0.25)\*(Predation rate attributable to coyotes). Predation rate on fawns by predators other than coyotes was estimated crudely from the literature (see text).

<sup>\*</sup>Includes deaths attributable to vehicle collisions, old age, and natural accidents or sickness.

Calculated as the percentage of the spring population comprised of fawns (see Hatter and Bergerud 1991).

<sup>1</sup>Calculated using the formula:  $\lambda = (1 - M)/(1 - R)$ , where M is the percentage of the spring population that died during the ensuing year and R is the percentage of the spring population comprised of fawns (see Hatter and Bergerud 1991).

	QC 1992	QC 1995-1997	CBL <sup>1</sup> 1995-1997
Annual Predation Rate (%)			
Telemetry			
Fawns <sup>2</sup>		16.4 (0.0-45.6)	18.3 (0.0-50.7)
Adults <sup>2</sup>		2.6 (0.0-6.3)	7.9 (2.6-13.2)
Scat analysis			
Fawns	34.1	16.5	16.4
Adults	20.0	11.8	7.2
Winter killing rates			
(deer killed • coyote <sup>-1</sup> • 100 <sup>-1</sup>	days) <sup>3</sup>		
Scat analysis	3.34	3.0	2.9
Winter snow tracking	3.6+3	2.7	2.3

Table 5.5. Comparison of coyote predation rates on deer estimated using radio-collared deer, coyote scat analysis, and winter snowtracking of radio-collared coyotes.

<sup>1</sup>Telemetry data was only available for CBL for so this comparison does not consider the CBH area.

<sup>1</sup>Pooled data for 1995-1996 in both study areas. Predation rates based on telemetry for fawns are based on data collected from deer >6 mo thus must be considered minimal. The 95% CI calculated by program Micromort (Heisey and Fuller 1985) are given in parenthesis.

<sup>1</sup>Winter predation rate estimates (Table 5.3) were adjusted to estimate kills  $\cdot$  coyote<sup>-1</sup>  $\cdot$  100<sup>-1</sup> days.

<sup>4</sup>Although I do not have comprehensive tracking data from this winter I am aware that at least one group in QC killed a minimum (based on intermittent tracking) of 8 deer in 80 days (minimum killing rate of 10 deer/ 100 days). Thus my prediction of high killing rates in QC during this winter seems reasonable. from 10 to 75 hares/ km<sup>2</sup>. Over the same range of deer densities the model suggests that the functional response to increasing deer densities exerted a greater influence on deer killing rates than the negative relationship between deer killing rates and hare density (Fig. 5.4).

The multiprey disc equation for hare:

hare killed • coyote<sup>1</sup> • 100 km<sup>-2</sup> = 
$$\frac{2.2 * (hare / km^2)}{(1 + (2.2 * 0.012 * hare / km^2) + (0.237 * 0.35 * deer / km^2)}$$
(5.5)

was significant at P = 0.001 ( $r^2 = 0.72$ , n = 11, Fig. 5.5). The model suggests a near linear functional response to increasing hare densities, and hare killing rates declined about 15% as deer densities increased from ~1.5 - 6.0 deer/ km<sup>2</sup> (Fig. 5.5).

The multiprey functional response was based on deer killing rates derived from snowtracking radio-collared coyotes, which accounted only for those kills made by group-living coyotes. Conversely, estimates based on the scat analyses and radio-telemetry accounted for predation by all coyotes. During this study single coyotes were implicated in significantly fewer deer kills than expected (Chapter 4), thus, killing rates estimated using the functional response may be higher than would be observed when considering all coyotes in a given area. I estimated that 39% of the coyotes occupying my study areas during this study were solitary (n = 30, Chapter 2). These solitary coyotes were either young coyotes temporarily disassociated from their parents, or coyotes that had dispersed and were still solitary. However, solitary



Fig. 5.4. The number of white-tailed deer killed • coyote<sup>-1</sup> • 100 days<sup>-1</sup> as a function of the relative densities of deer and snowshoe hare in the Queens County and Cape Breton study areas, winters 1995 through 1997. The multiprey functional response was estimated using the multi-prey disc equation (Charnov 1973, Hilborn and Sinclair 1979).



Fig. 5.5. The number of snowshoe hares killed • coyote<sup>-1</sup> • 100 days<sup>-1</sup> as a function of the relative densities of hare and white-tailed deer in the Queens County and Cape Breton study areas, winters 1995 through 1997. The multiprey functional response was estimated using the multi-prey disc equation (Charnov 1973, Hilborn and Sinclair 1979). coyotes were implicated in only 23% of all coyote-killed deer I examined. I corrected for this potential bias by multiplying the functional response by the following correction factor (*Cf*):

$$Cf = ((p_s * k_s) + p_q)$$
 (5.6)

where:  $p_s$  = the proportion of solitary coyotes in my study populations (0.39),  $k_s$  = the proportion of deer killed by solitary coyotes relative to group living coyotes (0.59), and  $p_g$  the proportion of group living coyotes in my study populations. This resulted in a scaling of the functional response by 0.84.

### Coyote numerical response

Although I had limited data, coyote density appeared to be linearly related to the combined biomass of deer and hare available during the previous year (y = 0.051x + 0.68,  $R^2 = 0.58$ , P = 0.08, n= 6, Fig. 5.6). At the highest coyote densities observed during this study (13.9/ 100 km<sup>2</sup>, CB 1997, Chapter 2), there was very little room for the establishment of new territories, even if existing territories contracted by 20-30%. Messier et al. (1986) reported that at a density of ~12.5/ 100 km<sup>2</sup>, the forested area they studied in southern Québec was saturated with coyote territories. Thus, although my limited data suggested a linear response, I imposed an asymptotic density of 16/ 100 km<sup>2</sup> for the coyote numerical response.

Predation rates on deer as a function of deer and hare densities

The model indicated that in the two prey system I studied, predation rates decreased sharply (depensatory) as deer densities



Fig. 5.6. The numerical response of coyotes in northeastern North America to changing prey biomass (the combined weight of white-tailed deer and snowshoe hare). I assumed that coyotes could consume 44 and 1.4 kg of useable biomass, respectively, from each deer and hare in winter.

increased from 0 - 1.5 deer  $/km^2$  (Fig. 5.7). Predation rates increased with hare density (change in elevation of the curve) but the shape of the curve remained unchanged. The model also predicted that coyote predation could drive deer populations to extinction if deer densities drop below 0.4/  $km^2$  assuming typical recruitment for deer in Nova Scotia (~25%, Fig. 5.7). If recruitment is improved to 30% the threshold density is lowered to ~0.1/  $km^2$ . Conversely, a reduction in deer recruitment to 20% increases this threshold density to 0.6 - 1.6 deer/  $km^2$ , depending on hare densities. Under typical conditions, deer populations should stabilize at densities between 3.4 and 4.2/  $km^2$ , but this equilibrium density is heavily dependent on deer recruitment and the abundance of snowshoe hares (Fig. 5.7).

Analysis of the proportional effects of the functional and numerical response on predicted predation rates (Fig. 5.8) revealed that, assuming moderate hare densities (~30/ km<sup>2</sup>), the influence of the functional response decreased rapidly with increasing deer densities and the functional response contributed to inverse density dependence above 0.5 deer/ km<sup>2</sup>(Fig. 5.8). The numerical response contributed to density dependence in the range of 1.5-6.5 deer/ km<sup>2</sup>, however, the total response was not density dependant at any range of densities because the two responses tended to cancel each other out (Fig. 5.8). At 6.5 deer/ km<sup>2</sup> the numerical response reached the asymptote we imposed on coyote density and the proportional effect plummeted quickly to zero (Fig. 5.8). Changing the hare density to



Fig. 5.7. Changes in the coyote predation rate (as calculated from the total response) with deer and hare density. The solid line represents deer population growth without coyote predation and the shaded area represents the effects of changing deer population growth ± 5%. Low, moderate, and high hare densities represent densities of ~15, 30, and 45 hares/ km<sup>2</sup>, as estimated by pellet counts. K represents the density at which net deer population growth (in the absence of coyote predation) is 0. The stable equilibrium condition induced by coyote predation is represented by (S), whereas (U) represents an unstable equilibrium.



Fig. 5.8. The proportional effects of the functional and numerical responses on the predation rate of coyotes preying on whitetailed deer in a system where deer and snowshoe hare represent the dominant prey available to coyotes. Values >1.0 would be indicative of density dependence whereas values <1.0 indicate an inversely density-dependent relationship. See Messier (1994) for details on the calculations. Proportional effects were calculated assuming moderate (~30 /km<sup>2</sup>) hare densities.

