ABSTRACT

Predation strongly affects the dynamics of northern vertebrate communities through direct and indirect pathways. Coyotes are one of the main predators of snowshoe hares, and hare populations are characterized by cyclic fluctuations with peaks every 8–11 years. Northern coyotes rely on hares as their primary food source, but they are also major predators of Dall sheep lambs. I examined the response of coyotes to the snowshoe hare population decline in the Alaska Range from 1999–2002 and evaluated the impact of coyote predation on other species in the vertebrate prey community. I first addressed these issues at the population level and then examined the foraging behavior of individual coyotes and social groups.

Snowshoe hare abundance declined 10-fold and had a strong effect on coyote diet composition. The absolute biomass of hares was a good predictor of the amount of carrion, voles, porcupine, and hare in the diet, and coyotes were relatively insensitive to changes in the abundance of alternative prey. Coyote selection for hares and porcupines increased as hare numbers declined, and per-capita consumption of porcupines increased 25-fold. Conversely, voles irrupted and represented 61% of available prey biomass by the end of the hare decline, but coyote selection for voles did not increase. Coyote per-capita consumption of Dall sheep was not affected by sheep or hare abundance. Because coyote predation on alternative prey was not dependent on alternative prey density, it was not a stabilizing influence on the prey community.

Coyote numbers declined nearly 2-fold during the snowshoe hare decline, with peak coyote numbers occurring 1½ years after the hare peak. Mortality and emigration increased immediately following the peak in coyote numbers, followed by reproductive failure during the low phase of the hare cycle. Coyote-inflicted mortality on Dall sheep lambs fell 3-fold when coyote reproduction failed. Lamb survival was negatively related to hare abundance, showing a limit cycle with a 2-year time delay. Thus, snowshoe hare abundance indirectly affects Dall sheep populations via a numerical response by coyotes.

Diet composition varied among individual coyotes and social groups. The pattern of snowshoe hare consumption by social groups largely mirrored the pattern of hare abundance in space and time, indicating that patchiness in prey abundance may have been the main cause of diet variation among coyote groups. Adult coyotes with higher proportions of hare and vole in their diets and lower proportions of porcupine and carrion had increased chances of surviving the hare decline and remaining in the study area.
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CHAPTER 1
GENERAL INTRODUCTION: PREDATION AND COMMUNITY DYNAMICS IN NORTHERN ECOSYSTEMS

Predation is a dominant influence in the dynamics of northern terrestrial vertebrates (Sinclair et al. 2000, Ruesink and Hodges 2001). The behavioral and numerical responses of predators to changes in prey density influences community dynamics through direct and indirect pathways (Krebs et al. 1996, Schmitz et al. 2004). Behavioral responses include changes in prey selection, activity levels, and spatial movements in response to prey density (Holling 1959, Murdoch 1969, Holt 1984). Numerical responses can occur through changes in survival and reproductive rates or aggregative responses to prey density (Erlinge et al. 1983, O'Donoghue et al. 1997). Variation in these responses results in different effects of predation in different communities. Predation can increase the amplitudes of fluctuations in prey abundance (van Baalen et al. 2001), dampen fluctuations (Fryxell and Lundberg 1994), increase the probability of prey extinctions (Holt 1977), or decrease the probability of extinctions (Krivan and Eisner 2003). In addition, individual variation in the responses of predators can affect population and community dynamics (Sherratt and MacDougall 1995, Fryxell and Lundberg 1998).

Direct effects of predation

Predator behavior

Predators directly impact prey populations by consuming individuals. The total number of prey individuals consumed depends on the predator population size and the number of prey individuals consumed per predator. As prey density changes, predator numbers and the per-capita predation rate often change as well, and these components of predation are known as the numerical and functional responses (Holling 1966). Holling (1959) described three basic forms of the functional response, only one of which allows predators to regulate prey numbers (the sigmoidal type III curve). The predation rate must accelerate as prey numbers increase in order for predators to regulate prey, which is a feature of the type III functional response (Sinclair 1989). The type III curve has rarely been demonstrated empirically, however (Holling 1959, Murdoch and Oaten 1975). Stabilizing predatory behavior may therefore be rare, or it may be
difficult to demonstrate because accurate data are needed at very low prey densities (Sinclair 1989).

Predator behaviors that can lead to stabilizing functional responses, such as prey switching, are easier to demonstrate empirically than the response curves themselves (Murdoch 1969, Lawton et al. 1974, Oaten and Murdoch 1975b, Akre and Johnson 1979, Bond and Kamil 1998). Prey-switching, in which selection for abundant species increases and selection for rare species decreases, results in positive frequency-dependent predation (Murdoch 1969). Frequency-dependent predation can dampen oscillations in prey populations and increase prey diversity. For example, predation by *Pisaster ochraceus* in the intertidal zone prevents *Mytilus californianus* from dominating the community, and thus prey diversity is greater with *Pisaster* than without (Paine 1966). Several studies have supported this concept of predator-mediated coexistence (e.g., Connell 1970, Caswell 1978, Crowley 1979, Henke and Bryant 1999). However, many studies that have evaluated prey switching and frequency-dependent predation have not found evidence of these behaviors, or have only found evidence in certain cases (Akre and Johnson 1979, Corbett and Newsome 1987, Jaksic et al. 1992, Dale et al. 1994, White et al. 1996, O'Donoghue et al. 1998a). Predators often strongly prefer particular prey types, and in these cases the absolute abundance of the preferred prey can determine prey choice rather than relative prey abundance (Davies 1977, Windberg and Mitchell 1990, Leckie et al. 1998). Prey-switching in response to absolute primary prey abundance can be destabilizing because predation on alternative prey is not density dependent (Norbury 2001).

**Predator numbers**

Predator densities can be strongly affected by prey abundance, and the numerical response of predators can in turn affect growth rates of prey populations. The predator-prey models of Lotka (1925) and Volterra (1926) formalize this interrelationship, and most population models are built from this foundation. Commonly a lag time in the numerical response of predators to changes in prey density occurs. Models indicate that this delayed density-dependent response can contribute to cyclic predator/prey dynamics (May 1981). For example, mammalian predators of snowshoe hares (*Lepus americanus*) track hare numerical trends with a 1-year time lag (Elton and Nicholson 1942, Keith 1963, O'Donoghue et al. 1997), and predation may hasten the decline and prolong the low phase of the hare cycle (Keith and Windberg 1978, Finerty 1980, Krebs et al. 1995).
In order to quantify the numerical response of predators, estimates of predator population sizes must be obtained. Large predators are notoriously difficult to count because they tend to be rare, secretive, and wide-ranging, and this methodological problem is a major challenge in wildlife ecology (Mills et al. 2000). Recent advances in molecular techniques have led to the development of a promising new method that can be used to monitor predator populations, known as fecal genotyping or molecular scatology (Taberlet et al. 1996). Millions of intestinal cells are present in animal feces, and DNA from these cells can be isolated and amplified by polymerase chain reaction (PCR) to produce a genetic fingerprint of the individual that produced the scat. Carnivores often defecate in conspicuous locations along trails and roads, and by obtaining genetic fingerprints from collected feces, ecologists can derive population estimates. To date, fecal genotyping has been used to estimate the population size of several elusive species, such as coyotes (Kohn et al. 1999), wombats (Banks et al. 2002), badgers (Frantz et al. 2003), wolverines (Flagstad et al. 2004), wolves (Lucchini et al. 2002, Creel et al. 2003), and forest elephants (Eggert et al. 2003). These studies used fecal genotyping to produce short-term population estimates, but no published studies have used this technique to monitor population dynamics over time.

**Indirect effects of predation**

Predation can cause indirect effects both vertically down food chains and horizontally within trophic levels. Trophic cascades demonstrate the vertical indirect effects of predation, because removal or addition of predators can indirectly affect primary producers via direct effects on consumers (Polis 1994, Schmitz et al. 2000). Horizontally, predators can alter community structure within consumer trophic levels by reducing competition, as mentioned above. However, predators often feed on species that do not compete directly with one another. In such cases, predation can facilitate indirect competition among these species and cause decreases in prey diversity (Bonsall and Hassell 1997). Predator-mediated competition, also known as apparent competition, occurs when the presence of one prey species leads to the reduced population size or exclusion of another prey species by increasing the abundance of a shared enemy rather than by direct competition (Figure 1.1; Holt 1977). Apparent competition has been demonstrated in numerous field and laboratory studies and can play a central role in structuring communities (for reviews see Jeffries and Lawton 1984, Holt and Lawton 1994, Chaneton and Bonsall 2000). If prey species vary in growth rates or resistance to predation, the
Figure 1.1. Apparent competition between two prey (hares and sheep) mediated by a shared predator (coyote). Adapted from Holt (1984).
most robust species can exclude other prey (Holt and Lawton 1994, Bonsall and Hassell 1997). Many studies have found that indirect competition among prey is asymmetrical, because the more robust species has a large negative impact on the less robust prey but the reverse is rarely true (Chaneton and Bonsall 2000).

Habitat segregation may facilitate coexistence among prey that share predators because predators may focus on the most profitable prey patch, thus creating temporary “enemy-free space” in the other prey patches (Holt 1984, Holt and Lawton 1994). Spatial segregation has been shown to facilitate the persistence of bivalve and gastropod populations that share predators (Schmitt 1987). In contrast, spatial overlap with the primary prey of canid and mustelid predators has resulted in high levels of nest predation in some grassland bird species (Vickery et al. 1992, Yanes and Suarez 1996).

The negative indirect effects of predation can also be reduced if the predator is limited by factors other than food supply (Holt 1977). Density-dependent mechanisms may limit a predator population before food does so (for example, if the predator is territorial or subject to predation). If the predator does not have a strong numerical response to additional prey, then the addition of a new prey species could relieve some of the predation pressure on existing prey. This situation could lead to positive indirect effects among prey species, known as apparent mutualism (Abrams and Matsuda 1996, Abrams et al. 1998). Prey-switching behavior can also lead to apparent mutualism, because the most abundant prey will draw predation away from other species (Abrams and Matsuda 1996, Abrams et al. 1998). A classic example of apparent mutualism is the relationship between lemmings and ground-nesting birds in the arctic. Nest predation is low during high lemming years, but predators switch to feeding on eggs when lemmings crash (Underhill et al. 1993, Summers et al. 1998, Bety et al. 2002, Blomqvist et al. 2002). Ground-nesting birds therefore have higher breeding success when lemmings are abundant. However, it is important to consider the time-scale of indirect effects. The short-term interaction among prey may appear to be indirect mutualism, but the long-term effects may be negative due to the predator’s numerical response (Holt 1977, Abrams and Matsuda 1996). If predators cannot persist without the primary prey species, then the long-term effect of primary prey on alternative prey will likely be negative despite the positive relationship when both species are present.
Individual variation among predators

Increasingly, ecologists are shifting focus from the population to the individual level. Each individual may utilize only a subset of the resources exploited by its population, and the degree of individual specialization within a population can have implications for ecology, evolution, and conservation (Bolnick et al. 2003). Individual specialization may reduce intraspecific competition (Kohda 1994), facilitate sympatric speciation (Schluter and McPhail 1992, Wilson 1998), and lead to lags in predator responses to changing prey abundance (Werner et al. 1981). Theoretical models have shown that variation among individuals can lead to outcomes that are not predicted when all individuals are assumed to be “average” (Lomnicki 1978, Huston et al. 1988, Judson 1994). For example, variation in dietary preferences among individuals can lead to bias in which the average population preference is disproportionately affected by individuals that prefer rare prey species (Sherratt and MacDougall 1995). Although complexity is increased when individual variation is considered, this approach provides a direct link between natural selection and population-level processes and thus can help to connect the fields of population biology, behavioral ecology, and evolutionary ecology (Wilson 1998).

When different prey items require different foraging tactics for successful capture, specialization on one prey type can greatly increase predator foraging efficiency (Werner et al. 1981, Serra et al. 1997). Development of search images and accumulation of hunting experience can increase the profitability of target prey (Dukas and Ellner 1993, Bernays and Funk 1999), and habitat separation of prey can increase the cost of prey-switching. Thus, switching amongst prey may lower foraging efficiency, which may partially explain the relative scarcity of studies demonstrating this behavior.

The diet of an individual can be influenced by intrinsic factors such as morphology, age, sex, size, and social status (Zerba and Collins 1992, Sandlin and Willig 1993, Skulason et al. 1993, Gese et al. 1996b, Molsher et al. 2000, Ishikawa and Watanuki 2002), as well as by external factors such as habitat, season, and prey abundance (Zerba and Collins 1992, Ben-David et al. 1997, Wilson 1998). Because these factors also affect an individual’s chance of survival or reproduction, individual diet and fitness may be linked (Pierotti and Annett 1991, Grant and Grant 1996, Votier et al. 2004). Alternative foraging strategies may differ in risks and payoffs and therefore confer different fitness consequences (Annett and Pierotti 1999).
The study system

Snowshoe hare population cycles

The snowshoe hare (*Lepus americanus*) is a keystone species in northern boreal forests; hare density has a large impact on most species in the community (Krebs et al. 1996, Ruesink and Hodges 2001). Snowshoe hare populations in northern boreal forests are characterized by cyclic fluctuations, with a period of 8–11 years and an amplitude of 10–25 (Hodges 2000). The cycle is caused by repeated changes in the survival and reproductive rates of hares (Keith and Windberg 1978, Krebs et al. 1996, Haydon et al. 1999). Long-term experiments in the Yukon found that adding food tripled hare density, excluding mammalian predators doubled hare density, and excluding predators while adding food caused a 10-fold increase in hare density (Krebs et al. 1995). Thus, food and predators interact to limit hare density. The sublethal effects of predation, such as high stress levels and habitat shifts of hares, may also contribute to the cyclic dynamics (Hik 1995, Boonstra et al. 1998).

Snowshoe hares have four major predators: great horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*), coyotes (*Canis latrans*), and lynx (*Lynx canadensis*; O'Donoghue 1997). All of these predator populations fluctuate cyclically in response to snowshoe hare numbers (Boutin et al. 1995). Coyotes are a relatively recent arrival in the north, having first appeared in the Yukon and Alaska approximately 100 years ago (Sherman 1981). It is not known whether the arrival of coyotes quantitatively impacted the densities of hares or other predators, but the qualitative population trends appear unchanged.