10 and 50 hares/  $km^2$ , respectively, affected only the elevation and slopes (slightly) of the curves, but not their relative positions.

### DISCUSSION

Age, sex, and condition of deer killed by coyotes

Coyotes killed proportionately more fawns than available in CB and QC (winters 1992 through 94 only). Winter conditions were relatively severe in QC during 1993 and 1994 (Patterson 1995), and were generally more severe in CB than QC (MacDonald 1996, Lock 1997). Given their relatively small size, increased snow depths may have increased the relative vulnerability of fawns to predation. Fawns predominated among deer killed by coyotes in Québec and Northern New Brunswick (Messier et al. 1986, Parker and Maxwell 1989), and winter conditions experienced during both of these studies were severe relative to my study.

Deer killed by coyotes during this study had FMF levels as high or higher than deer in the general populations (Fig. 5.3). Further, examination of the carcasses of deer killed by coyotes revealed no signs of arthritis or other debilitations which may predispose ungulates to predation (Mech et al. 1995). Although at least four of the deer killed by coyotes during winter in QC were ≥8 years old, I have no evidence that any of these deer were disadvantaged by their age. Messier et al. (1986), Lavigne (1992b), and Brundige (1993) also reported that deer killed by coyotes during winter were probably in as good or better condition as the general population.

During winter, coyotes often killed deer in situations where deer were disadvantaged either by deep snows or by poor footing on frozen lakes (Chapter 4). I also noted several cases where deer were ambushed in their beds and subdued before they could escape. These findings are similar to those reported for coyotes in the Adirondack Mountains of New York (Brundige 1993) and may help explain the general lack of selectivity for weaker individuals (very young or old deer). I conclude that mortality due to coyote predation during this study was largely additive to other mortality factors.

### Year-long predation rates and population balances

### Predation on deer fawns

The consumption of fawns during June and July exceeded hare in all study areas/ periods (Chapter 3). Harrison and Harrison (1984) speculated that it was more energetically efficient for adult coyotes attending pups to kill and transport fawns than other smaller prey items. In northern New Brunswick, predation by coyotes was identified as the single most important source of mortality for neonatal fawns (Ballard et al. 1999). However, predation by domestic dogs (*Canis familiaris*), bobcats, and black bears (overall) removed a greater proportion of fawns than coyotes alone. June to October survival rates of radio-collared fawns in Minnesota averaged 0.51 (Kunkel and Mech 1994) with wolves and black bears representing the only identified mortality sources (each removed an equal proportion of the fawns). Mathews and Porter (1988) identified predation by black bears as a major mortality source for white-

tailed deer fawns in the Adirondack Mountains of New York and emphasized the need for further quantification of the effects of this mortality factor.

Although I did not use telemetry to estimate survival rates of neonatal fawns, fawn survival through the first 9 months of life was assessed by comparing in utero reproductive rates of road-killed deer during each winter (multiplied by 0.9 to account for perinatal mortality-Verme 1977) with fawn: doe ratios observed during the next winter (also estimated from examining road-killed deer). Survival rate estimates for fawns varied from 40 - 80% and were positively correlated with snowshoe hare abundance (as indexed by the provincial harvest, Fig. 5.9). I suggest that during summer, covote predation was a major source of mortality for fawns in Nova Scotia and that high snowshoe hare densities buffered predation on fawns, similar to the findings of Hamlin et al. (1984) for coyotes and mule deer (Odocoileus hemionus) fawns in north-central Montana. The relatively low density of deer, and high use of fawns, by coyotes in QC suggests that predation by coyotes during summer may have had a substantial limiting effect on deer populations.

### Coyote functional response

During winter, deer killing rates observed during snowtracking (Chapters 4, 5), were correlated negatively with hare density and positively with deer density. Coyotes exhibited a Type II functional response to increasing deer density (Fig. 5.4, see also Fig. 3.5a). A Type II functional response, in combination with most types of numerical responses, causes predation to be depensatory at



Fig. 5.9. Relative survival of fawn white-tailed deer from birth through mid-winter in relation to the relative abundance of snowshoe hares. Fawn survival was assessed by comparing in utero reproductive rates during winters 1983 - 1995, with the fawn : doe ratios of road-killed deer during the next winter. The provincial harvest of hares was used an index of hare abundance.

high prey densities (Messier 1994, 1995). Further, there are more substandard (very old, weak, or young) deer available for predators at high prey densities (Messier and Crête 1985, Potvin et al. 1988). Thus, at higher prey densities predation mortality likely becomes at least partially compensatory. Although density-dependent reproduction and winter survival indicate that there are upper limits to the number of over-wintering deer that should be targeted as a management goal, the impact of coyote predation can be reduced by maintaining deer at relatively high densities (e.g., >2 deer/ km<sup>2</sup>).

### Coyote numerical response

The numerical response was based on the assumption that the availability of deer and hare to coyotes was directly related to the total abundance of the two prey species. However, deer are probably more difficult to capture than hares, thus the numerical response may be related more to deer vulnerability than to absolute deer density. I suggest that under typical conditions, the numerical response of coyotes may be influenced more by changes in density of hares, or other numerically significant, easier to capture alternate prey, than deer. The numerical response also suggests that in the absence of deer and hare, coyotes could subsist at a marginal density of 0.68/ 100 km<sup>2</sup>, an estimate that seems reasonable given the plasticity of foraging behavior exhibited by coyotes (Chapter 3, see also Samson and Crête 1997).

Total response and coyote predation on deer

The highest predation rates documented in this study were observed in QC during 1993-94 (Q1). Low deer densities, a lag in the coyote numerical response (resulting in a relatively high coyote: deer ratio), and unusually severe winter conditions appear to have been responsible for the high predation rate (Chapters 3, 4). Declining coyote numbers, and increased use of snowshoe hare, likely contributed to the decrease in predation rates on deer in QC by 1996-97 (Chapter 3). Winters are generally mild in QC and deer typically remain distributed throughout the entire area. When deep snow occurs, deer may be particularly vulnerable to predation (Patterson 1994, Chapter 4). In CB, predation rates on deer appear to have been mitigated by high deer densities and a relatively high use of snowshoe hare.

The full implication of any mortality factor can only be realized after being juxtaposed to other potential limiting factors on reproduction and survival (Messier and Crête 1985). With the exception of deer living in Kejimkujik National Park, hunting was the most significant limiting factor for deer in this study. Whitlaw et al. (1998), and McNay and Voller (1995) reported that predation was the major source of mortality for white-tailed deer in Northern New Brunswick and black-tailed deer (*Odocoileus hemionus columbianus*) on Vancouver Island, BC, respectively. However, most survival studies of white-tailed deer have concluded that hunting is the major cause of mortality in exploited populations (Nelson and Mech 1986a, Fuller 1990, Dusek et al. 1992). This study reinforces the importance of legal harvest as a tool for managing deer populations.

According to the balance models (Table 5.4), preventing the decline in deer densities following the winter of 1993 would have required the complete protection from harvest (both registered and unregistered) of all sex/ age classes of deer, during autumn 1992. However, reductions in harvest at that time may have been offset by increased winter mortality and possibly reduced recruitment because of the relatively severe winter conditions experienced during winter 1993 (Verme 1977, McCullough 1979, Huot et al. 1984, White and Bartmann 1998). Following the province-wide population boom in deer densities during the early 1980s, deer in Kejimkujik National Park experienced an equal if not greater decline in densities, despite complete protection from harvest mortality (Drysdale 1986, Patterson 1995). Prior to the decline, this population was at high densities and in poor physical condition (Drysdale 1986), suggesting that the lack of hunting was largely compensated for by high densitydependent winter mortality, and/ or reductions in recruitment. This emphasizes the need to prevent deer populations from erupting, because subsequent crashes appear to be very difficult to prevent.

Although harvest mortality may be largely compensatory at high deer densities, it can be largely additive to other limiting factors at low to moderate deer densities (Connolly 1981, Bartmann et al. 1992, Patterson et al., in prep.). Continued high harvests following the peak in deer densities in 1986 likely accelerated and prolonged the subsequent decline in deer densities in Nova Scotia

(Fig. 5.1). Given our general inability to prevent high rates of coyote predation from occurring under certain ecological conditions (low deer densities, severe winter conditions), managers must be ready to impose rapid restrictions on antlerless deer hunting when high predation rates or winter malnutrition losses are expected. The recent establishment of a zone-based antlerless harvest quota system in Nova Scotia should allow managers to rapidly compensate for non-hunting deer losses.