Coyotes in northern ecosystems

Coyotes are medium-sized carnivores that currently reside throughout most of North America (Figure 1.2). The range of the coyote has greatly expanded since European settlement, most likely due to activities such as agriculture and wolf control (Young and Jackson 1951). Coyote populations generally consist of resident and transient individuals, and residents often form reproductive pairs that maintain exclusive, year-round territories (Mills and Knowlton 1991, Gese 2001). Reproductive pairs produce an average of 4–6 young per year (range = 0–17), and reproductive output can be highly dependent on prey density (Knowlton 1972, Bekoff 1978). Coyote social groups usually consist of an adult pair and associated offspring, but most juveniles
Figure 1.2. Approximate present-day geographical ranges of snowshoe hares (*Lepus americanus*), coyotes (*Canis latrans*), and Dall sheep (*Ovis dalli*). The coyote range includes all areas with snowshoe hares. Location of the central Alaska Range study site is shown. Data from Forsyth (1999) and Bekoff (1977).
disperse from their natal territories during their first year (Harrison 1992). Thus, coyotes occur primarily as singletons, pairs, or small groups (3–5 individuals) but may form larger groups (>10 individuals) in rare situations where they prey on large ungulates such as elk (Bekoff 1978, Bowen 1978, Gese 2001).

Coyotes have been well studied in the southern portions of their range, but little is known about how they are functioning as new members of northern ecosystems. The few studies of coyotes in northern boreal forests have all found that snowshoe hares are the primary food of coyotes (Theberge and Wedeles 1989, Thurber et al. 1992, O'Donoghue 1997). Coyotes are considered to be prototypical generalist predators because they consume a variety of prey items such as small mammals, lagomorphs, large mammals, insects, birds, fruit, carrion, and vegetation (Young and Jackson 1951, Bekoff 1977). However, several studies have shown that coyotes can be selective predators, and changes in resource availability can strongly affect their patterns of resource use (Clark 1972, Windberg and Mitchell 1990, O'Donoghue et al. 1998a).

In areas where top predators have been removed, coyotes may limit the abundance of mesopredators such as foxes, raccoons, skunks, and cats (Crooks 2002, Kamler et al. 2003). In northern ecosystems, however, coyotes are subject to predation themselves, particularly by wolves (Canis lupus). Wolves are widely believed to limit the size and distribution of coyote populations (Carbyn 1982, Dekker 1989, Arjo 1999, Switalski 2003), but coyotes may benefit from scavenging wolf kills (Paquet 1992, Thurber et al. 1992, Arjo 1999).

Effect of coyotes on Dall sheep

Dall sheep (Ovis dalli dalli) range from northern British Columbia to the northwestern Canadian territories and Alaska (Figure 1.2; Geist 1971). Studies of Dall sheep in Alaska and the Yukon indicate that coyotes are a major predator of lambs (Burles and Hoefs 1984, Scotton 1998), and it is not known whether this relatively new source of mortality is sustainable. Dall sheep populations declined approximately 60% from 1984–1994 in Alaska and the Yukon, but sheep populations in both areas have stabilized in recent years (Figure 1.3). Wild sheep populations tend to be highly variable but are not characterized by repeated cycles (Hoefs and Bayer 1983, Clutton-Brock et al. 1991). In particular, reproductive success appears to depend on weather as well as predation (Hoefs and Cowan 1979, Hoefs and Bayer 1983, Ross et al. 1997).

The effects of predation on mountain sheep can vary widely. Isolated populations of bighorn sheep (Ovis canadensis) in the Sierra Nevada range are seriously threatened by
Figure 1.3. Population counts of Dall sheep (*Ovis dalli*) in the Alaska Range and the Ruby Range, Yukon, from aerial surveys. Unpublished data from S. Arthur (Alaska Department of Fish and Game) and J. Carey (Yukon Territory Government).
predation from cougars, *Felis concolor* (Wehausen 1996). Cougar predation can be highly variable: Ross et al. (1997) found that most cougars did not kill sheep, but one individual killed 9% of the total population and 26% of the lambs in a single winter. Nonetheless, some populations that experience heavy predation pressure can persist due to high lamb production (Hass 1989). Predation is important to the dynamics of mountain sheep, and unstable interactions between sheep and predators could lead to long-term declines or localized extinctions.

**Research objectives**

The overall goal of my thesis is to examine the behavioral and numerical responses of coyotes to major changes in the abundance of their primary prey, snowshoe hares, and to determine how these responses may in turn affect alternative prey species in the community, particularly Dall sheep. I first address these issues at the population level and then examine the foraging behavior of individual coyotes and social groups. I conducted this study from 1999—2002 in the central Alaska Range, during the decline phase of the hare cycle. The study site contained a mixture of northern boreal forest, subalpine shrub, and high-elevation alpine tundra habitats. This tapestry of habitat types resulted in relatively high prey diversity and abundance, and combined with the natural experiment of rapidly declining hare density, provided an ideal setting to empirically test foraging theories.

I have four main research objectives:

1) **Evaluation of coyote prey-switching behavior.** In Chapter 2, I compare coyote foraging patterns to prey availability in order to test for changes in coyote prey selection during the snowshoe hare decline. I determine whether coyote foraging decisions are based on primary or relative prey abundance, and I explore the potential consequences of coyote foraging behavior on alternative prey population dynamics and community stability.

2) **Estimation of the numerical response of coyotes to the hare decline.** In Chapter 3, I use fecal genotyping to estimate coyote population size and survival during nine intervals over three years, which I then relate to snowshoe hare abundance. I examine several factors that affect the
success and accuracy of fecal genotyping, and I evaluate the use of two open-population models for tracking changes in population size and survival over time.

3) *Examination of the indirect effects of snowshoe hares on Dall sheep.* In Chapter 4, I synthesize results from the two previous chapters and examine causes and rates of lamb mortality in order to test predictions about the nature of coyote-mediated interactions among hares and sheep. I use additional data collected prior to my study in order to examine snowshoe hare density and lamb mortality during a longer time series. The mechanisms underlying indirect relationships are evaluated as well as patterns of mortality and abundance.

4) *Examination of diet variation among individual coyotes.* In Chapter 5, I quantify differences in diet composition among individuals and social groups, and I explore the causes and consequences of this variation. I examine the prevalence of diet specialization in the coyote population as snowshoe hare abundance declines, and I explore the potential fitness consequences of diet choice.

Finally, I summarize the major findings of this thesis in Chapter 6 and suggest several avenues of future research.
CHAPTER 2
FORAGING ECOLOGY OF COYOTES IN ALASKA DURING A DECLINE IN FOOD SUPPLY

Introduction

The effect of predation on community stability has long been disputed. Theoretical models and empirical studies have shown that predation does not have the same effect in all communities. Predation can increase the amplitudes of fluctuations in prey abundance (van Baalen et al. 2001), dampen fluctuations (Fryxell and Lundberg 1994), increase the probability of prey extinctions (Holt 1977), or decrease the probability of extinctions (Krivan and Eisner 2003). Thus, the relevant question is not whether predation increases or decreases community stability; but rather, under what conditions is predation stabilizing or destabilizing?

A distinction is commonly made between specialist and generalist predators, and it has been hypothesized that predation by generalists leads to stability whereas predation by specialists leads to instability. For example, Hanski et al. (1991) propose that specialist predators in northern Fennoscandia drive large-amplitude population cycles in voles, whereas generalist predators in southern Fennoscandia dampen prey fluctuations. Likewise, the predator-mediated coexistence hypothesis states that frequency-dependent predation by “keystone” generalist predators can lead to coexistence among competing prey because the dominant competitor is prevented from excluding inferior competitors (Paine 1966, Caswell 1978, Henke and Bryant 1999). By selectively preying upon the most abundant prey, keystone generalist predators dampen fluctuations in prey abundance and promote coexistence.

Although several cases of keystone predation have been documented (most famously, *Pisaster* in intertidal communities; Paine 1966), predation by generalists can also reduce the likelihood of prey coexistence by inducing “apparent competition” among prey that do not compete directly (Holt 1977). Apparent competition often occurs when a primary prey species supports a dense predator population that also feeds on a secondary prey species, and this predation can reduce secondary prey populations or drive them extinct (Holt and Lawton 1994, Bonsall and Hassell 1997). Thus, generalist predators have been shown to increase prey diversity and stability in some cases and reduce diversity and stability in others.

Prey switching is a foraging behavior commonly associated with generalist predators that can affect community stability (Murdoch and Oaten 1975, Oaten and Murdoch 1975b, Abrams 13
This behavior is a specific pattern of change in resource selection in which a predator's selection for a prey species increases when that species is abundant and decreases when it is scarce (Murdoch 1969). Theoretically, switching among alternative prey can increase the stability of a predator-prey system by dampening fluctuations in populations and reducing the effects of apparent competition (Oaten and Murdoch 1975b, Holt 1977, Erlinge et al. 1984, Abrams and Matsuda 1996). Prey switching has been documented in several studies (Lawton et al. 1974, Murdoch et al. 1975, Akre and Johnson 1979, O'Donoghue et al. 1998a), but studies have also documented cases in which generalist predators did not switch prey (Akre and Johnson 1979, Corbett and Newsome 1987, Jaksic et al. 1992, Dale et al. 1994, White et al. 1996, O'Donoghue et al. 1998a). Murdoch (1969) found that predatory snails would not switch prey if their preference for one prey item was strong, but they would switch if preference was weak. Predators often have strong preferences for particular prey types, and in these cases the absolute abundance of the preferred prey can determine prey choice rather than relative prey abundance (Davies 1977, Windberg and Mitchell 1990, Leckie et al. 1998). When prey-switching occurs in response to absolute primary prey abundance, switching behavior can be destabilizing because predation on alternative prey is not density dependent (Norbury 2001).

Predators may have strong preferences for the most profitable prey type, and optimal foraging theory predicts that predators should always include the most profitable prey item in their diet regardless of its abundance (Stephens and Krebs 1986). Less profitable prey should be added in decreasing order of profitability when the abundance of the most profitable prey falls below a threshold (Stephens and Krebs 1986, Oksanen et al. 2001, van Baalen et al. 2001). Theoretical models show that optimal foraging by predators should destabilize dynamics in most situations (Krivan and Sikder 1999, Oksanen et al. 2001, van Baalen et al. 2001, Bolker et al. 2003). However, if alternative prey occur in different habitats than primary prey, adaptive foraging may lead to habitat switching when the primary prey declines in abundance, and this behavior can increase stability (Holt 1984, Oksanen et al. 2001, Schmidt 2004). Most studies of foraging behavior and stability have been theoretical, and relatively few studies have examined these theories empirically. In this paper, I evaluate the foraging behavior of coyotes (*Canis latrans*) in an area with considerable habitat heterogeneity and examine the consequences of their behavior for the vertebrate prey community.

Coyotes are known to consume a wide variety of prey items and have long been regarded as prototypical generalists (Young and Jackson 1951, Bekoff 1977). However, several studies have shown that coyotes can be selective predators, and changes in resource availability can
strongly affect their patterns of resource use (Windberg and Mitchell 1990, O’Donoghue et al. 1998b). In northern Canada and Alaska, the snowshoe hare (Lepus americanus) is the primary prey for coyotes (Thurber et al. 1992, O’Donoghue 1997). Snowshoe hare populations fluctuate cyclically, with a period of 8–11 years and an amplitude of 10–25-fold (Hodges 2000). A 10-year study in the Yukon found that coyotes did not switch from snowshoe hares to alternative prey when hares declined (O’Donoghue et al. 1998a).

The goals of this study are to examine the behavioral response of coyotes to a steep decline in snowshoe hare abundance in the central Alaska Range and to assess the impact of changes in coyote foraging behavior on alternative prey, such as Dall sheep (Ovis dalli). A previous study of Dall sheep mortality in this study area found that coyotes were the main predator of lambs (Scotton 1998). The study site contained a patchy mixture of northern boreal forest, sub-alpine shrub, and high-elevation alpine tundra habitats (Figure 2.1). This tapestry of habitat types resulted in relatively high prey diversity and abundance, and combined with the natural experiment of rapidly declining hare density, provided an ideal setting to empirically test foraging theories. I tested two alternative hypotheses:

H1: Coyote selection for hares would be high regardless of hare density and alternative prey would be added to the diet when hare density reached a low threshold. Absolute hare density would be the best predictor of coyote diet.

H2: Coyote selection for hares would decrease as hare abundance declined because coyotes would leave hare habitat to forage for alternative prey such as Dall sheep or voles. Relative prey density would be the best predictor of coyote diet.

Study Area

This study was conducted from May 1999 to July 2002 in the central Alaska Range (Figure 2.1; 63° 57' N, 147° 18' W). The area encompassed 1,000 km² of mountains and foothills on the northern edge of the Alaska Range, approximately 80 km south of Fairbanks. Elevation ranged from 600–2100 m. Potential coyote prey species included snowshoe hare (Lepus americanus), Dall sheep (Ovis dalli), moose (Alces alces), caribou (Rangifer tarandus), ground squirrel (Spermophilus parryii), voles (Clethrionomys rutilus, Microtus spp.), red squirrel (Tamiasciurus hudsonicus), porcupine (Erethizon dorsatum), ptarmigan (Lagopus spp.), and grouse (Dendragapus canadensis and Tympanuchus phasianellus). Other major predators in the
Figure 2.1. Central Alaska Range study area (63° 57' N, 147° 18' W) showing the three major habitat classifications (boreal forest, sub-alpine shrub, alpine meadow) and home ranges of five radiocollared coyote pairs (polygons). Each home range is the 100% minimum convex polygon enclosing all locations of each pair from 1999–2002.
area included grey wolves (Canis lupus), red fox (Vulpes vulpes), pine marten (Martes americana), wolverine (Gulo gulo), lynx (Lynx canadensis), grizzly bear (Ursus arctos), and black bear (Ursus americanus). Snowshoe hare habitat consisted of willow (Salix spp.) and alder (Alnus spp.) thickets and closed-canopy white spruce (Picea glauca) forests, and these cover types made up approximately 43% of the study area (boreal forest, Figure 2.1). Moose, red squirrel, grouse, and porcupine also occurred primarily in these lower-elevation cover types. Hare habitat bordered Dall sheep habitat, which consisted of alpine meadows and bare rock at higher elevations and some sub-alpine shrub areas (1000–2600 m; Figure 2.1). Ground squirrels and ptarmigan occurred primarily in these higher elevation habitats, and voles occurred in grassy meadows that were distributed throughout the study area. The home ranges of most radiocollared coyotes included both high and low elevation habitats (Figure 2.1).