During winter, the use of deer by coyotes was inversely related to hare density (Chapter 4), likely because coyotes showed a Type I functional response to changes in hare density (Chapter 3). This suggests that coyote predation on deer may decline with increasing hare densities. This appears to be the case with predation on fawns during summer (Fig. 5.9). However, coyote predation on deer >6 months was greatest from December to April (see also Whitlaw et al. 1998, and Ballard et al. 1999) and the total response indicated that year-long predation rates on deer actually increased with hare density. This occurred because the positive numerical response of coyotes to increasing densities of snowshoe hare outweighed the relaxation of the functional response to deer afforded by this alternate prey. Pekins and Mautz (1990) and Patterson et al. (1998) suggested that when available, covotes preferred to feed on deer rather than hare. The present results agree with the suggestion I put forward in chapter 3; that coyote populations supported at elevated densities by alternate prey will continue to feed preferentially on deer, regardless of deer density.

Similar scenarios where the presence of an alternate prey species increases predation rates on the primary prey have been proposed for wolf-moose-caribou (*Rangifer tarandus*) (Bergerud and Elliot 1986, Seip 1992) and wolf-moose-bison (*Bison bison athabascae*) (Gates and Larter 1990) systems in British Columbia and the Northwest Territories, respectively. This contrasts with the conclusion of Abrams and Matsula (1996) that positive indirect effects of one prey on the equilibrium density of others should occur frequently. However, Abrams and Matsula (1996) acknowledged the lack of field data supporting their conclusion.

Under typical conditions, my model predicts that deer populations should stabilize at densities between 3.4 - 4.2/ km<sup>2</sup> (Fig. 5.7). Because the predation curve is depensatory rather than density-dependent at this equilibrium density, predation limits, but does not regulate deer at these densities, (Sinclair and Pech 1996). Food competition must be considered the only potentially regulatory agent for deer in Nova Scotia; with predation merely lowering the equilibrium density (from K to S, Fig. 5.7). Given that factors other than deer density may influence coyote predation on deer (Chapter 4), and the direct influence of weather, hunting, and density-dependent relations with habitat on deer population growth and demography (Mech et al. 1987, Fryxell et al. 1991, Messier 1991), deer densities are unlikely to remain stable and should fluctuate around this density (S) over time. A similar hypothesis was proposed by Crête and Lemieux (1996) for a coyote-deer system on

the Gaspé peninsula of Québec, and for the moose-wolf system on Isle Royale (Messier 1991).

My model also predicts that because coyote populations can subsist on alternate prey, coyote predation could extirpate deer populations when deer densities drop below 0.2 - 0.6/ km<sup>2</sup>, given typical recruitment for deer in Nova Scotia (~25%, Fig. 5.7). However, white-tailed deer are unlikely to be extirpated in most jurisdictions of northeastern North America because hunting would typically be greatly reduced or eliminated at such low deer densities. The resulting boost in production (~10 - 25%) would likely boost deer population growth sufficiently to escape limitation by coyotes.

The only case were local extinction may be expected would be along the northern fringes of the range of the white-tailed deer where winter severity may effect malnutrition losses (up to 40% in a single winter - Huot et al. 1984) and increase predation by coyotes to the extent that the elimination of sport hunting would be insufficient to prevent severe population declines. This appears to have been the case in the Gaspé Region of Québec and northern New Brunswick during the late 1980s and early 1990s (Parker 1995, Crête and Lemieux 1996, Samson and Crête 1997). The presence of additional limiting factors, such as bear or bobcat predation, may also lower deer recruitment and hinder efforts to promote deer population growth.

This study provides evidence that, although coyote predation can be a significant limiting factor for deer in Nova Scotia, it is

unlikely to be regulatory. Deer densities were seldom stable in Nova Scotia prior to the arrival of the coyote (Benson and Dodds 1977, Patton 1991). Given the annual variation in many of the factors influencing the magnitude of coyote predation on deer (densities of deer and alternate prey, winter severity), and the direct impacts of hunting and winter severity on deer populations, this trend is likely to continue. Coyote predation, because of its depensatory nature, will likely exacerbate future population fluctuations. However, when deer populations are driven to low densities from one or more limiting factors, alternate prey may enable coyote densities to remain high enough to prevent deer population growth, despite the occurrence of mild winters and restrictive hunting.

# 6. WINTER NUTRITIONAL CONDITION OF EASTERN COYOTES IN RELATION TO PREY DENSITY

#### INTRODUCTION

Originally restricted to the Great Plains of Western North America, coyotes only recently expanded their range into northeastern North America (Moore and Parker 1992). Throughout most of the forested regions of the Northeast, white-tailed deer and snowshoe hare have become the primary prey of the eastern coyote (Parker 1986, Messier et al. 1986, Chapter 3). Both of these prey species show considerable spatial and temporal fluctuations in abundance (Fryxell et al. 1991, Eaton 1993).

Prey abundance may influence the relative nutritional status of coyotes, which in turn may directly affect social and demographic characteristics. Pregnancy rates and litter sizes of coyotes declined with snowshoe hare abundance in Alberta (Todd and Keith 1983). Similarly, female coyotes in the Gaspé region of Québec exhibit exceptionally low fecundity, probably due to low prey abundance (Poulle et al. 1995, Samson and Crête 1997). Several researchers (Messier and Barrette 1982, Harrison and Harrison 1984, Poulle et al. 1995) noted that eastern coyotes, particularly adults rearing young, are typically emaciated during early summer. Carcasses collected during winter generally have moderate fat reserves (Poulle et al. 1995), suggesting that it may be easier for coyotes to obtain adequate food resources during winter relative to other seasons. Despite these observations, few studies have attempted to relate nutritional condition of coyotes to the abundance of major prey species.

Numerous indices have been developed to assess the relative condition of birds and mammals; however, most are related to fat reserves (Harder and Kirkpatrick 1994, Huot et al. 1995). The analysis of urine collected from snow (*Urinalysis* - Delgiudice et al. 1987) can be used to assess the nutritional status of free ranging mammals during winter. Metabolic byproducts resulting from the digestion of meat exhibit definite patterns of excretion (related to protein intake) in urine expelled by carnivores (Delgiudice et al. 1987, Mech et al. 1987, Ramsay et al. 1991).

Urea : creatinine (U : C), and potassium : creatinine (K : C) ratios were significantly lower in a sample of fasted, as opposed to fed, captive wolves (Delgiudice et al. 1987). Further, U : C ratios were considerably higher in snow-urine samples collected from the immediate area surrounding the carcasses of deer killed by wolves than for samples collected randomly along wolf trails (Mech et al. 1987). These studies indicated that the analysis of multiple urine samples collected from free ranging wolves could reveal changes in the nutritional status of wolves over time. Each pack need only be sampled frequently enough throughout the winter to obtain a valid index of the actual mean time since feeding. It would then be reasonable to conclude that a pack that has a significantly longer time since feeding should be in poorer condition than a pack that feeds more frequently (Mech et al. 1987). I tested the hypothesis that local abundance of white-tailed deer and snowshoe hare can affect the nutritional condition of eastern coyotes using U : C ratios from urine samples.

### METHODS

I used urinalysis as the basis for a comparison of the nutritional condition of coyotes living in territories containing different densities of white-tailed deer and snowshoe hare. I defined nutritional condition as: "The state of body components controlled by nutrition and which in turn influence an animal's fitness" (Harder and Kirkpatrick 1994).

Suitability of urinalysis as an indicator of relative nutritional condition of coyotes

Several authors (Saltz et al. 1995, White et al. 1995a, 1995b) have criticized the suitability of urinalysis. Two major concerns are:

- Among ungulates, different age/ sex classes show marked differences in nutritional condition as winter progresses. Therefore mean U : C ratios from randomly collected samples will be largely influenced by the age and sex ratios of the herd in question.
- High U : C ratios in ungulates may indicate either high intake of dietary protein or an advanced state of starvation (catabolism of lean body tissue).

I addressed the first concern by analyzing urine only from known (radio-collared) individuals and their associates. I tracked groups of coyotes containing the breeding pairs of coyotes and other associates presumed to be their offspring (Chapter 2). I do not
believe the second concern to be a problem to my study because none of 17 radio-collared coyotes killed and examined during winter exhibited any signs of malnutrition (see also Poulle et al. 1995). Finally, the studies of Delgiudice et al. (1987) and Mech et al. (1987) validated the use of urinary U : C ratios as an indicator of the time since last feeding for both captive and wild timber wolves, a close relative of the eastern coyote (Wayne and Lehman 1992).