Methods

Prey abundance

Snowshoe hares. Snowshoe hare abundance was estimated using a combination of mark-recapture estimates from live-trapping and fecal pellet counts. Procedures for handling live animals were conducted in accordance with Animal Care protocols approved by the University of British Columbia, and permits were granted by the Alaska Department of Fish and Game. A 9.4 ha live-trapping grid was established in June of 1999 to obtain annual estimates of hare density. Tomahawk live traps (n = 84) were placed at 40-m intervals in a white spruce forest. Traps were baited with apple, carrot, and alfalfa cubes, and traps were locked open and baited for a week prior to trapping in order to familiarize the hares with the traps. Traps were set at 2000 h and checked at 0730 h the next morning for five consecutive nights. Captured hares were marked with ear tags (Monel #1, National Band and Tag Co., Newport, KY). The program CAPTURE (Otis et al. 1978) was used to calculate mark-recapture estimates for hares, ground squirrels, and voles, using the jackknife heterogeneity estimator (Boulanger and Krebs 1996). The trapping grid was surrounded by open habitat inhospitable to hares, so the mark-recapture estimate was converted to a density estimate by dividing the number of hares by the area of the trapping grid.

The trapping grid was not established in preferred hare habitat, because the grid was too large to fit in the narrow, discontinuous strips of willow and alder that were preferred habitat in
this area. As a result, a mark-recapture estimate could only be obtained in 1999, when hares were most abundant. Hare fecal pellets were counted on 126 plots within the trapping grid to calibrate pellet counts with the mark-recapture estimate. Several studies have shown that pellet plot counts are precise and accurate indicators of hare abundance (Krebs et al. 2001, Murray et al. 2002). Additional pellet plot grids in three habitat types (spruce, alder, and willow) were established throughout the study area \( n = 11 \). At least 50 permanent plots spaced 15 m apart were established on each grid. Circular plots of 25-cm radius \( (0.20 \text{ m}^2) \) were used on grids with high pellet density, and plots of 50-cm radius \( (0.79 \text{ m}^2) \) were used on grids with low pellet density. Plots were counted and cleared once per year (for details of the pellet count protocols, see Prugh and Krebs 2004). Pellet counts are an index of hare abundance during the previous year, so there is a lag between changes in hare abundance and changes in pellet counts. To correct for this, I averaged the pellet counts from time \( t \) and time \( t + 1 \) when estimating hare abundance at time \( t \).

**Ground squirrels.** The abundance of ground squirrels was also determined by a combination of mark-recapture estimates and population indices. A 1.3 ha live-trapping grid was established in a sub-alpine area with a mix of dwarf birch \( (Betula nana) \) and alpine vegetation, and mark-recapture estimates were obtained annually during July 1999–2001. An additional live-trapping grid was established in the alpine July 2001. Tomahawk live-traps \( n = 48 \) were spaced 20 m apart, and traps were covered with branches to provide shade. Traps were locked open and baited with peanut butter for two days prior to trapping, and trapping sessions occurred for three consecutive days. Traps were set at 0730 h and checked at 0930 h and 1200 h, and they were locked open until the following morning. Trapped squirrels were weighed, ear-tagged, and sexed. For density estimates, a buffer strip was added to the area of the grid. The width of this strip was the average movement distance of squirrels between recaptures (46.8 m).

Tracking boards were used to obtain population indices at four sites in the alpine habitat (as well as on live-trapping grids), because this index has been shown to correlate well with mark-recapture estimates at a range of densities (Hubbs et al. 2000). Tracking board grids were \( 30 \times 300 \text{ m} \), and every ground squirrel burrow within this area was flagged. Tile samples \( (5 \times 7 \text{ cm}) \) were rubbed with paraffin-based oil, dipped in unscented talcum powder, and secured in the burrow entrance with a nail. Tiles were placed in all flagged burrows at 0730 h and retrieved nine hours later. The number of boards with ground squirrel tracks was used as the index of
abundance. The three-year average calibration of tracks per squirrel (obtained from trapping grids) was used to estimate squirrel density on all tracking board grids.

**Voles.** Vole abundance was estimated using a combination of mark-recapture estimates and minimum-number-alive (MNA) indices. A 0.36 ha live-trapping grid was established in a shrub/meadow habitat of mixed sedges and dwarf birch, and mark-recapture estimates were obtained annually during August 1999–2001. Longworth live-traps \((n = 50)\) were spaced at 10-m intervals and covered with plywood for rain protection. Three grids of the same design were established to obtain MNA indices in wet meadow, shrub/meadow, and spruce forest habitats. Traps were baited with upholstery cotton, oats, sunflower seeds, and apple, and they were locked open for one night prior to obtaining an MNA index. Traps were set at 2000 h and checked the following morning at 0800 h. For the MNA indices, voles were weighed and when possible, species and sex were determined. On the mark-recapture grid, an MNA index was obtained (in order to calibrate the MNA indices with the mark-recapture density estimates), and traps were then locked open for an additional four nights, followed by a mark-recapture session of 3–5 consecutive trap nights. Handling was the same for mark-recapture sessions as for MNA indices, and ear tags were used for individual identification. A buffer strip the width of the average vole movement between recaptures (18.7 m) was added to the area of the trapping grid for density estimates.

**Dall sheep.** Annual estimates of Dall sheep abundance were obtained by aerial surveys in June 1999–2001 from a Robinson R22 helicopter. Lambs, ewes, rams, and yearlings were counted in separate categories throughout the study area. Surveys were conducted using the same pilot and observer each year, in similar weather conditions and at the same time of year.

**Carrion.** Wolf and hunter-killed moose, caribou, and Dall sheep carcasses were commonly scavenged by coyotes. The number of hunter-killed ungulates in the study area was calculated from harvest records at the Alaska Department of Fish and Game (ADF&G), and the number of wolf-killed ungulates was determined from a wolf kill rate study conducted by ADF&G in the study area during winters 1998 and 2000. Carcass density was similar in both years, so I used the average carcass density for the three years of this study. The kill rate in summer months was assumed to be half the rate of winter kills due to changes in wolf social structure and diet (M. McNay, ADF&G, personal communication).
Porcupine. An estimate of porcupine abundance was not obtained in the study area because they were rarely seen (four sightings in three years) and not considered to be an important prey item at the outset of the study. Based on other studies of porcupines and the scarcity of sign in our area, we assumed that porcupine density remained constant and low (0.7 per ha) for the duration of this study (Sweitzer 1996, Zimmerling 2001).

Biomass calculations

Biomass of hares, ground squirrels, and voles per hectare was calculated by multiplying the average weight of live-trapped animals by the respective density estimates. For Dall sheep lambs, the biomass calculation was based on a model incorporating birth rates, mortality rates, and growth rates each year (data from ADF&G and Shackleton et al. 1999), and the yearly average biomass was used. Adult Dall sheep were not included in the biomass calculation, because coyotes rarely killed adult sheep in this area (Arthur 2003). Carrion biomass was estimated by monitoring fresh wolf-killed carcasses during winter months to estimate the proportion left after abandonment by wolves. For hunter-killed ungulates, 30% of the biomass was assumed to be available to scavengers, based on the amount of meat that hunters were legally required to remove from harvested animals (Alaska Department of Fish and Game 2003). Wolf and hunter-killed ungulates were separated into species, sex, and age categories and multiplied by the appropriate biomass based on ADF&G data.

To facilitate comparison of relative prey biomass, a GIS habitat map was used to quantify available habitat in the study area for hares, ground squirrels, voles, and porcupines based on 24 land cover classifications (Bureau of Land Management 2002). The habitat-specific density estimates for each prey type were multiplied by the hectares of available habitat to provide an estimate of total prey biomass in the study area. Estimates of lamb and carrion biomass were calculated based on counts in the entire study area, so these were not adjusted for habitat.

Coyote diet

Scat analysis. Coyote feces were collected during summer (May–August) and winter (January–March) 1999–2002. Scats were collected opportunistically in summer as we traveled in the study area on foot, and they were collected on snowmobile trails and by backtracking coyotes in winter. Scats were autoclaved to kill Echinococcus eggs (Colli and Williams 1972). Sterile samples were washed in nylon mesh bags using a clothes washing machine on gentle cycle, and
samples were air-dried before analysis. Dried scats were carefully examined and all food items present were recorded. The relative amount of each item in the scat was estimated on a scale of 1-5, with 1 = trace amount (<2%), 2 = 2–25%, 3 = 26–50%, 4 = 51–75%, and 5 = 76–100% of scat contents. Hairs, teeth, and claws were compared to reference specimens and guide books (Moore et al. 1974) for identification. Hair medulla patterns were examined under a microscope for identification, and scale impressions were made for all moose and caribou hairs, as well as other hairs that were difficult to identify. Occurrences of moose and caribou in scats were assumed to be the result of scavenging and categorized as carrion, because studies of these species in this area did not find coyotes to be a significant source of mortality (Boertje et al. 1996). Diet from scats is reported as % weighted occurrence:

\[
\text{% weighted occurrence}_{prey_i} = \frac{X_i Y_i}{\sum_{i} X_i Y_i}
\]

where \( X_i \) = occurrence of prey \( i \) in scats and \( Y_i \) = relative amount of prey \( i \) in scats (weighting value), divided by the total weighted occurrences of all prey items in the diet.

Items with a weighting value of "1" (trace amount) were excluded from analyses. When annual diet is reported, summer and winter scats are pooled (May–August and January–March). I refer to summer 1999/winter 2000 as year 1, summer 2000/winter 2001 as year 2, and summer 2001/winter 2002 as year 3.

Snow tracking. Diet information was also collected by following coyote tracks during winters 2001 (143.8 km) and 2002 (140.7 km). Fresh coyote tracks were located by traveling on snowmobile trails after fresh snowfalls. When a track was encountered, it was backtracked on foot, and the following events were recorded: kills, visits to old kills (scavenging), caching, and retrieval of food from caches. The study area was stratified and tracks were chosen from within these areas to ensure equal representation from each area. Diet was calculated by summing food-related events recorded for each prey species and dividing this by the total number of food-related events.

Data analysis

Repeated measures analysis of variance was used to test for changes in snowshoe hare, ground squirrel, and vole abundance among years. Hare data were log transformed to meet the assumptions of ANOVA. Diet diversity was calculated using Simpson's index of diversity on a
random subsample of 72 scats each season (Krebs 1999, p. 443), and linear regression was used to examine the effect of hare abundance on diet diversity.

To test for prey switching, the selection ratio for each prey item (% weighted occurrence in diet/relative biomass in study area) was compared among years using Bonferroni adjusted Chi-squared tests (after Manly et al. 2002, p. 57-58). After Bonferroni adjustment, significance of pairwise comparisons were tested at $\alpha = 0.017$ to maintain an overall $\alpha$ of 0.05 over all three comparisons. Separate tests were conducted using diet data from scats and snow tracking. If the selection ratio for a prey item was low when the prey was scarce and increased when the prey was abundant, I considered this evidence of prey switching. Selection ratios were only used as “ballpark” estimates of predator preference in this study, because occurrence of items in scats may not be directly proportional to biomass ingested for each prey type. Small prey tend to be over-estimated and large prey tend to be under-estimated by scat analysis due to differences in the ratio of indigestible (hair and bone) to digestible (muscle and organ) material (Johnson and Hansen 1979). This problem affects only the absolute value of the selection ratio, however, and changes in selection ratios over time should accurately reflect changes in coyote selection for prey. It should also be noted that selection ratios can be sensitive to the prey items chosen for analysis (Manly et al. 2002). Re-analysis of this dataset with various combinations of species indicated the selection ratios reported here are fairly robust to changes in prey species included in the analyses.

Regression analyses were used to examine the relationship between available prey biomass and coyote diet, using both relative and absolute measures of prey biomass and occurrences in coyote scats. For regression analyses, $\alpha = 0.05$. Analyses were conducted using JMP-IN 4.0 (SAS Institute) and Excel (Microsoft Inc.).

Results

Prey abundance

The abundance of snowshoe hares declined nearly 6-fold from 1999–2001 (Figure 2.2a, $F_{1,8} = 68.8$, $P<0.0001$), and hare biomass declined from 68% of total prey biomass in 1999 to
Figure 2.2. Yearly estimates of (a) hare, (b) ground squirrel, (c) vole, (d) lamb, and (e) total prey biomass in the Alaska Range, 1999–2001. Estimates were adjusted for habitat coverage and represent average total biomass in the 1,000 km$^2$ study area. Error bars represent 90% confidence intervals of bootstrapped means. Lamb estimates (d) were from total counts. Carcass and porcupine estimates were included in total prey biomass calculations (e).
Figure 2.3. Relative available biomass of six prey species monitored in the Alaska Range, 1999–2001. Carrion biomass was too negligible (0.3–0.4%) to be visible in this graph.
Figure 2.4. Relative occurrence of prey items in coyote scats (weighted by the approximate volume of items in each scat) collected in the Alaska Range from 1999–2002. Sample sizes (n scats) are shown above bars. The “other” diet category included mainly birds and vegetation. Year 1 = summer 1999/winter 2000, year 2 = summer 2000/winter 2001, and year 3 = summer 2001/winter 2002.
20% of total prey biomass in 2001 (Figure 2.3). The hare decline resulted in an overall decline in prey biomass from 1999–2001 (Figure 2.2e), although this decline in prey abundance was partially mitigated by the vole irruption in 2001 (Figure 2.2c; \( F_{1,3} = 9.22, P = 0.056 \)). By 2001, voles represented 61% of available prey biomass (Figure 2.3). Ground squirrel abundance was moderate and stable across all years (\( F_{1,2} = 4.81, P = 0.16 \)). The high variance of these estimates indicates that squirrel distribution was patchy (Figure 2.2b). Dall sheep lamb biomass declined 50% between 1999 and 2000 and remained low in 2001 (Figure 2.2d). Lamb biomass represented only 1% of total prey biomass each year (Figure 2.3). After abandonment by wolves, 14.6% of carcass biomass was available to scavengers on average (\( n = 8, 95\% \) CI ± 13.46%). Approximately 85% of the carrion provided by wolves and hunters was moose. Hunters provided twice as much carrion as wolves but only during the fall hunting season, whereas wolf kills were available year-round. Combined hunter and wolf carrion represented only 0.3–0.4% of the total available prey biomass (Figure 2.3). Based on an assumed density of 0.7 porcupines per hectare, porcupines represented 1.4–2.2% of the total prey biomass (Figure 2.3).