## Collection and processing of urine samples

I collected urine samples while snow tracking radio-collared coyotes belonging to eight territorial family groups from January to March, 1995 through 1997. Urine soaked snow was collected in plastic freezer bags and kept frozen until processing. Each sample was labeled as to date and location as well as the pack ID and number of coyotes being followed. Samples were stored at -20°C.

Samples were later thawed out and centrifuged at 2000 g to remove dirt, and in some cases, blood cells. Aliquots were then refrozen at -20°C. I assayed the samples for urea and creatinine using spectrophotometry with the Cobas Mira Plus Bioanalyzer (Roche Diagnostics, Mississauga, ON). I used creatinine (kinetic) and urea (rate) assay kits from Diagnostic Chemicals Limited. Samples were initially diluted at 12.5 : 1. Further adjustments were made if the initial assays indicated the samples were either too concentrated or too dilute to produce reliable results. Urea nitrogen concentrations of samples were expressed relative to the concentrations of creatinine to correct for variations in expelled urine concentration and dilution by snow. Creatinine excretion is considered to be relatively constant over time and thus provides a valid index for comparing urinary metabolites (Delgiudice et al. 1987, White et al. 1995a).

I assayed 688 coyote urine samples. I tested the accuracy of these assays by testing duplicate samples of known concentrations ranging from two to 800  $\mu$ m/ L (0.02 - 9.05 mg/ dL) for creatinine, and 1 to 10 mmol/ L (2.8 - 28 mg/ dL) for urea nitrogen. I calculated an average difference of 3.9  $\pm$  1.9 % (n = 34) and 5.9  $\pm$  1.8 % (n = 12) for the creatinine and urea standard assays, respectively. In both cases the estimated concentrations were consistently higher than the actual values. I did not consider this bias problematic to my analysis because it appeared to affect the entire range of concentrations in a consistent and predictable manner. However, the preliminary assays indicated that I could not reliably measure creatinine and urea concentrations below 10  $\mu$ m/ L (0.112 mg/ dL) and 1 mmol/ L (2.8 mg/ dL), respectively. Censoring all samples with concentrations of either creatinine or urea below these values resulted in the removal of 55 samples. I censored an additional 66 samples because they either came from territories with inadequate prey abundance data (n = 39) or could not be accurately assigned to a specific radio-collared family group (n = 27). Therefore the total number of samples included in analyses was 567.

#### Statistical analyses

I compared mean U : C ratios using analysis of covariance (ANCOVA) with study area as the primary explicative variable and month as a covariable. Significant differences were determined using Tukey's LSD for unequal sample sizes (Sokal and Rohlf 1995). I used Spearman rank correlations (Sokal and Rohlf 1995) to examine the correlations between U : C ratios and deer and hare densities, and winter traveling group size (Chapter 2). Because the use of deer or hares by eastern coyotes may depend on the relative density and vulnerability of both species (Chapters 3, 4), it may be inappropriate to correlate any behavioral or physiological parameters to the relative availability of one without statistically controlling for the other. I used Kendall's partial rank order correlation ( $T_{xy,z}$ , Siegel and Castellan 1988) to assess the relative contribution of deer and hare densities to U : C ratios. Values are presented as means ± 1 standard error (SE). The minimum level of significance accepted for all tests was P = 0.05.

#### RESULTS

#### Comparison of samples collected along trails vs. kill sites

The mean U : C value for 28 samples collected within the immediate vicinity of 11 white-tailed deer carcasses being fed upon by coyotes was 84.0  $\pm$  6.1 versus 52.0  $\pm$  1.5 for all remaining samples pooled ( $U_{536, 29} = 2756$ , P < 0.001, Table 6.1). Coyotes often remained in the vicinity of large prey carcasses for several days resulting in a large number of urine samples being deposited in these areas. I randomly selected one urine sample per day for each day a coyote group was located at a deer carcass site for inclusion in all subsequent comparisons.

sample plots in parentheses, data from Chapters two and three) for '52 urine soaked snow samples collected while snowtracking radio-collared coyotes belonging to eight territorial packs in Nova Scotla, January - March, 1996-1997. Table 6.1. Urea nitrogen: creatinine ratios (tSE) and relative deer and have densities (1 SE, No. of

urine       study       nit cogen(1)       reactinine       (r)       Hate       Hate </th <th></th> <th>No.</th> <th></th> <th>Urea</th> <th></th> <th></th> <th></th> <th></th> <th>Mean</th>		No.		Urea					Mean
Pack ID       amples       Area       (mg/d1)       (us/d1)       (u		ur i ne	Study	ni t rogen (U)	Creatinine (C)		llare		dreat
Pack ID       sampton       Title 1       23.6 for 31 for	4	po l cmeo	Area	(ma/ dl)	(mg/dl)	0±0	pellets/m	Deet / km	3120
Devonshits       Tupper lake 96       25       0C       37.6.15.1       1.23.10.23       45.8.15.1       5.9.11.0.1115       1.6.10.3       (1)       2.4       (1) <th< td=""><td>Pack ID</td><td>no refute</td><td>JO</td><td>56.318.9</td><td>4.57 ± 1.42</td><td>22.614.2</td><td>2.610.9105)</td><td>2.4 (1.0 (10)</td><td><b>7</b> • 7</td></th<>	Pack ID	no refute	JO	56.318.9	4.57 ± 1.42	22.614.2	2.610.9105)	2.4 (1.0 (10)	<b>7</b> • 7
Tupper lake 97       40       CC       26.5 1 2.8       0.81 1 0.10       45.3 1 5.1       5.9 1 1.0 (115)       1.6 1 0.3 (9)       2.3         Tupper lake 97       40       CC       26.5 1 2.8       1.69 1 0.17       28.1 1 3.8       1.7       9.8 1 2.0 (15)       2.3         Rupper lake 97       40       CC       26.5 1 2.8       1.69 1 0.17       28.1 1 3.8       1.7       9.8 1 2.0 (15)       2.1         Rden 95       29       CBL       37.4 1 3.6       1.69 1 0.17       28.1 1 3.1       2.9 1 1.0 (15)       9.8 1 2.0 (15)       2.1         Rden 97       57       CBL       30.3 1 4.7       0.50 1 0.06       53.8 1 4.7       5.6 1 1.1 (43)       9.2 1 1.9 (11)       2.1         Rden 97       81       81       63.6 1 12.5       1.54 1 0.30       55.2 4 3.2       5.7 1 1.1 (43)       9.2 1 1.9 (10)       2.0         Mapte Brook 96       28       CBL       31.7 1 3.3       0.84 1 0.12       49.9 1 7.5       2.7 1 1.1 (43)       9.4 1.1.0 (6)       1.1         Iona 97       81       65       1.49       0.50 1 0.22       49.9 1 7.5       2.7 1 1.5 (7)       0.6       1.1	pevonshire	 		37.6 1 5.1	1.23 1 0.23	45.8 1 5.6	(87) 8.0 1 6.1	2.4 I U.H (7)	1.7
Tupper lake 91     30     CBL     29.1     1.69     10.11     28.1     1.38     1.69     10.11     29.4     9.8     1.0     161     2.4     2.0     161     2.4     2.0     161     2.4     2.0     163     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     1.0     2.1     1.1     2.1     1.1     1.1     1.1     1.1     1.1     1.1     1.1     1.1     1.1	Tupper Lake 96	C 2		26.5 1 2.8	0.81 1 0.10	45.3 1 5.1	6,944.0.115)	1.6 1 11.3 (9)	2.4
Eden 95     33     CBL     37.4 ± 3.6     1.65 ± 0.17     27.4 ± 3.1     2.9 ± 0.5 (164)     9.8 ± 7.9 ± 1.6     1.9     2.9       Eden 96     29     CBL     37.4 ± 3.6     1.65 ± 0.17     27.4 ± 3.1     4.7 ± 1.1     (147)     9.2 ± 1.9<(11)     2.1       Eden 97     57     CBL     38.1 ± 3.3     1.05 ± 0.13     47.7 ± 3.1     4.7 ± 1.1     (147)     9.2 ± 1.9<(11)     2.1       Reden 97     57     CBL     30.3 ± 4.7     0.50 ± 0.06     53.8 ± 4.7     5.6 ± 1.1.1     (64)     1.4 ± 1.1.0     (6)     2.1       Mapte Brook 96     28     CBL     31.7 ± 3.3     0.50 ± 0.30     55.2 ± 3.2     5.7 ± 1.1.1     (64)     1.8 ± 0.4     (6)     1.1       Iona 97     81     CBL     31.7 ± 3.3     0.64 ± 0.12     48.9 ± 7.5     7.9 ± 11.1     (64)     1.8 ± 0.4     (6)     1.1       Roseburn 96     34     CBH     35.2 ± 3.2     0.84 ± 0.12     48.9 ± 7.5     1.2 ± 1.1.5     (61)     0.6     2.1       Skye Mt. 96     23     CBH     4.9 ± 0.21     6.2 ± 4.5     9.3 ± 1.1.5     (111)     0.6     1.1	Tupper Lake 97	40		201478	1.69 1 0.17	28,1 1 3.8	1.7'	9.8 i 2.0 (16)	, <b>1</b>
Eden 96     29     CBL     37.44.1.3.0     1.05 1.0.13     47.7 1.3.1     4.7.1 1.1.1 (147)     6.2 1.1.9 (11)     7.3       Reden 97     57     CBL     38.1 1.3.3     1.05 1.0.13     47.7 1.3.1     4.7.7 1.3.1     4.7.1 1.1.1 (147)     6.2 1.1.0 (10)     7.3       Maple Brook 96     28     CBL     30.3 1.4.7     0.50 1.0.06     53.8 1.4.7     5.6 1.1.1 (147)     6.2 1.1.0 (10)     7.3       Maple Brook 96     28     CBL     30.3 1.4.7     0.50 1.0.30     55.2 1.3.2     5.7 1.1.1 (147)     6.2 1.0.4 (6)     1.1       Iona 97     81     81     CBL     31.7 1.3.3     0.84 1.0.12     49.8 1.4.2     7.8 11.1.5 (64)     0.6     1.1       Roseburn 96     34     CBH     31.7 1.3.3     0.84 1.0.12     48.9 1.7.5 1.7 1.2.0 (71)     0.8     2.7       Skye Mt. 96     23     CBH     52.0 1.4.9     1.49 1.0.41     65.8 1.4.5     9.3 1.1.3 (111)     0.6     7.1       Skye Mt. 91     69     CBH     41.6 1.7.5     2.70 1.0.47     62.8 1.4.5     9.3 1.1.3 (111)     0.6     7.1       Skye Mt. 91     69     CBH     41.8 1.3.5     0.21	Eden 95	5.5			1 69 1 0 17	21.4 1 1.1	2.9 1 0.5 (164)	(91) 0'Z I 8'6	2.4
Eden 97     57     CBL     38.1 ± 3.3     1.03 ± 0.10     53.8 ± 4.7     5.6 ± 1.11     (64)     3.4 ± 1.0     (6)     1.1       Maple Brook 96     28     CBL     30.3 ± 4.7     0.50 ± 0.06     53.8 ± 4.7     5.7 ± 1.11     (64)     1.4 ± 1.0     (6)     1.1       Iona 97     81     CBL     30.3 ± 4.7     0.50 ± 0.30     55.2 ± 3.2     5.7 ± 1.11     (64)     1.8 ± 0.4     (6)     1.1       Iona 97     81     CBH     31.7 ± 3.3     0.84 ± 0.12     48.9 ± 7.5     5.7 ± 1.15     (64)     0.6     1.1       Roseburn 96     34     CBH     31.7 ± 3.3     0.84 ± 0.12     48.9 ± 7.5     7.8 ± 1.1.5     (61)     0.6     1.1       Roseburn 96     23     CBH     52.0 ± 4.9     1.49 ± 0.21     48.9 ± 7.2     7.8 ± 1.1.5     (11)     0.6     2.1     2.1       Skye Mt. 96     23     CBH     52.0 ± 4.9     1.49 ± 0.21     48.9 ± 7.5     2.7 ± 2.0     (11)     0.6     7.5     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     2.1     3.6 <t< td=""><td>Eden 96</td><td>29</td><td>CBL</td><td></td><td></td><td>1.1 + 7.74</td><td>4.7 1 1.1 (147)</td><td>6.2 ± 1.9 (11)</td><td>7. fr</td></t<>	Eden 96	29	CBL			1.1 + 7.74	4.7 1 1.1 (147)	6.2 ± 1.9 (11)	7. fr
Maple Brook 96       28       CBL       30.3 ± 4.7       0.50 ± 0.06       53.8 ± 4.7       5.7 ± 1.11       641       1.8 ± 0.4       651       1.1         Iona 97       81       CBL       51.5 ± 12.5       1.54 ± 0.30       55.2 ± 3.2       5.7 ± 1.11       641       1.8 ± 0.4       651       1.1         Roseburn 96       34       CBH       31.7 ± 3.3       0.84 ± 0.12       48.8 ± 4.2       7.8 ± 1.56       1.1       0.6       1.1         Roseburn 96       34       CBH       52.0 ± 4.9       1.49 ± 0.21       48.9 ± 7.5       7.8 ± 1.5       0.6       1.1         Skya Mt. 96       23       CBH       52.0 ± 4.9       1.49 ± 0.21       48.9 ± 7.5       9.3 ± 1.3       1111       0.6       7.8         Skya Mt. 91       101       CBH       101.5 ± 17.5       2.70 ± 0.41       62.8 ± 4.5       9.3 ± 1.3       1111       0.6       7.8       7.8       7.9       7.9       7.8       7.8       7.8       7.9       7.9       7.8       7.9       7.9       7.8       7.9       7.9       7.8       7.8       7.9       7.9       7.8       7.9       <	Eden 97	57	CBL	38.1 1 3.9	61'N I 60'I			(9) (1 1 1 1 1 1	2.2
Tona 97       B1       CBL       65.6 ± 12.5       1.54 ± 0.30       55.2 ± 3.2       5.7 ± 1.1       (64)       1.8 ± 0.4       (6)       1.1         Roseburn 96       34       CBH       31.7 ± 3.3       0.84 ± 0.12       48.8 ± 4.2       7.8 ± 1.5       (64)       0.6       1.1         Roseburn 96       34       CBH       52.0 ± 4.9       1.49 ± 0.21       48.8 ± 4.2       7.8 ± 1.5       (71)       8.8       2.7       2.1         Skye Mt. 96       23       CBH       52.0 ± 4.9       1.49 ± 0.21       48.9 ± 7.5       5.3 ± 1.3 (111)       0.6       3.         Skye Mt. 97       101       CBH       41.6 ± 10.15       1.7.6 ± 0.41       65.8 ± 4.5       9.3 ± 1.3 (111)       0.6       3.         River       7.       69       CBH       44.8 ± 3.6       0.94 ± 0.11       66.3 ± 4.5       9.3 ± 1.3 (111)       0.6       3.         Benys Mt. 97       69       CBH       44.8 ± 3.6       0.94 ± 0.11       66.3 ± 4.5       9.3 ± 1.3 (111)       0.6       3.         Denys Mt. 97       69       CBH       44.8 ± 3.6       0.49 ± 0.22       84.0 ± 6.1       0.6	Maple Brook 96	28	CBL	30.3 ± 4.7	0.50 1 0.06	53,8144.7			
Numeration     34     CBH     31.71     3.3     0.84     0.12     48.8     4.4.2     7.4     1.5     64.1     0.6     1.1       Ryse Mt. 96     23     CBH     52.0     4.9     1.49     0.21     48.9     7.5     12.7     2.0     7.1     3.8       Skye Mt. 96     23     CBH     52.0     4.9     1.49     0.21     48.9     7.5     12.7     2.7     2.7     2.7     2.7     2.5     2.5     3.4     5.7     4.6     1.1     0.6     4.5     2.7     2.6     2.7     2	10 EQCI	81	CBL	65.6 1 12.5	1.54 1 0.30	55.2 ± 3.2	5.7 1 1.1 (64)	1.8 ± 0.4 (6)	-
Roseburn 96     34     CBH     52.0 ± 4.9     1.49 ± 0.21     48.9 ± 7.5     12.7 ± 2.0 (71)     0.8     2.       Skye Mt. 96     23     CBH     52.0 ± 4.9     1.49 ± 0.21     48.9 ± 7.5     1.3 (111)     0.6     7.       Skye Mt. 97     101     CBH     101.5 ± 17.5     2.70 ± 0.47     62.8 ± 4.5     9.3 ± 1.3 (111)     0.6     7.       River       0.1     0.41     62.8 ± 4.5     9.3 ± 1.3 (111)     0.6     7.       River       0.15 ± 17.5     2.70 ± 0.47     62.8 ± 4.5     9.3 ± 1.3 (111)     0.6     7.       River     97     69     CBH     44.8 ± 3.6     0.94 ± 0.11     66.3 ± 4.6     10.7 ± 1.9 (77)     0.2     4.       Denys Mt. 97     69     CBH     44.8 ± 3.6     0.69 ± 0.22     84.0 ± 6.1     0.2     4.0 ± 6.1     10.7 ± 1.9 (77)     0.2     4.     4.6     10.7 ± 1.9 (77)     0.2     4.     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6     4.6	10114		naz	1 1 1 1 1 1	0.84 1 0.12	48,8 ± 4,2	7.8 11.5 (63)	0.6	н
Skye Mt. 96     23     CBH     52.0 ± 4.9     1.49 ± 0.21     48.9 ± 0.5     1.3 (111)     0.6     1.       Skye Mt. 97     101     CBH     101.5 ± 17.5     2.70 ± 0.47     62.8 ± 4.5     9.3 ± 1.3 (111)     0.6     1.       River     River     101     CBH     101.5 ± 17.5     2.70 ± 0.47     62.8 ± 4.5     9.3 ± 1.3 (111)     0.6     1.       River     97     101     CBH     44.8 ± 3.6     0.94 ± 0.11     66.4 ± 4.6     10.7 ± 1.9 (77)     0.2     3.       Denys Mt. 97     69     CBH     44.8 ± 3.6     0.94 ± 0.11     66.4 ± 6.6     1.0.7 ± 1.9 (77)     0.2     3.       Deer kill sites     28     POOLED     58.0 ± 17.6     0.69 ± 0.22     84.0 ± 6.1     1.0.4 ± 0.4     4.6     1.0.7     4.6	Roseburn 96	34	CDU				(1/) 0 6 1 6 61	. 8 . 0	2. Н
Skye Mt. 97     101     CBH     101.5 ± 17.5 2.70 ± 0.47     62.8 ± 4.5 9.3 ± 1.3 (111) 0.6     1.4       River     River     Buys Mt. 97     69     CBH     44.8 ± 3.6     0.94 ± 0.11     66.3 ± 4.6 10.7 ± 1.9 (77) 0.2     4       Denys Mt. 97     69     CBH     44.8 ± 3.6     0.94 ± 0.11     66.3 ± 4.6 10.7 ± 1.9 (77) 0.2     4       Deer kill sites     28     POOLED 58.0 ± 17.6 0.69 ± 0.22     84.0 ± 6.1     1     4       Peer kill sites     28     POOLED 58.0 ± 17.6 0.69 ± 0.22     84.0 ± 6.1     1     4       I Hare pellet data not was available during this winter. This estimate was calculated based on the relative hate have barvests in Inverness County (the county containing the CH study area) from 1995, 1997 relative to pellet rounts     1	Skye Mt. 96	23	СВН	52.0 1 4.9	1,49 ± 0.21	48.9 1 4.9		-	-
River Denys Mt. 91 69 CBH 44.8 ± 3.6 0.94 ± 0.11 66.3 ± 4.6 10.7 ± 1.9 (71) 0.2 3. Deer kill sites 28 POOLED 58.0 ± 17.6 0.69 ± 0.22 84.0 ± 6.1 Hare pellet data not was available during this winter. This estimate was calculated based on the relative hate harvests in Inverness County (the county containing the CB study area) from 1995 1997 relative to pellet counts	Skye Mt. 97	101	CBH	101.5 1 17.5	2,70 ± 0.47	62.8 ± 4.5	(111) ٤.1 ± ٤.6	0,6	-
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Deer kill sites 28 POOLED 58.0 ± 17.6 0.69 ± 0.22 84.0 ± 6.1 <sup>1</sup> Hare pellet data not was available during this winter. This estimate was calculated based on the relative hare harvests in Inverness County (the county containing the CB study area) from 1995 1997 relative to pellet counts	Denys Mt. 97	69	CBH	44,813,6	0.94 ± 0.11	66.3 ± 4.6	10.1 4.1 4 7.01	. n.	
<sup>1</sup> Hare pellet data not was available during this winter. This estimate was calculated based on the relative hate harvests in Inverness County (the county containing the CB study area) from 1995. 1997 relative to pellet counts 	Deer kill sites	28	POOLED	58.0 1 17.6	0.69 ± 0.22	84.0 ± 6.1			
harvests in Inverness County (the county containing the CB study area) from 1945 1997 relative to pellet counts	<sup>1</sup> Hare bellet da	Ita not was	available	during this v	dinter. This est	imate was cale	mlated based on	the relative hat	z
	harvests in Inv	erness Coun	nty (the c	ounty containi	ng the CB study	,61 moit (Pate	ts 1997 telativ	tries, telleng of a	2. -
	-	10	1.661 90						