**Coyote diet**

A total of 1590 coyote scats were collected from 1999–2002. Snowshoe hare was the most prevalent item in coyote scats during years 1 and 2, but carrion surpassed hares as the top prey in year 3 (Figure 2.4). Hare occurrences decreased in the diet as hare abundance declined, whereas carrion, porcupine, and vole occurrences increased, and ground squirrels, Dall sheep, and other items (mainly birds and vegetation) remained unchanged in the diet (Figure 2.4). The proportion of porcupine in the diet increased from 0.53% in year 1 to 13.6% in year 3, and voles increased from 5.0% in year 1 to 10.9% in year 3 (Figure 2.4). The diversity of prey items in coyote scats was negatively related to snowshoe hare abundance (Figure 2.5, \( R^2 = 0.85, F_{5,4} = 22.5, P = 0.009 \)). Diet diversity showed no seasonal trends: diversity was slightly higher in summer than winter in year 3 but was slightly lower in years 1 and 2. Thus, hare abundance had a stronger influence on coyote diet breadth than seasonal changes in the prey community.

**Prey preference and switching**

Selection ratios were calculated for each prey type each year to test for prey switching. There was no significant change in the selection ratio for hares between years 1 and 2, but coyote selection for hares increased significantly between years 2 and 3 (Table 2.1, \( P < 0.001 \)).
Table 2.1. Yearly estimates of the selection ratios (relative occurrence in scats/relative available biomass) of coyotes for 6 prey types in the Alaska Range, 1999–2002. Year 1 = summer 1999/winter 2000, year 2 = summer 2000/winter 2001, and year 3 = summer 2001/winter 2002. Results from $\chi^2$ tests of differences between selection ratios among years are reported. After Bonferroni adjustment, the critical $\chi^2$ value is 5.99. Statistically significant differences ($P < 0.0167$) are in bold.

<table>
<thead>
<tr>
<th>Selection ratios</th>
<th>Manly's $\alpha$</th>
<th>$\chi^2$ values</th>
</tr>
</thead>
<tbody>
<tr>
<td>hare</td>
<td>0.88</td>
<td>1.00</td>
</tr>
<tr>
<td>squirrel</td>
<td>0.23</td>
<td>0.11</td>
</tr>
<tr>
<td>vole</td>
<td>0.31</td>
<td>0.30</td>
</tr>
<tr>
<td>lamb</td>
<td>6.04</td>
<td>6.39</td>
</tr>
<tr>
<td>porcupine</td>
<td>0.43</td>
<td>2.30</td>
</tr>
<tr>
<td>carrion</td>
<td>96.19</td>
<td>56.64</td>
</tr>
<tr>
<td>N scats</td>
<td>376</td>
<td>537</td>
</tr>
</tbody>
</table>

27
Table 2.2. Occurrences of food-related events (kills, scavenging, caching) encountered while snow-tracking coyotes, and relative prey biomass available in the Alaska Range, winters 2001–2002. Selection ratios are the relative occurrences of each prey type in the diet divided by relative available prey biomass. Results from $\chi^2$ tests of differences between selection ratios in 2001 and 2002 for each prey type are reported. The critical $\chi^2$ value was 3.84 ($\alpha = 0.05$). No differences were statistically significant.

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Occurrences</th>
<th>Prey biomass</th>
<th>Selection ratio</th>
<th>Manly's $\alpha$</th>
<th>$\chi^2$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>hare</td>
<td>16</td>
<td>8</td>
<td>0.70</td>
<td>0.11</td>
<td>0.57</td>
</tr>
<tr>
<td>vole</td>
<td>4</td>
<td>8</td>
<td>0.26</td>
<td>0.84</td>
<td>0.39</td>
</tr>
<tr>
<td>lamb</td>
<td>1</td>
<td>2</td>
<td>0.01</td>
<td>0.01</td>
<td>1.70</td>
</tr>
<tr>
<td>porcupine</td>
<td>1</td>
<td>4</td>
<td>0.03</td>
<td>0.03</td>
<td>0.89</td>
</tr>
<tr>
<td>carrion</td>
<td>18</td>
<td>27</td>
<td>0.00</td>
<td>0.00</td>
<td>197.36</td>
</tr>
<tr>
<td>total</td>
<td>40</td>
<td>49</td>
<td>1</td>
<td>1</td>
<td>200.91</td>
</tr>
</tbody>
</table>
Figure 2.5. Relationship between coyote diet diversity and snowshoe hare biomass in the Alaska Range, 1999–2002. Each datapoint represents the Simpson’s diversity index for a random subsample of scats \((n = 72)\) from each season \((n = 6)\), plotted against the corresponding snowshoe hare biomass estimate.
Although the percent occurrence of hares in the diet decreased by 23.8% between years 2 and 3, the availability of hares decreased by 40.8%. Thus, coyote selection for hares actually increased as hares declined.

Voices were the most abundant prey by year 3, but the selection ratio for voles did not increase (Table 2.1). Carrion was the most preferred prey, because proportional occurrence in the diet was much higher than proportional availability each year (Table 2.1). Coyote selection for carrion decreased between years 1 and 2 ($\chi^2 = 16.10, P < 0.001$) and then increased between years 2 and 3 ($\chi^2 = 6.90, P = 0.009$). Selection for ground squirrels and Dall sheep did not change significantly among years. The selection ratio for porcupines increased significantly each year (Table 2.1, $P < 0.001$).

**Diet from snow tracking**

Coyote diet was quantified by recording feeding events found while snow-tracking coyotes in winters 2001 and 2002 (Table 2.2). The dietary information obtained from snow-tracking and scat analysis was remarkably similar. As with scats, data from snow tracking showed that hares and carrion were the most common food items. Changes in diet composition from 2001 to 2002 also were similar between methods: percent occurrence of hares decreased, and occurrence of voles, porcupine, and carrion increased in the diet. Changes in selection ratios among years showed similar patterns for both methods, but no comparisons of selection ratios among years were significant for data from tracking (Table 2.2). The main difference between the two methods was that carrion was more prevalent in the diet estimated by tracking in both years. The importance of carrion was likely over-estimated in the tracking data due to coyotes visiting old carcasses without feeding.

**Predicting coyote diet**

Snowshoe hare biomass was a good predictor of the percent occurrence of hare, carrion, vole, and porcupine in coyote scats (Figure 2.6). Absolute hare biomass explained more of the variation in prey occurrence than relative hare biomass (Table 2.3). As hare biomass increased, occurrence of hare in scats increased (Figure 2.6a; $R^2 = 0.73$, $F_{5,4} = 10.99$, $P = 0.03$), occurrence of carrion decreased (Figure 2.6b; $R^2 = 0.70$, $F_{5,4} = 9.36$, $P = 0.038$; without outlier, $R^2 = 0.99$, $F_{4,3} = 260.7$, $P < 0.001$), occurrence of porcupine decreased (Figure 2.6c; $R^2 = 0.94$, $F_{5,4} = 63.16$, $P = 0.001$), and occurrence of voles decreased (Figure 2.6d; $R^2 = 0.92$, $F_{5,4} = 47.39$, $P = 0.002$). Ground squirrels hibernate in winter so we could not include them in this analysis.
Table 2.3. Regression analyses of the percent occurrence of five prey species in coyote scats versus absolute hare biomass and relative hare biomass. \( N = 6 \) seasonal datapoints for each regression, except for carrion (no outlier) \( n = 5 \). A linear function was used to predict occurrence of hares, carrion, and lamb in the diet, and an exponential decay function was used for vole and porcupine. Significant relationships are in bold. Figure 2.6 shows graphs of the regressions with absolute hare biomass.

<table>
<thead>
<tr>
<th>Prey in diet</th>
<th>Absolute hare biomass</th>
<th>Relative hare biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Equation</td>
<td>R(^2)</td>
</tr>
<tr>
<td>hare</td>
<td>( y = 0.454 + 0.0000035*x )</td>
<td>0.73</td>
</tr>
<tr>
<td>vole</td>
<td>( y = 0.329<em>exp(-0.002</em>x) )</td>
<td>0.92</td>
</tr>
<tr>
<td>porcupine</td>
<td>( y = 0.318<em>exp(-0.003</em>x) )</td>
<td>0.94</td>
</tr>
<tr>
<td>carrion</td>
<td>( y = 0.56 - 0.0004*x )</td>
<td>0.7</td>
</tr>
<tr>
<td>(no outlier)</td>
<td>( y = 0.595 - 0.0000048*x )</td>
<td>0.99</td>
</tr>
<tr>
<td>lamb</td>
<td>( y = 0.084 - 0.000002*x )</td>
<td>0.06</td>
</tr>
</tbody>
</table>
Figure 2.6. Relationship between prey occurrence in coyote scats and available snowshoe hare biomass in the Alaska Range, 1999–2002. Percent of coyote scats containing (a) snowshoe hare, (b) moose or caribou carrion, (c) voles, and (d) porcupine are plotted against the corresponding snowshoe hare biomass estimate for each season (n = 6 seasons). Dashed line (b) is the linear regression excluding the outlier (n = 5). Sample sizes of scats for each estimate vary from 72–407. Regression equations, R² values, and P-values of analyses are reported in Table 2.3 (absolute hare biomass).
Occurrences of carrion, porcupine, and vole in coyote scats were better predicted by hare biomass than by any other prey biomass (including their own), but Dall sheep occurrence in scats could not be predicted by hare biomass (Table 2.3; $R^2 = 0.06, F_{5,4} = 0.24, P = 0.65$) or any other prey biomass (including sheep). Vole biomass was also a good predictor of vole occurrence in the diet (linear function; $R^2 = 0.80, F_{5,4} = 16.2, P = 0.016$), but this may have been an artifact of the negative correlation between vole and hare biomass ($R = -0.81, P = 0.05$).

**Discussion**

Snowshoe hares were the primary prey of coyotes in the mountainous Alaska Range, a finding in agreement with previous studies of northern coyotes (Thurber et al. 1992, O'Donoghue et al. 1998b). Coyote selection for hares did not decrease when hare abundance declined; in fact, their selection for hares actually increased, and the absolute density of hares was the best predictor of coyote diet composition. These findings support my first alternative hypothesis (H$_1$), which was based on predictions of optimal foraging theory when predators forage in a fine-grained environment. My second hypothesis (H$_2$), which predicted that selection for hares would decline due to habitat switching by coyotes foraging in a coarse-grained environment, was not supported. The alternative prey types that coyotes relied on most heavily when hare abundance was low (carrion and porcupine) occurred in the same habitat as hares, so coyotes were able to include these items in their diet while foraging in snowshoe hare habitat. Additionally, what appeared to be a patchy, heterogeneous habitat landscape in my study area may have been utilized as a fine-grained environment by coyotes. The home ranges of most radiocollared coyotes in this area included all major habitat types (Figure 2.1) and coyotes moved among habitat patches on a daily basis during all years (ADF&G, unpublished telemetry data). Although habitat patchiness is often shown to increase the stability of predator-prey interactions in theoretical analyses (Holt 1984, Oksanen et al. 2001, Schmidt 2004), relatively few studies have demonstrated this effect in the field (Schmitt 1987, Seip 1992).

**Profitability and thresholds**

As predicted by H$_1$, alternative prey were added to the diet of coyotes as hare density declined, but not in the pattern expected. Optimal foraging theory predicts that predators should consume only the most profitable prey when it is above a threshold density and consume
alternative prey when primary prey density falls below this level (Stephens and Krebs 1986). There was no evidence of a threshold hare density that affected inclusion of alternative prey in the coyote diet. Alternative prey were consumed during peak hare abundance, and the addition of new prey items to the diet was linear during the hare decline (Figure 2.5). Partial preferences and a gradual shift in diet, which is considered "semi-optimal" (Oksanen et al. 2001), is often observed in field studies and may occur due to imperfect knowledge, sampling, or nutritional constraints (Belovsky 1981, Stephens and Krebs 1986). It is also possible that hare density never exceeded the level beyond which it would become advantageous for coyotes to ignore all other prey items encountered. Additionally, coyotes are subject to predation themselves and may alter foraging patterns depending on risk levels and their nutritional state (Dekker 1989, Bateson 2002, Switalski 2003).

Use of the term "profitable" may lead to some confusion, because this term may or may not account for prey density. In the optimal foraging literature, profitability is the energy gained per energy expended to capture and consume a prey item. Because optimal foraging theory predicts a profitable item should be consumed regardless of its density, this can be thought of as "intrinsic profitability." Many factors will influence the intrinsic profitability of a prey item, such as size, vulnerability, and nutritional content (Stephens and Krebs 1986). However, this measure disregards the energy expended while searching for the prey item, which will be strongly affected by prey density. I will use the term "net profitability" when including search time in the measure of energy expended. For a species that has a high intrinsic profitability ranking but is rare, it may be advantageous for the predator to attack this prey if it is encountered opportunistically, but it may not be advantageous to specifically search for it.