Although I counted all deer pellets deposited after 1 November, most deer had migrated from the CBH area by early January, when the bulk of winter field work began. Therefore pellet counts overestimated the density of overwintering deer in CBH. The density estimates presented here are based on aerial and ground surveys and should better represent the actual winter densities of deer (Chapter 2). The unadjusted density estimates based on the pellet surveys are : Roseburn 96, 1.4  $\pm$  0.7 (6); Skye Mt. 96, 2.4  $\pm$  0.4 (7); Skye Mt. 97, 1.3  $\pm$  0.5 (8); River Denys Mt. 97, 3.0  $\pm$  0.7 (7). Seasonal and geographic differences in U:C

The mean U : C value was highest in the CBH study area  $(60.3 \pm 2.7, n = 227)$  and lowest in the QC study area  $(43.8 \pm 2.9, n = 86)$  (Table 6.1). The mean value for the CBL area was  $45.8 \pm 1.8$  (n = 228). Overall, study area had a significant influence on U : C ( $F_{(2,547)} = 14.6, P < 0.001$ ). The mean value in CBH was significantly greater than in CBL and QC (Tukey's LSD, P < 0.001). There was no significant difference in mean U : C between CBL and QC (Tukey's LSD, P = 0.86).

Tracking studies of eastern coyotes (Hilton 1976, Huegal and Rongstad 1985, Parker and Maxwell 1989) suggest that per capita food consumption may increase as winter progresses and deer become more vulnerable to predation. Although ANCOVA revealed that U : C values differed significantly among months after controlling for study area ( $F_{(1,547)} = 6.4$ , P = 0.012), there was not a progressive increase from January through March (Fig. 6.1). In QC and CBL, the mean U : C ratios decreased from January to February, but increased in March to levels above those found at any other time during winter (Fig. 6.1). In the CBH study area, the mean U : C ratio was highest in February but there was relatively little difference among months (Fig. 6.1).

#### The influence of deer and hare abundance on U:C

U : C was positively correlated with hare densities ( $r_s = 0.75$ , P = 0.004, Fig. 6.2a), and negatively with deer density ( $r_s = -0.70$ , P = 0.01, Fig. 6.2b). Pack size did not appear to have



Fig. 6.1. Mean monthly urea : creatinine ratios (± SE) for 552 urine soaked snow samples collected in the Queens County (QC), Cape Breton Highland (CBH), and Cape Breton Lowland (CBL) study areas, Nova Scotia, January to March, 1996-1997.



Fig. 6.2. The relationship between mean urinary urea nitrogen : creatinine (U:C) ratios collected from urine-soaked snow while snow-tracking radio-collared coyotes, and the relative densities of (a) snowshoe hare and (b) white-tailed deer within each coyote territory.

a significant influence on U : C ( $r_s = 0.39$ , P = 0.21). Kendall partial rank order correlation's indicated that both deer and hare densities remained significantly correlated with U : C after statistically controlling for the influence of the other ( $T_{uc^*deer,nare} = -0.40$ , P = 0.03,  $T_{uc^*hare,deer} = 0.38$ , P = 0.039).

# DISCUSSION

Although I can conclude that prey abundance influences the mean U : C ratios of coyotes, I cannot determine the degree to which low U : C ratios relate directly to malnutrition. That determination could only be made after consideration of baseline data from coyotes known to be suffering from various degrees of malnutrition. However, even without such data, I feel comfortable with the assertion that higher mean U : C ratios were associated with more frequent feeding as suggested by Delgiudice et al. (1987) and Mech et. al. (1987). I further assume that packs feeding more often would likely be in relatively better nutritional condition than packs which fed less often (those exhibiting significantly lower U : C ratios).

Mean U : C ratios of urine samples collected near deer killed by coyotes in this study (84.0  $\pm$  6.1) were remarkable similar to that from 234 wolf urine samples collected near deer killed by wolves in Minnesota (80.8  $\pm$  2.6, Mech et al. 1987). The overall mean U : C ratio for urine samples collected along coyote trails (51.9  $\pm$  1.5) was higher than the mean U : C ratio for urine samples collected along wolf trails (43.7  $\pm$  6.9, Mech et al. 1987). Relative to coyotes, large prey generally makes up a larger proportion of the winter diet of wolves (Mech et al. 1987, Potvin and Jolicoeur 1988, Chapter 3). Poulle et al. (1995) demonstrated that coyotes hunting primarily large game during winter generally accumulate enough body fat to last through extended fasts (through gorging when a kill is made). Nonetheless, given the number of days during which no food is consumed (search time between kills) the mean daily excretion of urinary metabolites related to protein intake should be lower, as documented during this study. Similarly, the lower mean rate of urea excretion in wolves is probably related to longer fasting and greater energy expenditure between feedings relative to coyotes that have the ability to feed more frequently on smaller prey.

Although the negative correlation between deer density and U : C may seem surprising, areas containing the lowest deer densities during winter tended to have the highest hare densities  $(r_s = -0.64, P = 0.025, Table 6.2)$ . Although capable of killing deer year-round, coyotes are most successful when deep snows hinder deer movements (Messier and Barrette 1985, Parker and Maxwell 1989, Chapter 4). Further, during this study high densities of deer were associated with reduced vulnerability to predation (Chapter 4). Thus deer density did not relate directly to deer availability per se, vulnerability appeared to be a critical factor (Chapter 4). The negative correlation between U : C and deer density provides further evidence of the dominant influence of hare density (Fig. 6.2).

Larger groups of coyotes are generally associated with a greater foraging efficiency in areas where ungulates are a major food source (Bowen 1981, Gese et al. 1988, Parker and Maxwell 1989). However, group size did not exert a significant influence on mean U : C ratios during this study. Considering that U : C was not positively correlated with deer density, the lack of correlation between U : C and winter traveling group size is expected.

## Seasonal trends in U : C

Mean U : C ratios decreased from January to February in both the QC and CBL study areas. However, ratios remained consistently high in CBH. February coincides with the peak of breeding in eastern coyotes (Parker 1995). Although some researchers have suggested an increase in coyote sociality resulting in increased predation on deer during the breeding season (Parker and Maxwell 1989, Dibello et al. 1990), this may be oversimplifying the case. Although coyote predation on deer often increases as winter progresses (Heugal and Rongstad 1985, Parker and Maxwell 1989, Dibello et al. 1990), this increase does not generally occur until after mating. During five winters of snow tracking radio-collared coyotes I often observed the breeding pair temporarily disassociate from the rest of the family group around the time of conception for up to two weeks (Chapter 2). For family groups relying on hunting deer as a primary food source, this may cause a decrease in food intake for the duration of this disassociation. In this sense, it is not

surprising that packs living in areas with high densities of snowshoe hares were probably in good nutritional condition throughout the winter, whereas packs more reliant on hunting deer fed relatively less often during the breeding season in February.

## Urinalysis as an indicator of nutritional condition in carnivores

I believe that the analysis of urine voided in snow accurately reflected the relative winter nutritional condition of coyotes in Nova Scotia. I demonstrated a positive relationship between the density of a primary prey species and mean U : C ratios and assumed that this reflected the relative nutritional condition of coyotes. I suggest that urinalysis can be used to measure the relative fitness of coyotes occupying different areas during winter. However, I do not know the U : C value below which coyotes would be experiencing serious nutritional restriction. Baseline information from coyotes known to be suffering different degrees of nutritional restriction would facilitate the future use of this method as a measure of nutritional condition.

Considering the basic nature of the relationship between protein intake and the excretion of urea nitrogen in most carnivores, I concur with Mech et al. (1987) that this technique should be useable with most carnivores inhabiting regions that have snow for a significant part of the year. The analysis of samples collected from coyotes or other top predators across a broad area has potential for use as an indicator of total prey availability in different areas. However, due to the labor involved in collecting a statistically significant number of samples, the technique will likely remain largely restricted to situations where samples can be collected in adjunct with other research projects.

## 7. CONCLUSIONS AND GENERAL DISCUSSION

### Main conclusions

The main objectives of this study were to determine the spatial distribution, and social organization and predatory behaviour of eastern coyotes in relation to the local abundance of white-tailed deer and snowshoe hares. In addition, I wanted to develop a model of coyote predation on deer in a system where deer and hares were the dominant food items of coyotes.

Coyotes responded to variations in deer and hare densities with major demographic and behavioural changes. I will first summarize the major findings of the study and then will follow with a general discussion of the influence of prey variation on eastern coyote life history. Finally I will discuss the significance of alternate prey in influencing predation of whitetailed deer by eastern coyotes.

The most important findings of this study were:

- White-tailed deer and snowshoe hares were the principal food items of coyotes in all study areas. Coyotes appeared to prefer deer to hares as a food source and I estimated that coyotes killed 76 - 86 % of the deer they consumed.
- 2) Coyotes were territorial and territory sizes were negatively correlated with the total biomass of deer and hare. Similarly, coyote densities appeared to increase with prey abundance.
- Juvenile dispersal during autumn was higher in an area with low prey abundance. Some juveniles delayed dispersal until

late winter or beyond, and during winter most territories were occupied by groups of coyotes consisting of the breeding pair and non-dispersing offspring during winter.

- 4) Group formation and cohesion was independent of principal prey type (deer vs. hare). Human exploitation appeared to contribute significantly to the decrement of pack size during winter.
- 5) Coyotes did not use areas containing higher densities of deer proportionally more than expected (based on availability). In one study area (CBL), coyotes actually used areas of low deer density more than expected. Similarly, proportionally more deer were killed in areas of low density suggesting increased vulnerability of deer to predation.
- 6) Most groups of coyotes engaged in one or more extraterritorial excursions. Excursions were more common during winter and appeared to be related to procuring deer or livestock carcasses for food. Coyotes living in CBH (very high hare densities) were implicated in the largest number of excursions despite appearing to the least food restricted of all coyotes examined during the study.
- 7) Coyotes exhibited functional responses to the densities of both deer and hare. However, the response to increasing deer density was less pronounced than the response to hare density, probably because deer vulnerability was more important than abundance per se in determining killing rates of deer.

- 8) Deer killing rates were negatively correlated with hare densities, and survival of fawns during summer was positively correlated with hare abundance.
- 9) Larger (≥4) groups of coyotes were more successful in killing deer. Similarly, success of coyotes chasing deer was positively associated with increasing snow depths. Coyotes killed proportionally more deer during late winter likely owing to increased deer vulnerability and an innate preference for deer to hares.
- 10) Year-long predation rates were estimated at 25.0 and 13.6% in the QC study area during 1992-93 (Q1) and 1996 - 97 (Q2), respectively; and at 9.0% in the CB study area during 1996-97. Predation on fawns during summer accounted for a large portion of the total estimates, but predation on adult deer was substantial during Q1. Coyote predation was less significant than hunting (legal and illegal) as a limiting factor for deer.
- 11) Predation rates on deer decreased sharply (depensatory) as deer densities increased from 0 - 1.5 deer  $/km^2$ . Predation rates increased with hare density. This occurred because the positive numerical response of coyotes to increasing hare densities outweighed the relaxation of the functional response to deer afforded by this alternate prey. The model predicted that coyote predation could drive deer populations to extinction when deer densities drop below 0.2 - 0.6/  $km^2$  given typical recruitment for deer in Nova Scotia (~25%). The model

suggested that under typical conditions deer populations should stabilize at densities between 3.4 - 4.2/ km<sup>2</sup> but this equilibrium density was heavily dependent on deer production and the abundance of snowshoe hares.

#### General Discussion

The influence of prey availability on coyote social organization and space use

The size of exclusive territories used by family groups of coyotes in this study was inversely related to the abundance of the main prey items (deer and hare), as previously reported for bobcats (*Felis rufus*, Litviatis et al. 1986), squirrels (*Tamiasciurus sp.*, Smith 1968), and chipmunks (*Tamias striatus*, Mares et al. 1976). Conversely, Messier (1985) reported that territory sizes of wolves increased with the density of the principal prey (moose) in Québec. This occurred because higher moose densities supported larger packs of wolves that could then effectively exploit larger territories.

Although winter pack sizes of coyotes examined during this study were largely independent of deer and hare densities (Chapter 2), this result may have been influenced by relatively high levels of human exploitation (Chapter 2). Higher rates of autumn dispersal by juveniles were associated with low prey abundance (Chapter 2), and winter nutritional condition of coyotes was positively related to deer and hare densities (Chapter 6). Further, packs living in areas with little access to deer but high snowshoe hare densities were as large and cohesive as those living in areas with high deer densities. Overall, it appears that in the absence of human exploitation, high prey abundance may have resulted in larger group sizes during winter.