Prey selection

In contrast to a recent study of coyote foraging in the Yukon, where voles were the most common alternative prey in the diet (O'Donoghue 1997), carrion was the most commonly-used alternative prey in our study area. This was surprising, considering voles were the most abundant food source by the end of the hare decline and carrion represented a negligible component of available prey biomass. Occurrence of voles in scats doubled as hares declined and was likely influenced by hare abundance, but voles ranked only fourth in dietary importance when hares were scarce. Coyote selection for voles did not increase in response to the hare decline or the vole irruption, contrary to the predicted response of a prey-switching generalist. A coyote would have to catch approximately 53 voles to equal the biomass of one snowshoe hare,
and since voles occur primarily in open meadows and snowshoe hares prefer dense cover, coyotes cannot search efficiently for hares and voles at the same time. Thus, the abundant biomass of voles in the study area did not appear to raise their net profitability above that of less abundant prey types.

The strong selection for carrion during all years, on the other hand, suggests that it had high intrinsic and net profitability. Carrion does not need to be pursued and hunted down, so the handling costs of this prey item are negligible. After a carcass was discovered, coyotes returned to it repeatedly (unpublished tracking data), so it was a reliable food source that required little search time. However, use of carrion increased as hare abundance declined, suggesting that use of carrion has some costs, relative to use of hares. Wolves and humans (providers of the carrion) are known to kill coyotes (e.g., Polis et al. 1982, Paquet 1992, Switalski 2003, Wilmers et al. 2003), whereas the risks associated with hunting hares are minimal. Furthermore, coyote territory size may decrease when hares are abundant (Mills and Knowlton 1991, Patterson and Messier 2001), and smaller home ranges may reduce the number of carcasses available to coyotes.

Although coyotes are an important predator of Dall sheep lambs (Scotton 1998, Arthur 2003), Dall sheep was a small component of coyote diet in all years, and consumption of sheep was not related to hare or sheep abundance. Thus, variation in per-capita coyote predation on Dall sheep may be affected more by weather or sheep condition (Windberg and Mitchell 1990, Delgiudice 1998, Patterson and Messier 2000) than by prey abundance. Most coyote predation on Dall sheep occurred during the spring lambing season (Arthur 2003), when young lambs were most vulnerable and coyotes were rearing pups in high-elevation dens. Although coyotes did kill some lambs during winter, they appeared to require particular snow conditions (deep drifts) in order to effectively hunt sheep. Dall sheep may therefore be effectively unavailable to coyotes during most of the year, as are ground squirrels (which hibernate from September–April; Forsyth 1999). The ephemeral nature of these resources may partially explain why coyote selection for Dall sheep and ground squirrels did not increase when hares declined.

When hares were at peak abundance, coyote consumption of porcupine was rare. This finding was expected, given the scarcity of porcupine sign in the area and the danger associated with hunting porcupines (two radiocollared coyotes in this study area evidently died as a result of ingesting porcupine quills [Chapter 4]). Despite these considerations, coyote utilization of porcupines increased 25-fold in response to the hare decline. Similarly, Thurber et al. (1992) found that porcupines were the most common alternative prey for coyotes during a cyclic low in
snowshoe hare numbers on the Kenai Peninsula in Alaska. I cannot rule out the possibility that coyotes increased consumption of porcupines due to an irruption in porcupine numbers, because I did not assess porcupine populations. This seems unlikely, however, because sightings of porcupines and porcupine tracks were infrequent and did not increase during the study. In addition, porcupines only have one young per year (Woods 1973), which limits their capacity for rapid population growth. Adult porcupines weigh approximately 7.5 kg (Zimmerling 2001), which is approximately equivalent to six snowshoe hares or 342 voles. Thus, porcupines may have been the most profitable under-exploited prey item available when hare populations declined.

**Community stability**

Although porcupines were not the most common food item in the coyote diet during any year, they experienced the greatest increase in predation pressure compared to other prey. Coyote predation on porcupines may have had a destabilizing effect on the porcupine population due to the sudden increase in predation pressure. Such a case was reported in the Great Basin Desert, when cougars switched from mule deer to porcupines and caused the near-extinction of a porcupine population (Sweitzer et al. 1997).

In general, coyote predation on alternative prey species was not density dependent, which should have been destabilizing (Sinclair 1989). For example, the lack of feedback between coyote and Dall sheep population dynamics means that coyotes could potentially drive sheep populations extinct. Because coyotes rely primarily on hares but are major predators of sheep, they could drive sheep populations to low levels without suffering adverse consequences. However, the cyclic dynamics of snowshoe hares may prevent coyotes from driving alternative prey extinct in northern areas, because heavy predation pressure should be periodic rather than sustained. Instead, coyote predation may trigger population cycles in alternative prey because predation patterns are closely linked to the snowshoe hare cycle. Such secondary predator-driven population cycles have been reported for several species in northern ecosystems, such as greater snow geese (Bety et al. 2002), ptarmigan, and ground squirrels (Boutin et al. 1995). In my study area, porcupines are the most likely alternative prey to exhibit secondary population cycles due exclusively to prey switching by coyotes. No data exists on porcupine population trends in Alaska or the Yukon, but emerging results from Quebec indicate that populations show major cyclic peaks every 22 years and minor peaks every 11 years (Berteaux et al. 2004).
Coyotes in Texas were found to be “keystone” generalist predators, because rodent diversity declined when coyotes were removed from treatment sites (Henke and Bryant 1999). By preying preferentially on the most abundant species, coyotes in Texas prevented competitive exclusion among rodents. Northern coyotes do not appear to have the stabilizing influence of a keystone generalist predator, however. Coyotes in the Yukon foraged as specialists on snowshoe hares and did not switch to alternative prey when hares declined (O'Donoghue et al. 1998a). In my study area, the absolute biomass of snowshoe hares was a better predictor of coyote diet composition than relative prey biomass. Voles were the only alternative prey in which coyote predation was related to alternative prey biomass, but this was likely an artifact of the negative correlation between vole and hare numbers.

Assuming that the net profitability of available prey types is the main factor affecting diet choices of predators, I hypothesize that in order for predation to increase the stability of a prey community, the net profitability of prey items must be determined primarily by prey abundance. Positive frequency-dependent predation (i.e., selectively preying upon the most abundant prey), which is the mechanism by which generalist keystone predators stabilize prey populations, should only occur in situations where the most profitable prey is always the most abundant prey. This statement implies that the intrinsic profitabilities of available prey items must be similar, because the only difference in my definition of net versus intrinsic profitability is the inclusion of search time (which will mainly be determined by prey density). Unfortunately, measuring the intrinsic profitability of a prey species is extremely difficult and will differ for each predator, so it may be difficult to predict situations in which predation should have a stabilizing effect. In vertebrate communities, prey size may be a major determinant of intrinsic profitability, and it may be possible to use this information to help make predictions (Sinclair et al. 2003). For example, coyotes exhibiting frequency-dependent predation in Texas were choosing from several similarly-sized rodents (Henke and Bryant 1999), whereas the sizes of coyote prey in my study area varied by several orders of magnitude.

The specialist-generalist dichotomy

Coyotes are classified as generalist predators, but their foraging behavior and population dynamics in northern areas seem to be driven primarily by snowshoe hare abundance, and in this sense they may function as specialists on snowshoe hares (O'Donoghue et al. 1998a). The distinction between specialist and generalist predators may be somewhat artificial for several reasons. Predators may change from foraging as specialists to foraging as generalists as
conditions change, both within and between communities (Krivan 1996), and individual predators within populations may vary in their degree of diet specialization (Bolnick et al. 2003). In addition, these terms are not well defined: specialist predators rely primarily on one prey type but often consume alternative prey (e.g., Lynx canadensis; O’Donoghue et al. 1998b), so it is unclear how wide a predator’s diet niche must be in order to be categorized as a generalist (Roper 1994). Predators that are categorized as specialists may have morphological adaptations that increase the efficiency of hunting a particular prey type (e.g., Dejean et al. 1999), but most predators fall somewhere on a continuum between complete diet generalization and specialization. In terms of predicting the effect of predators on community dynamics, the dichotomy may illuminate some broad-scale patterns (Murdoch et al. 2002) but may not be as useful when examining specific communities in detail. My study suggests that further examination of the interaction between predator behavior and prey characteristics may be a fruitful avenue of future research.
CHAPTER 3
MONITORING COYOTE POPULATION DYNAMICS BY GENOTYPING FECES

Introduction

Large predators are notoriously difficult to count because they tend to be rare, secretive, and wide-ranging. Non-invasive genetic sampling, in which genetic fingerprints are constructed from DNA extracted from hair or feces, has been used to obtain short-term population estimates for several mammalian species (e.g., Kohn et al. 1999, Banks et al. 2002, Eggert et al. 2003). To date, this method has not been used to study changes in a population over time. We used fecal genotyping to monitor the population dynamics of coyotes (Canis latrans) in Alaska over three years (2000-2002). Snowshoe hares (Lepus americanus) are the staple prey of northern coyotes (Thurber et al. 1992, O'Donoghue et al. 1998b), and the hare population declined approximately 10-fold during this study (Chapter 4). We hypothesized that coyote population size and survival would decline in response to the snowshoe hare decline, as was found elsewhere (Todd et al. 1981, O'Donoghue et al. 1997).

Accurate estimates of population parameters such as survival, recruitment, and abundance are crucial to the conservation and management of natural populations. Capturing, marking, and re-capturing animals is commonly used to estimate these parameters (see Seber 1986, Pollock et al. 1990, Lebreton et al. 1992, Schwarz and Seber 1999). For species that are too difficult to capture, collecting and genotyping shed DNA (commonly in the form of feces and hairs) can be considered equivalent to capturing the animal that deposited the genetic sample. Mark-recapture models can then be used to estimate parameters such as population size and survival.

Mark-recapture models assume that individuals are uniquely identifiable and that there is no error in their identification. When establishing individual identity through genotypes, however, there is always the chance of an identification error. Waits and Leberg (2000) found that typical levels of genotyping error (~5%) can lead to greatly inflated population estimates. Therefore, two preliminary goals of our study were to estimate (1) the probability of failing to distinguish different individuals ("the probability of identity," Taberlet and Luikart 1999), and (2) the probability of creating a new individual through genotyping errors. Additionally, we
investigated factors that affected DNA amplification success rates, such as sample age and storage method, because long-term studies may store samples for several years prior to analysis.

Mark-recapture statistical models generally fall under two categories: closed-population and open-population models. Closed-population models, such as Petersen and Schnabel estimators, assume populations are closed to births, deaths, immigration and emigration (Otis et al. 1978). Open-population models, such as Jolly-Seber, Cormack-Jolly-Seber, and Pradel models, do not assume population closure. Previous non-invasive genetic studies used closed-population models to estimate abundance because sampling in these studies occurred over a relatively short time period (e.g., Banks et al. 2002, Boulanger et al. 2002, Frantz et al. 2003).

The primary objective of this study was to evaluate the feasibility and utility of applying open-population models to long-term fecal genotyping data. We applied two open-population models to our three-year fecal genotyping dataset, and we used data from a concurrent radio-telemetry study to evaluate model performance. One model allowed us to integrate fecal data and supplementary mortality data, and we used this model to evaluate the benefits of combining a fecal sampling scheme with a traditional radio-telemetry study. Finally, we address our hypothesis that coyote population size and survival would decline in response to food stress as a "case study" to show how fecal genotyping can be used to monitor wildlife populations over time.

Methods

Sample collection

We collected a total of 1,237 scats in the central Alaska Range (63° 57' N, 147° 18' W; Figure 3.1) during November 1999–March 2000, January–March 2001, and January–March 2002. From these, we selected 834 scats for genetic analysis by random sampling without replacement. We obtained tissue samples from 17 radiocollared coyotes (Arthur 2003) and 5 coyotes trapped for fur or found dead in our study area from 1998–2002. The study area encompassed approximately 1,000 km² of mountains and foothills on the northern edge of the Alaska Range, and we established >150 km of snowmobile trails along the three major river drainages (Figure 3.1). Trails were travelled routinely to search for coyote scats, and we also collected scats while following coyote tracks on foot. The study area was stratified and tracks were chosen from within these areas to ensure equal representation from each area. Distances
Figure 3.1. Central Alaska Range study area (63° 57' N, 147° 18' W) showing major scat collection routes along the three main rivers (Wood River, Dry Creek, West Fork) and the two trials between river drainages (dashed lines). Point symbols represent locations of genotyped coyote feces, with a different symbol for each of the 56 individuals. Polygons show composite home ranges of radiocollared coyote pairs, 2000–2002. Elevation increased to the south and mountain peaks (2000–2600 m) occurred between river drainages south of the connecting trails.
travelled in search of scats were recorded as a measure of scat collection effort. We recorded the GPS location, estimated maximum age of the scat (based on travel and snowfall history), and our certainty level that the scat was from a coyote. Coyote scats could have been confused with those of grey wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), lynx (*Lynx canadensis*), and dogs (*Canis familiaris*).

**Sample storage, DNA preservation and extraction**

Due to cold winter temperatures, feces froze upon defecation. Collected scats were stored outdoors (average temperature = $-14.7^\circ$C) for 1–2 weeks before being flown to Fairbanks and stored at $-30^\circ$C. At the end of each field season, samples were prepared at the University of Alaska Fairbanks for DNA preservation. Approximately 100 mg of frozen fecal material was collected by scraping the surface of each sample with a scalpel and placing shavings into 2 ml vials.

Scats collected in the 1999/2000 and 2001 field seasons were stored in 1.5 mL DET buffer (20% DMSO, 0.25 M EDTA, 100 mM Tris, pH 7.5 and NaCl to saturation; Seutin et al. 1991). Samples from the 2002 field season were stored frozen in vials without the buffer. All vials were stored at $-80^\circ$C until DNA extraction. Scats from 1999/2000 were stored for 45 months prior to DNA isolation, scats from 2001 were stored for 33 months, and 2002 season scats were stored for 14 months.

DNA samples were transported frozen to the Genetics Data Centre at the University of British Columbia for genetic analyses. We extracted DNA from fecal samples using QIAamp DNA Stool Mini-Kits (Qiagen) after centrifuging samples for 10 minutes and removing the storage buffer. Scats stored without the buffer were processed directly. Extracted DNA was eluted with 150 µl of the provided elution buffer. Negative controls were included in each batch of DNA isolation to monitor for contamination. DNA isolation and amplification were conducted in separate labs to minimize the risk of contaminating stock DNA with post-PCR products, and aerosol-barrier tips were used for all procedures.

We examined four factors that we hypothesized could affect DNA amplification success rates: (1) supernatant color (which varied widely), (2) storage method (buffer or not), (3) storage time, and (4) age of scat at the time of collection. For a subset of 140 samples, we recorded the color of the sample after mixing with the ASL buffer (Qiagen protocol) on a scale of 1–5, with “1” being clear and “5” being black/brown. We compared the color of successful versus unsuccessfully-amplified samples using a Chi-square contingency test. For this test, data were
combined into three categories: light (scale value 1 or 2), medium (3), or dark (4 or 5). We compared mtDNA amplification success rates of samples stored in buffer versus no buffer, and of samples stored for 33 months versus 45 months, using Chi-square contingency tests. The effect of the estimated maximum age of a scat at the time of collection on amplification success was evaluated with logistic regression. All analyses were conducted using JMP-IN software (SAS Institute, Inc.).

Species verification and microsatellite analysis

We screened each fecal DNA sample with a mitochondrial DNA test to ensure the isolated DNA was from a coyote. We modified the method developed by Adams et al. (2003) for our genetic tests. Briefly, ScatID primers (Adams et al. 2003) were used to amplify a section of the cytochrome-\(b\) region of mtDNA, and the PCR product was digested with Taq\(^\alpha\)I restriction enzyme (New England Biolabs Inc.). Samples that did not amplify or showed non-coyote products were removed from the dataset. Of the 834 samples, DNA from 647 (78%) amplified successfully. Of the successful samples, 596 (92%) were coyote. One non-coyote sample was a lynx and the rest were red fox, wolf, or dog (we could not distinguish these species). For details of the species verification test, see Prugh and Ritland (in press).

Coyote microsatellite DNA was amplified in 10-\(\mu\)l reactions containing: 2.5 \(\mu\)l DNA extract (directly from kit extraction), 0.5 pmol forward IRD-labelled and reverse primers, 1x reaction buffer, 1.5 mM MgCl\(_2\), 1 unit AmpliTaq polymerase (Roche), 0.2 mM dNTPs, and 1mg/mL BSA. Negative controls were run with each batch of PCR. We amplified DNA in PTC-100 thermocyclers (MJ Research, Inc.) using the following program: initial denaturation at 94°C for 5 min; 35 cycles of 45 s at 94°C, 45 s at 58°C, and 45 s at 72°C; final extension of 72°C for 5 min. PCR products were visualized on 7% polyacrylamide gels using a Licor 4200 autosequencer. Gels were analyzed using SAGA genotyping software (MX version, Licor Inc.).

Probability of identity and genotyping error rates

The probability of identity (P\(_{ID}\)) is dependent upon the number of loci used to construct the genotype, the heterozygosity of the loci, and the relatedness of individuals within the population (Waits et al. 2001). DNA was amplified from our coyote tissue samples (\(n = 22\)) at 11 microsatellite loci, and we used these allele frequencies to calculate heterozygosity and P\(_{ID}\). We calculated P\(_{ID}\) for unrelated individuals as a lower bound (P\(_{ID-RAND}\)) and P\(_{ID}\) for siblings (P\(_{ID-SIB}\)) as an upper bound using equations from Waits et al. (2001). Based on our P\(_{ID}\) values (see
Results), we used our best 6 loci for individual identification (all tetra repeats: FH2137, FH2159, FH2140, FH2235, FH2096, FH2001; http://www.fhcrc.org/science/dog_genome/).

The genotyping error rate was determined by replicating PCR amplification five times for 45 fecal samples at five loci. A consensus genotype was constructed by examining the five replicates, and each replicate was compared to the consensus genotype to determine the per-replicate, per-locus error rate. Error due to allelic dropout and false alleles were recorded separately. Based on these results, we adopted the comparative multiple-tubes approach developed by Frantz et al. (2003). Based on this protocol, we replicated PCR at least twice for heterozygous samples and three times for homozygous samples. Samples were replicated a maximum of five times at each locus and were included in the dataset if they had consensus genotypes at four or more loci.

We used simple formulas to estimate the probability of creating a new individual with genotyping errors. The probability of allelic dropout in a consensus genotype is:

\[ P_D = \sum P_{DR}^3 \]

where \( P_{DR} \) is the per-replicate, per-locus dropout rate, summed across loci. The probability of a false allele in a consensus genotype is:

\[ P_F = \sum P_{FR}^2 \]

where \( P_{FR} \) is the per-replicate, per-locus false allele rate, summed across loci. The total probability of obtaining a false multi-locus consensus genotype (i.e., individual) is:

\[ P_{ERROR} = P_D + P_F \]

We grouped identical and near-identical multi-locus genotypes to look for potential errors by sorting in Excel (Microsoft, Inc.) and using the program GIMLET (Valiere 2002). Samples that only differed by one or two alleles from other samples were examined for scoring inconsistencies by aligning all replicates side-by-side using SAGA genotyping software (Licor, Inc.). Samples without matching genotypes were subjectively evaluated to determine whether they were likely to be unique individuals or erroneous genotypes. Criteria such as band intensity, clarity, and repeatability were used to visually scrutinize questionable samples, and poor quality samples (for example, samples with faint bands that were difficult to score) were removed from the dataset.
Sex identification

We determined the sex of each unique individual by choosing one fecal sample per individual and amplifying a 104 bp region of the SRY gene on the Y-chromosome with primers designed specifically for canids (5'-3' CTCGCGATCAAAGGCGCAAGAT upstream and 3'-5' TTCGGCTTCTGTAAGCATTTT C downstream; Meyers-Wallen et al. 1995b). With this method, only DNA from males amplifies. We therefore amplified the 177 bp canine HPRT gene as an internal control to distinguish between females and failed reactions (5'-3' GTAATGATCAGTCAACGGGGGAC upstream and 3'-5' CCAGCAAGCTTGCAACCTTAACAA downstream; Meyers-Wallen et al. 1995b). The PCR reactions contained the same reagents as our mtDNA species ID test, and the thermocycler program was the same as it was for our microsatellite reactions.

Although our primers were designed for canids, these regions of the genome are highly conserved among mammals and it may be possible to amplify DNA from prey remains in coyote feces. Therefore, the wrong sex could be recorded if a female coyote ate a male mammalian individual. Murphy et al. (2003) found high rates of false sex identification using captive grizzly bear (Ursus arctos) feces. To test the accuracy of sex identification from our coyote feces, we amplified five scats each from two male and two female radiocollared coyotes for which we had multiple fecal genotypes. An additional 18 fecal genotypes matched coyote tissue genotypes, and we compared the result of fecal DNA sexing to the known sex for these samples.

Estimation of population parameters

To apply mark-recapture models to our dataset, we divided each winter into “capture sessions” such that each month represented a different sampling interval. We did not estimate survival or population size in November or December 1999 because lack of snow limited fecal collections to the Dry Creek drainage during those months. A capture history was constructed for each coyote by recording whether or not it was “captured” during each interval. Only fecal samples were counted as captures; radio locations of collared coyotes were not included. For the Burnham joint live and dead encounters model, we also recorded whether the animal was found dead (either opportunistically or with radio-telemetry) during the interval. These capture histories were imported to the program MARK for analysis (White and Burnham 1999). We evaluated the accuracy of the Burnham model by graphically comparing the estimated survival rates of the radiocollared coyotes to their true survival rates. We calculated true survival rates by
dividing the number of collared coyotes known to have died by the number of collared coyotes known to be in the study area during each interval.

The first model we considered was the Cormack-Jolly-Seber (CJS) model, which estimates apparent survival ($\phi$) and recapture rates ($p$) of coyotes. Apparent survival is:

$$\phi = S \times F$$

where $S$ is the survival rate and $F$ is the fidelity rate ($1 - \text{emigration rate}$). Recapture rates are calculated for all time periods except the first, because there are no possible recaptures in the first interval. Survival estimates are calculated for all intervals except the last, because they represent the chance of surviving to the next interval. We used the CJS model as an example of how fecal genotyping data can be used in an open-population model without supplementary mortality data. We then used the Burnham joint live and dead encounters model, which allowed us to include mortality data from radio-telemetry and opportunistic encounters in order to estimate real survival ($S$), fidelity ($F$), recapture rates ($p$), and the probability of recovering dead animals ($r$).

In both models, parameter estimates were obtained using a general linear equation:

$$\ln\left(\frac{\theta}{1-\theta}\right) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + ... + \beta_s X_s + \varepsilon$$

where $\theta$ is the parameter of interest (e.g., $\phi$, $p$, $S$), $X_s$ is the value of the $s$th covariate, $\beta_i$ is the slope of the $s$th covariate (obtained through maximum-likelihood), and $\varepsilon$ is the error (Lebreton et al. 1992). We used the following covariates to model heterogeneity: sex, location, sampling effort, year, and whether or not a coyote was radiocollared. Location was recorded as the river drainage (Wood River, Dry Creek, or West Fork) where the majority of a coyote's scats were collected.

Within each model type (CJS or Burnham), models with different combinations of covariates were ranked and weighted according to Akaike information criterion ($\text{AIC}_c$; Burnham and Anderson 2002). Based on the recommendations of Lebreton et al. (1992), we began with the fully parameterized model (excluding interactions due to the limited dataset). We then checked for lack of fit using a bootstrapping goodness of fit test in MARK before analyzing reduced parameter models. When we had a final set of model results, we used model averaging to obtain parameter estimates and standard errors. Model averaging is generally preferable to the use of estimates from the best model alone because it accounts for model selection uncertainty in the parameter and variance estimates (Buckland et al. 1997, Burnham and Anderson 2002).
These open-population models do not produce estimates of population size directly within MARK. Therefore, we used the estimated recapture rates (\( \hat{p} \)) from the CJS model to derive estimates of coyote abundance using a simple Horvitz-Thompson-type estimator developed by McDonald and Amstrup (2001). This estimator is:

\[
\hat{N}_t = \sum_{s=1}^{n} \frac{I_{st}}{\hat{p}_{st}}
\]

where \( \hat{N}_t \) is the estimated population size at time \( t \), \( I_{st} \) is “1” if animal \( s \) was captured during time \( t \) and “0” if it was not, and \( \hat{p}_{st} \) is the maximum-likelihood estimate of the recapture rate of animal \( s \) at time \( t \). The approximate variance of \( N_t \) is:

\[
\text{var}(\hat{N}_t) = \sum_{s=1}^{n} \left( \frac{I_{st}(1 - \hat{p}_{st})}{\hat{p}_{st}^2} + \frac{I_{st}\sigma_{pst}^2}{\hat{p}_{st}^3} + \frac{I_{st}(1 - \hat{p}_{st})\sigma_{pst}^2}{\hat{p}_{st}^4} \right)
\]

Results

Factors affecting amplification success

Samples stored in the DET buffer had higher amplification success rates than samples stored at -80°C without buffer, despite the fact that buffered samples were stored 19–31 months longer prior to DNA extraction. The success rate of scats stored in buffer was 83.6% (\( n = 495 \)) versus 65.9% without buffer (\( n = 407 \); \( \chi^2_{1,900} = 38.3, P < 0.001 \)). Of the scats stored in buffer, samples that were stored for 33 months had higher amplification success than samples stored for 45 months (91% vs. 79% respectively, \( \chi^2_{1,493} = 13.9, P < 0.001 \)).

DNA extracts that were lighter in color had higher rates of amplification success than darker extracts: 90% of “light” extracts amplified successfully (\( n = 41 \)), 64% of “medium” extracts amplified successfully (\( n = 61 \)), and 48% of “dark” extracts amplified successfully (\( n = 40 \); \( \chi^2_{2,139} = 17.1, P < 0.001 \)). All samples in this trial were stored at -80°C without buffer for 14 months prior to extraction.

We found a weak, and perhaps biologically unimportant, effect of scat age on amplification success. The probability of successful amplification decreased slightly as the age of scats at the time of collection increased (logistic regression \( \chi^2_{1} = 4.9, P = 0.02, n = 834 \)).
Table 3.1. Genotyping error rate estimates for coyote fecal samples collected in the Alaska Range. Five replicate PCRs were conducted for 45 samples at five loci. $P_{DR}$ is the allelic dropout rate, $P_{FR}$ is the false allele rate, and $P_{ERROR}$ is the total estimated error rate when homozygotes were replicated three times and heterozygotes were replicated twice.

<table>
<thead>
<tr>
<th>locus</th>
<th>average $P_{DR}$</th>
<th>$P_{DR}$ 95% CI $^\dagger$</th>
<th>average $P_{FR}$</th>
<th>$P_{FR}$ 95% CI $^\dagger$</th>
<th>$P_{DR}^3$</th>
<th>$P_{FR}^2$</th>
<th>$P_{ERROR}$</th>
<th>$P_{ERROR}$ 95% CI $^\dagger$</th>
</tr>
</thead>
<tbody>
<tr>
<td>FH2001</td>
<td>0.086</td>
<td>0.036–0.137</td>
<td>0.015</td>
<td>0–0.041</td>
<td>0.00065</td>
<td>0.00023</td>
<td>0.00088</td>
<td>0–0.002</td>
</tr>
<tr>
<td>FH2137</td>
<td>0.019</td>
<td>0–0.073</td>
<td>0.014</td>
<td>0–0.035</td>
<td>0.00001</td>
<td>0.00019</td>
<td>0.00020</td>
<td>0–0.001</td>
</tr>
<tr>
<td>FH2140</td>
<td>0.061</td>
<td>0.008–0.114</td>
<td>0.014</td>
<td>0–0.037</td>
<td>0.00022</td>
<td>0.00020</td>
<td>0.00043</td>
<td>0–0.001</td>
</tr>
<tr>
<td>FH2159</td>
<td>0.008</td>
<td>0–0.031</td>
<td>0.032</td>
<td>0–0.113</td>
<td>0.00000</td>
<td>0.00102</td>
<td>0.00102</td>
<td>0–0.015</td>
</tr>
<tr>
<td>FH2235</td>
<td>0.049</td>
<td>0–0.108</td>
<td>0.023</td>
<td>0–0.065</td>
<td>0.00012</td>
<td>0.00051</td>
<td>0.00062</td>
<td>0–0.005</td>
</tr>
<tr>
<td>FH2096$^\ddagger$</td>
<td>0.045</td>
<td>0–0.093</td>
<td>0.020</td>
<td>0–0.058</td>
<td>0.00020</td>
<td>0.00043</td>
<td>0.00063</td>
<td>0–0.005</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.00119</td>
<td>0.00259</td>
<td>0.00378</td>
<td>0–0.029</td>
</tr>
</tbody>
</table>

$^\dagger$ Negative lower confidence intervals were set to 0.