Harrison (1992a) suggested that there was little evidence of sociality between adult eastern coyotes and pups aged >1 year. Further, he found no evidence of groups of resident adult coyotes exceeding two individuals. However, I documented three instances where packs (≥3 individuals) contained members other than the breeding pair and young of the year (Chapter two). Similarly, Brundige (1993) reported that a newly formed group of eastern coyotes contained three animals prior to any breeding. These observations suggest that group living by eastern coyotes must confer important advantages. However, in some areas, low densities and diversity of potential foods might preclude pack formation by eastern coyotes, as previously suggested by Harrison (1992a).

Potential advantages of grouping in carnivores include: higher killing rates when exploiting large prey (Gese et al. 1988, Brundige 1993, see also Chapter four), defense of territory and/ or prey carcasses (Bowen 1981, Bekoff and Wells 1980), access to the opposite sex (Gittleman 1989, Moehlman 1989), facilitation of learning (Andelt 1985, Schmidt and Mech 1997), avoidance of the risk of dispersal (Andelt 1985, Messier 1985, Schmidt and Mech 1997), and the potential inheritance of the natal territory and achievement of breeding status (Gittleman 1989, Moehlman 1989, Brundige 1993, Schmidt and Mech 1997). As pointed out by Brundige (1993), the challenge remains to determine which factors cause grouping behaviour and which are effects.

Andelt (1985) reported that large group sizes of coyotes in Texas resulted primarily from high habitat saturation and low exploitation by humans, whereas foraging ecology and territory defense appeared to be of secondary importance. Bowen (1981) believed that prey size determined group size in coyotes in Alberta. Similarly, Brundige (1993) suggested that pack formation by eastern coyotes in New York was necessary for coyotes to economically exploit white-tailed deer.

Although, per capita consumption of deer in Brundige's (1993) study was actually highest for pairs of coyotes, he believed that increased hunting success and the reduced interval between kills reduced the costs of procuring prey and facilitated a lower per capita intake rate by larger groups of coyotes. Under this scenario the difference between energy costs and benefits was presented as a major reason for grouping (Brundige 1993).

Although larger ( $\geq$ 4) groups of coyotes were more successful in killing deer in this study, overall killing rates of deer were relatively low (Chapter 4) and there was little indication that group size contributed to the overall nutritional condition of coyotes (Chapter 6). Further, winter group size and cohesiveness was no different for groups exploiting primarily snowshoe hare or deer (Chapter 2).

This study supports the idea that territoriality and group formation by eastern coyotes probably serve to enhance the genetic fitness of the breeding pair by improving the survival of immobile pups during summer, and of juveniles prior to dispersal. Although young remaining in parental territories might reduce the fitness of the parents and subsequent offspring through intraspecific competition (Bradbury and Vehrencamp 1977), Bekoff and Wells (1982) reported that transients and non-breeding helpers did not negatively affect survival or weight of coyote pups. Further, forcing juveniles to disperse prematurely would decrease their survival and directly reduce the parents' fitness. During this study breeding pair members were quickly replaced after being killed (Chapter 2). Although I could not always determine the identity of the new breeding coyotes, a radio-marked yearling coyote (resident group member) inherited the status of breeding male in the River Denys Mountain territory (CBH) after the former breeding male was shot.

If territoriality serves to improve the survival of immobile pups during summer, the maintenance of an exclusive territory should be most critical during the pup-rearing period. I am not aware of any cases of non-territorial eastern coyotes raising pups. However, Messier and Barrette (1982) reported that solitary coyotes in Québec had good fat reserves and appeared to be as healthy as group living coyotes. Thus, solitary coyotes

(transients) probably do not attempt to maintain territories because they are not necessary for non-breeding coyotes (as opposed to the idea that they simply can not defend a territory against pairs or groups), as suggested by Messier and Barrette (1982). Although, the size and distribution of food resources may strengthen the tendencies towards a given social system (Messier and Barrette 1982, Gese et al. 1988), increased reproductive fitness, and inclusive fitness for non-dispersing juveniles, probably represent the ultimate factors influencing group formation and cohesion among eastern coyotes.

Influence of deer and hare abundance on predation of deer

Deer and hare abundance both appeared to exert a strong influence on coyote predation rates on deer (Chapters 4, 5). The overall impact of variations in deer and hare abundance on predation of deer by coyotes can best be understood by discussing individually the major components of the predator response, i.e. the numerical and functional responses.

Although based on limited data, coyote density appeared to be positively related to the total biomass of deer and hares (Chapter 5). Even if a single deer contributes as much biomass as ~30 hares, deer were generally less numerous and more difficult to capture than hares. Thus, the numerical response may be related more to deer vulnerability than to absolute deer density. Under typical conditions, I suggest that the numerical response of coyotes may be influenced more by changes in density of hare, or other numerically significant, easier to capture alternate prey, than deer.

Although coyotes exhibited functional responses to the densities of both deer and hare (Chapters 3-5), multiple regression indicated that killing rates of deer were influenced primarily by hare density, whereas deer density was not a significant variable in the model. An inverse relationship between deer and hare densities ( $r_s = -0.64$ , P = 0.03, n = 12; Table 6.2) may have resulted in a significant relationship between killing rates of deer and the abundance of both deer and hare even if killing rates were truly related only to the density of hares (colinearity). Further, because deer appear to generally be difficult for coyotes to kill (low killing rates and rate of chase initiation, Chapter 4), it is possible that killing rates of deer are influenced more by deer vulnerability than density per se. Although this remains a possibility, other lines of evidence suggest that at low to intermediate deer densities  $(<3.5/ \text{ km}^2)$ , killing rates of deer by coyotes were influenced by deer abundance.

Killing rates observed during snow-tracking (Chapter 5), suggested a type II functional responses for coyotes preying on deer. I used log-transformed data for deer density in a multiple regression model to assess the relative contributions of deer and hare abundance, and mean winter travelling group size of coyotes on killing rates of deer to partially compensate for the nonlinear functional response (Chapter 4). Although the logged deer density estimates provided a better fit for the linear regression, using a logarithmic transformation on the deer density estimates did not truly linearize the data because of the asymptote associated with a Type II functional response. Thus, the data transformation may have obscured some aspects of the true functional relationships between killing rates and deer and hare densities.

The multi-prev functional response (which considered the influence of deer and hare densities simultaneously; Chapter 5) represented a more biologically justified model of the influence of both prey species on per capita killing rates of deer. This model suggested a response that was basically Type 2, and indicated that deer density exerted a greater influence on per capita killing rates than hare density (Fig. 5.6). When the multi-prey functional response was coupled with a Type I numerical response (Chapter 5), the total response had a slope of less than one. This, along with the positive intercept in the numerical response (because coyotes can persist at low densities in the absence of deer and hare by exploiting alternate prey -Samson and Crête 1997) resulted in a predation rate that was strongly depensatory at low deer densities. This is consistent with the finding that individual deer were less vulnerable to predation at high densities (Chapter 4).

# Influences of predation by eastern coyotes on deer population dynamics

Based on the total response of coyotes to changes in deer and hare density, I predicted that deer populations in Nova

Scotia should stabilize at densities between 3.4 - 4.2/ km<sup>2</sup> (Fig. 5.7). Because the predation curve was depensatory rather than density-dependent at this equilibrium density, predation limits, but does not regulate deer at these densities, (Messier 1991, Sinclair and Pech 1996). Food competition must be considered the only potentially regulatory agent (Fig. 5.1); with predation merely lowering the equilibrium density (from K to S, Fig. 5.7). Given that factors other than deer density influence coyote predation on deer (see Chapter 4), and the direct influence of weather, hunting, and density-dependent relations with habitat on deer population growth and demography (Mech et al. 1987, Fryxell et al. 1991, Messier 1991), deer densities are unlikely to remain stable and should fluctuate around this density (S) over time. A similar hypothesis was proposed by Crête and Lemieux (1996) for a coyote-deer system on the Gaspé peninsula of Québec, and for the moose-wolf system on Isle Royale (Messier 1991).

This study provides evidence that, although coyote predation can be a significant limiting factor for deer in forested areas were deer and hares represent the principle prey items of coyotes, it is unlikely to be regulatory. However, when deer populations are driven to low densities from one or more limiting factors, alternate prey may enable coyote densities to remain high enough to prevent deer population growth, despite the occurrence of mild winters and restrictive hunting. The coyote has adapted well to forested habitats of northeastern North

America and will likely remain an important component of northeastern ecosystems for time to come.

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