$^\ddagger$ No estimates were obtained for this locus, so the average of the other five loci was used in order to estimate total error. An alternative method of calculating error from the final data confirmed that FH2096 had fairly “average” error rates.
Figure 3.2. Number of scats collected per coyote in the Alaska Range, 1999–2002. A total of 544 feces were genotyped from 56 coyotes.
The mean estimated age of successfully amplified scats was 13.3 days (95% CI = 12.1–14.6), versus 16.4 days (95% CI = 14.0–18.8) for unsuccessfully amplified scats.

**Probability of identity and genotyping error rates**

The average heterozygosity of our six loci was 0.74 (range = 0.68–0.79). The probability of identity using all loci was 0.0002 for unrelated individuals (\( P_{ID-RAND} \)) and 0.005 for siblings (\( P_{ID-SIB} \)). We included multi-locus genotypes with 4–6 loci, so the maximum probability of obtaining the same genotype for different individuals (i.e., \( P_{ID-SIB} \) for our four least heterozygous loci) was 0.033. Of the 544 multi-locus genotypes in the final dataset, 26 samples were genotyped at 4/6 loci, 78 were genotyped at 5/6 loci, and 440 were genotype at all 6 loci, for a weighted average \( P_{ID} \) range of 0.0004–0.0067.

The average per-locus, per-replicate dropout rate (\( P_{DR} \)) was 0.045 (95% CI = 0.006–0.084), and the average per-locus, per-replicate false allele rate (\( P_{FR} \)) was 0.018 (95% CI = 0.01–0.04; Table 3.1). Using the modified multiple-tubes approach (after Frantz et al. 2003), the average number of replicates conducted per sample, per locus was 2.8 (SE = 0.11) including failed reactions and 2.4 (SE = 0.07) excluding failed reactions. The probability of obtaining a false 6-locus genotype after replication (\( P_{ERROR} \)) was 0.004 (95% CI = 0–0.03; Table 3.1). Based on these data, we could expect anywhere from 0–16 erroneous genotypes in our sample of 546 genotypes.

We matched identical and near-identical genotypes to find samples that may have been erroneous, using the logic that samples without matching genotypes were the most likely samples to contain errors. Of the 546 samples, 27 had no matching genotypes. Two of these samples appeared to be of poor quality (see criteria in Methods) and were removed from the dataset. Eleven of these samples differed from another genotype at only one locus. We assumed these samples had genotyping errors and assigned them the identity of the closely matching genotype to reduce the possibility of falsely identifying an individual and thereby inflating our population estimate. We decided that the remaining 14 unmatched samples in our dataset were most likely unique individuals rather than genotyping errors. One sample matched the genotype of a radiocollared coyote, and the others were of high quality and differed from other genotypes at ≥3 loci.
Table 3.2. Top 10 Cormack-Jolly-Seber models run in program MARK to calculate maximum-likelihood estimates of the apparent survival rates ($\phi$) and recapture rates ($p$) of coyotes in the Alaska Range, 1999–2002. Twenty-two models were tested and ranked according to their AICc values. Models included the following covariates: whether a coyote was radiocollared (collar), sampling effort (effort), sex, location, or year (models including year and location were not among the top 10 models). Some models included time variation (t), where the parameter ($\phi$ or $p$) was estimated during each time interval.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$ AICc</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th># parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$(collar) $p$(collar+t)</td>
<td>307.4</td>
<td>0.0</td>
<td>0.55</td>
<td>1.00</td>
<td>13</td>
</tr>
<tr>
<td>$\phi$(collar) $p$(collar+effort)</td>
<td>309.0</td>
<td>1.6</td>
<td>0.24</td>
<td>0.44</td>
<td>5</td>
</tr>
<tr>
<td>$\phi$(collar) $p$(collar*effort)</td>
<td>311.2</td>
<td>3.8</td>
<td>0.08</td>
<td>0.15</td>
<td>6</td>
</tr>
<tr>
<td>$\phi$(collar) $p$(t)</td>
<td>311.8</td>
<td>4.5</td>
<td>0.06</td>
<td>0.11</td>
<td>12</td>
</tr>
<tr>
<td>$\phi$(collar) $p$(effort)</td>
<td>313.3</td>
<td>5.9</td>
<td>0.03</td>
<td>0.05</td>
<td>4</td>
</tr>
<tr>
<td>$\phi$(sex+collar) $p$(sex+collar+t)</td>
<td>314.8</td>
<td>7.4</td>
<td>0.01</td>
<td>0.02</td>
<td>17</td>
</tr>
<tr>
<td>$\phi()$ $p$(effort)</td>
<td>316.0</td>
<td>8.6</td>
<td>0.01</td>
<td>0.01</td>
<td>3</td>
</tr>
<tr>
<td>$\phi$(collar) $p$(collar)</td>
<td>317.3</td>
<td>9.9</td>
<td>0.00</td>
<td>0.01</td>
<td>4</td>
</tr>
<tr>
<td>$\phi()$ $p$(collar)</td>
<td>317.6</td>
<td>10.2</td>
<td>0.00</td>
<td>0.01</td>
<td>3</td>
</tr>
<tr>
<td>$\phi$(collar+t) $p$(collar+t)</td>
<td>318.8</td>
<td>11.4</td>
<td>0.00</td>
<td>0.00</td>
<td>22</td>
</tr>
</tbody>
</table>
Table 3.3. Top 10 Burnham joint live and dead encounter models run in program MARK to calculate maximum-likelihood estimators of the survival rates (S) and recapture rates (p) of coyotes in the Alaska Range, 1999–2002. Twenty-two models were tested and ranked according to their AICc values. Models included the following covariates: whether a coyote was radiocollared (collar) and sampling effort (effort). Some models included time variation (t), where the parameter (S or p) was estimated during each time interval. For all models, we fixed the parameter for site fidelity (F) at 1 and the dead animal recovery probability (r) at 1 for radiocollared coyotes. All models estimated “r” for uncollared coyotes, with no time variation, in addition to the parameters listed.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th># Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(collar) p(collar+t)</td>
<td>347.0</td>
<td>0.0</td>
<td>0.51</td>
<td>1.00</td>
<td>14</td>
</tr>
<tr>
<td>S(collar) p(collar+effort)</td>
<td>349.0</td>
<td>2.0</td>
<td>0.19</td>
<td>0.37</td>
<td>6</td>
</tr>
<tr>
<td>S(collar) p(t)</td>
<td>350.4</td>
<td>3.3</td>
<td>0.10</td>
<td>0.19</td>
<td>13</td>
</tr>
<tr>
<td>S(collar+t) p(collar+effort)</td>
<td>350.9</td>
<td>3.8</td>
<td>0.08</td>
<td>0.15</td>
<td>16</td>
</tr>
<tr>
<td>S(collar) p(effort)</td>
<td>352.3</td>
<td>5.3</td>
<td>0.04</td>
<td>0.07</td>
<td>4</td>
</tr>
<tr>
<td>S() p(collar+effort)</td>
<td>352.9</td>
<td>5.9</td>
<td>0.03</td>
<td>0.05</td>
<td>5</td>
</tr>
<tr>
<td>S(collar+t) p(effort)</td>
<td>353.1</td>
<td>6.0</td>
<td>0.03</td>
<td>0.05</td>
<td>14</td>
</tr>
<tr>
<td>S(collar+t) p(collar+t)</td>
<td>353.7</td>
<td>6.6</td>
<td>0.02</td>
<td>0.04</td>
<td>24</td>
</tr>
<tr>
<td>S() p(t)</td>
<td>355.29</td>
<td>8.24</td>
<td>0.01</td>
<td>0.02</td>
<td>12</td>
</tr>
<tr>
<td>S(t) p(collar+t)</td>
<td>356.0</td>
<td>8.9</td>
<td>0.01</td>
<td>0.01</td>
<td>23</td>
</tr>
</tbody>
</table>
Sex identification

All fecal samples from coyotes of known sex matched the correct sex ($n = 34$ samples from $11$ males and $7$ females). This included five replicate scats each for two male and two female coyotes. In addition, we analyzed three replicate scats from three coyotes of unknown sex, and the replicates showed $100\%$ agreement for each coyote. In total, $38$ tests assigned the correct sex and none were incorrect.

Coyote population dynamics

We identified $56$ unique individuals from the $544$ scats in our final dataset, $24$ females and $32$ males (Appendix I). The number of scats per individual ranged from $1\sim49$ (Figure 3.2), indicating considerable capture heterogeneity among individuals. Ten coyotes were present during all three years of the study, $11$ were present for two years, and $35$ were present during one year. All $15$ radiocollared coyotes that were present during scat collection and for which we obtained tissue or blood samples (we did not obtain a sample from one coyote) matched $\geq 1$ fecal genotype. All tissue samples from coyotes that were either fur-trapped or found dead in the study area during scat collection ($n = 4$) matched the genotype of $\geq 1$ fecal sample as well. Therefore, the chance of “capturing” a coyote present in our study area through fecal genotyping was very high. Moreover, we were able to non-invasively identify almost four times as many coyotes with fecal genotyping as we were with traditional capture methods.

The Cormack-Jolly-Seber model. The bootstrapping goodness-of-fit test showed that our fully-parameterized CJS model fit the data reasonably well (bootstrapping $P = 0.15$, $\hat{c} = 1.15$). We then examined reduced-parameter models and found that the best model included “radiocollar” as a covariate for both apparent survival ($\phi$) and the recapture rate ($p$), and the recapture rate varied over time (Table 3.2). The top five models included radiocollaring, sampling effort, or both as covariates. Coyotes that were radiocollared had higher survival and recapture rates than uncollared coyotes (Figure 3.3; Likelihood Ratio Tests, survival: $\chi^2_1 = 4.87$ $P = 0.03$; recapture: $\chi^2_1 = 4.75$ $P = 0.03$). Sex differences in survival and recapture rates were minimal, and models including this covariate were given little weight (Table 3.2). Likewise, location and year had minimal effects on survival and recapture rates and were therefore absent from the top $10$ models listed in Table 3.2 (out of $22$ models tested). Sampling effort explained
Figure 3.3. Estimated apparent survival ($\phi$) and recapture ($p$) rates of radiocollared and uncollared coyotes in the Alaska Range, 2000–2002. Error bars represent 95% confidence intervals. These maximum-likelihood estimates were obtained using the Cormack-Jolly-Seber model “$\phi$(collar) $p$(collar)” in program MARK.
Figure 3.4. Maximum-likelihood estimates of recapture rates of (a) radiocollared coyotes and (b) uncollared coyotes in the Alaska Range during each sampling interval. Estimates were obtained from Cormack-Jolly-Seber models in program MARK by model averaging, and error bars represent 95% confidence intervals.
approximately 32% of the variation in recapture rates. Recapture rates were lowest in January each year, when we were establishing our trails (Figure 3.4).

Estimates of population size derived from these recapture rates showed an increasing population that reached a peak of 35 coyotes in January 2001 and declined to 20 coyotes by March 2002 (Figure 3.5). Radiocollared coyotes accounted for 23–50% of the population at any given time during the study. The uncertainty surrounding these estimates was high (Figure 3.5). On average, 16.9% of this variation was attributable to model selection uncertainty.

*Burnham joint live and dead encounters model.* Our fully-parameterized Burnham model was a good starting point for evaluating reduced-parameter models (bootstrapping P = 0.21, \( \hat{c} = 1.08 \)). Based on the results of the CJS model, we did not include sex, location, or year as covariates in the Burnham model. As with the CJS model, the Burnham model with the most support included radiocollaring as a covariate for survival (S) and recapture rates (p), and recapture rates varied over time (Table 3.3). We predicted that coyote survival would decline during our study due to a decline in snowshoe hare abundance. We examined survival trends by using estimates from the most supported model that allowed survival to vary over time (S(collar+t) p(collar+effort), Table 3.3). Survival declined in 2001, when the coyote population size was highest, but survival increased in 2002 (Figure 3.6). The confidence intervals for estimated survival rates included the true survival rates of radiocollared coyotes in all time intervals except two, and in both cases true survival was 1 (Figure 3.6). Compared with estimates from the equivalent CJS model, the Burnham survival estimates were more precise (average Burnham CV = 14%, CJS = 17%) and deviated less from true survival rates (Burnham sum-of-squares = 0.05, CJS SS = 0.16).

The Burnham model also estimated site fidelity (F) and the probability of finding dead animals (r). We fixed “r” at 1 for radiocollared coyotes, and our estimated probability of finding dead uncollared coyotes was 0.11 (SE = 0.06). Due to our relatively small dataset, the models could not estimate both survival (S) and fidelity (F). When survival was held constant, F was estimated as 0.98 (SE = 0.03) for collared coyotes and 0.87 (SE = 0.05) for uncollared coyotes. Our radio-telemetry data agree, because 2 out of 16 radiocollared coyotes emigrated during the study, which is a per-interval fidelity rate of 0.99. In order to reduce the number of estimated parameters in our models, we fixed F at 1 for all coyotes. Therefore, survival rates (S) in our Burnham models were actually apparent survival rates (S*F).
Figure 3.5. Total estimated coyote population size in the Alaska Range study area during each sampling interval, derived from the recapture rates in Figure 3.4. Error bars represent 95% confidence intervals.
Figure 3.6. Maximum-likelihood estimates of the survival rates of (a) radiocollared coyotes and (b) uncollared coyotes in the Alaska Range during each sampling interval. Estimates were obtained from the Burnham joint live and dead encounter model “S(collar+t) p(collar+effort)” in program MARK. Error bars represent 95% confidence intervals. The dashed line (a) is the true survival rate of radiocollared coyotes.
Estimates of recapture rates from the Burnham model were nearly identical to recapture rate estimates from the CJS model, as were the derived population size estimates and variation. Thus, the Burnham model provided more accurate and precise survival estimates than the CJS model but did not increase the accuracy or precision of abundance estimates.

Discussion

Applying open population models to our 3-year fecal genotyping dataset provided insights into the response of coyotes to changes in food supply. We identified nearly four times as many coyotes with fecal genotyping as we did with traditional captures in the radio telemetry study, and we had ≥1 genotyped fecal sample for every coyote known to be in the study area (n = 19). Supplementary radio telemetry data was useful when estimating survival rates but did not increase the accuracy or precision of population estimates. When necessary precautions are taken to ensure data accuracy and appropriate mark-recapture models are used, fecal genotyping can be a practical technique for long-term wildlife monitoring.

Amplification success

Freezing at standard temperatures (−20 to −80°C) is probably not a sufficient storage method for long-term preservation of fecal DNA. Mitochondrial DNA amplification success rates were 18% higher for samples stored frozen in DET buffer compared with samples stored frozen without buffer, despite the fact that buffered samples were stored approximately two years longer. Frantz (2003) also had higher success rates with badger feces stored in DET buffer versus frozen. Other storage methods, such as drying samples with silica beads or storage in ethanol (or both), have also been used to preserve DNA (Goossens et al. 2000, Murphy et al. 2002, Nsubuga et al. 2004). Our amplification success rates were high (80–90%) with feces that had been stored in DET buffer for three or four years. To our knowledge, these are the longest storage times for fecal DNA reported in the literature, and we were therefore pleased to have such high amplification success rates. However, success rates were 12% lower with samples stored in buffer for four years versus three years. Thus, the shelf-life of fecal DNA, though potentially quite long, is not indefinite.
The scats in our dataset varied considerably in the length of time they could have been in the field prior to collection (1–90 days), but this variable did not have a strong impact on amplification success. The cold winter temperatures and constant snow cover during our study may have reduced the activity of bacteria in the fecal material and prevented contact with organisms in the environment that degrade DNA.

One of the challenges of amplifying DNA from feces is the presence of PCR inhibitors, such as polysaccharides from food residue, in fecal material (Monteiro et al. 1997). In fact, PCR inhibitors may pose more of a problem for amplification than DNA quality or quantity. We found that the color of the fecal extract, which may be an indicator of inhibitor level, had a stronger impact on amplification success rates than sample age or storage method. The success rates from dark scats, which likely have high levels of PCR inhibitors, were 42% lower than success rates from light scats. Morin et al. (2001) point out that inhibitors reduce the efficiency of PCR and therefore produce results that mimic low DNA template concentrations. They found high variability in the amount of amplifiable DNA in feces using quantitative PCR (Morin et al. 2001). Variation in the perceived DNA quantity may be determined by the amount of PCR inhibitors in the sample as well as the number of intestinal cells collected from the feces. Future research is needed to determine whether fecal extract color is related to PCR inhibitors and what factors cause these levels to vary among feces.

Reliability of sex determination

Unlike Murphy et al. (2003), who found that sex determination from captive grizzly bear feces was unreliable, our sex test was 100% reliable with coyote fecal DNA. Our primers were more specific, and coyote digestive processes might degrade prey DNA more effectively than bear digestion. Williams et al. (2003) also found that these primers accurately sexed coyote samples, even in mixtures with high concentrations of sheep DNA.

Genotype reliability

In this study we were more concerned about falsely identifying individuals (genotyping error) than about failing to differentiate unique individuals with matching genotypes (the shadow effect; Mills et al. 2000). Several studies have shown that genotyping error is a more serious problem than the shadow effect. For example, Creel et al. (2003) found that Yellowstone wolf population estimates from fecal genotyping were up to 5-fold higher than true numbers. Mills et al. (2000) showed that the closed population $M_{h,jackknife}$ CAPTURE model can produce relatively
unbiased population estimates despite the presence of shadow effect, whereas Waits (2000) found that this model can produce extremely biased estimates with common levels of genotyping error.

Our total per-replicate, per-locus error rate (6.3%) was lower than in most fecal genotyping studies, which have reported error rates of 5–35% (Flagstad et al. 1999, Kohn et al. 1999, Bayes et al. 2000, Ernest et al. 2000, Goossens et al. 2000, Lathuilliere et al. 2001, Morin et al. 2001, Banks et al. 2002, Lucchini et al. 2002, Creel et al. 2003, Eggert et al. 2003, Frantz et al. 2003). After employing the comparative multiple tubes method to reduce error (Frantz et al. 2003), our mean error rate was 0.4%, which should produce fairly unbiased population estimates based on simulations (Waits and Leberg 2000). However, we found that it was important to consider the uncertainty surrounding error rate estimates, because the number of genotypes in our dataset that were likely erroneous (13) was closer to upper end of our 95% confidence interval (0–16 expected erroneous genotypes) than it was to the mean (2 expected errors).

The equations we used to calculate genotyping error rate assume that the chance of having an error in one replicate is independent of the chance of having an error in a second replicate. For low quality samples this is probably not the case, and this may explain why we found more errors than expected. Creel (2003) highlighted the importance of considering variation in sample quality and recommended using a matching approach to reduce bias. We found the matching of near-identical genotypes and the careful scrutiny of samples without matches to be useful means of removing potentially erroneous genotypes. Unfortunately, the evaluation of unmatched samples is subjective and therefore complicates estimation of the probability of having erroneous genotypes in the final dataset.

Population dynamics of coyotes

The coyote population in our study area declined nearly 2-fold during the snowshoe hare decline, with a 1½-year time lag. The hare population peaked in our study area in summer 1999 and winter 2000 (Chapter 2), whereas the coyote population peaked in 2001. Likewise, coyotes in the Yukon tracked the snowshoe hare population in a classic predator-prey cycle with a 1-year time lag and a 4-fold change in density during the hare decline (O'Donoghue et al. 1997). The estimated survival rates of coyotes decreased after the peak in coyote numbers but then recovered, which is a mortality pattern that has also been documented in northern lynx populations (Poole 1994, O'Donoghue et al. 1997).
Utility of open population models

We found that fecal genotyping data could be used in open population models to study coyote population dynamics. The basic structure of the Cormack-Jolly-Seber model as implemented in program MARK is highly flexible, with a focus on model building and model selection that allows the researcher to model capture heterogeneity in a biologically relevant manner (Lebreton et al. 1992, White and Burnham 1999). The model selection process highlighted factors that affected coyote survival and recapture rates, such as radiocollaring and sampling effort, while factors such as sex, year, and location were shown to have little impact on these parameters.

Differences in survival, site fidelity, and recapture rates between collared and uncollared coyotes probably occurred because we attempted to radiocollar resident adult pairs rather than juveniles, and the telemetry data showed that home ranges of collared coyotes were within the boundaries of our study area (Figure 3.1). Nearly all juveniles in the population were uncollared, and juvenile coyotes have lower survival and higher dispersal rates than adults (Windberg 1995, Crete et al. 2001). Recapture rates probably were lower for uncollared adult coyotes because they were more likely to be transient or to have home ranges extending beyond the edges of our study area. In effect, “radiocollaring” may have been a proxy for age or resident status in our models, albeit an imperfect one.

The modified CJS model (Burnham joint live and dead encounters model) allowed us to include mortality data gathered opportunistically and through radio-telemetry, and this increased the accuracy and precision of the estimated survival rates but had no impact on estimates of recapture rates or population size. By using radiocollaring as a grouping variable, we not only learned that survival, site fidelity, and recapture rates differed among groups, but we could evaluate the accuracy of the survival estimates. Both models proved to be fairly accurate, and the Burnham model was more accurate and precise than the CJS model. If accurate and precise survival estimates are important goals of a study, we recommend supplementing fecal surveys with radio-telemetry when possible. If the primary goal is to track changes in population size over time, however, telemetry data may be unnecessary.

Confidence intervals surrounding our population estimates were wide, making strong inferences about population trends difficult. The usefulness of open population models may therefore be limited to fecal genotyping studies with relatively large sample sizes. Closed population estimators tend to be more precise, but using these models to estimate the size of open populations can lead to inflated estimates, because recapture rates will be biased low
Since genotyping error can also inflate estimates, fecal genotyping studies should be particularly cautious about violating the assumption of population closure. Bayesian techniques may be able to handle sparse data more effectively than traditional models, but most Bayesian models assume population closure (Gazey and Staley 1986, Garthwaite et al. 1995, Ananda 1997). The joint recovery/recapture open-population model developed by King and Brooks (2002), which combines CJS and Bayesian techniques, may be particularly promising for fecal genotyping datasets.

While considerable attention has been paid to the impact of genotyping error on population estimates (and rightly so), the usefulness of fecal genotyping will increase if more attention is focused on the development and appropriate use of population models. In particular, there is a need for a robust open-population model designed for data that are collected continuously. Many carnivore studies collect scats continuously over field seasons of several months in which births, deaths, immigration, and emigration may occur. The covering of feces by snow or the risk of DNA degradation in summer can make it more practical to collect scats continuously than during discrete intervals, particularly since it is necessary to have relatively large samples. Furthermore, animals deposit scats continuously regardless of the researcher’s collection schedule. It is unclear how the division of such data into arbitrary capture intervals affects the estimation of population parameters. Mark-recapture models for continuous data have been developed for closed populations (Wilson and Anderson 1995), but none currently exist for open populations. Rarefaction analysis, which is appropriate for continuously collected data, does not allow for capture heterogeneity and therefore can produce biased results (Krebs 1999 p. 415, Eggert et al. 2003), and it is not appropriate for open populations. Capture heterogeneity is ubiquitous and presents a major challenge for both closed and open population estimation (Pledger and Efford 1998), so any model used to estimate population parameters needs to adequately model capture heterogeneity.
CHAPTER 4
COYOTE-MEDIATED INTERACTIONS AMONG SNOWSHOE HARES AND DALL SHEEP

Introduction

Predation plays a key role in structuring communities. Frequency-dependent predation (i.e., selective foraging on the most abundant prey) may increase prey diversity because dominant prey are prevented from competitively excluding other species (Paine 1966, Caswell 1978, Crowley 1979). However, predators often feed on species that do not compete directly with one another, and predation can decrease prey diversity by facilitating indirect competition among these species. Predator-mediated competition, also known as apparent competition, occurs when the presence of one prey species leads to the reduced population size of another prey species due to the effects of a shared enemy rather than direct competition (Holt 1977). Apparent competition has been demonstrated by numerous studies in the field and laboratory and can play a central role in structuring communities (for reviews see Jeffries and Lawton 1984, Holt and Lawton 1994, Chaneton and Bonsall 2000). Predators are often dependent on one prey species but feed secondarily on other prey types, and high numbers of primary prey may support dense predator populations and thus lead to population declines and extinctions in secondary prey populations (Seip 1992, Sinclair et al. 1998).

Alternatively, one prey species may have a positive indirect effect on another prey species via shared predation, and this interaction is known as apparent mutualism (Holt 1977, Abrams et al. 1998). This can occur if an abundant species draws predation away from another due to positive frequency-dependent predation or predator satiation (Abrams and Matsuda 1996, Abrams et al. 1998). A classic example of this interaction is the relationship between lemmings and ground-nesting birds in the arctic. Nest predation is low during high lemming years, but predators switch to preying on eggs when lemmings crash (Underhill et al. 1993, Summers et al. 1998, Bety et al. 2002, Blomqvist et al. 2002). Thus, birds have higher nesting success when lemmings are abundant. In theory, prey-switching can lead to short-term apparent mutualism, but the long-term indirect effects may be negative due to the predator’s numerical response (Holt 1977, Abrams and Matsuda 1996). If predators cannot persist without the primary prey species, then the long-term effect of primary prey on alternative prey will likely be negative despite the
positive relationship when both species are present. In this paper, we will refer to positive indirect effects as apparent mutualism even though the long-term effects of the interaction may be negative. The distinction between short-term apparent mutualism and competition can help to predict the community response to changing prey densities. For example, if the short-term interaction among prey is apparent competition, then population crashes in the primary prey should benefit alternative prey, whereas crashes may be devastating for alternative prey if apparent mutualism is the dominant interaction.

Coyotes (Canis latrans) are primarily dependent on snowshoe hares (Lepus americanus) in northern ecosystems (Thurber et al. 1992, O'Donoghue 1997), but they are also major predators of Dall sheep lambs, Ovis dalli (Scotton 1998). Dall sheep range from northwestern British Columbia to the northwestern Canadian territories and Alaska (Forsyth 1999), and coyotes are a relatively new predator of Dall sheep, having arrived in the north approximately 100 years ago (Young and Jackson 1951). Low levels of Dall sheep recruitment in the early 1990's prompted concern about the declining trajectory of sheep populations and highlighted the need for a greater understanding of factors affecting lamb survival (Arthur 2003). Snowshoe hare populations in northern boreal forests are characterized by cyclic fluctuations with peaks every 8–11 years (Hodges 2000). In the mountainous areas of northwestern North America, snowshoe hare habitat often borders Dall sheep habitat, and coyotes forage in both habitat types. The goal of this study was to determine whether fluctuations in snowshoe hare numbers indirectly affect Dall sheep populations in the Alaska Range due to shared predation by coyotes.

Snowshoe hare numbers declined considerably in our study area from 1999–2003, and we monitored lamb survival rates and causes of mortality during this period to test for indirect effects of hares on sheep. We tested two alternative hypotheses:

**H1: Apparent competition.** Lamb survival would be negatively related to hare abundance, because coyote numbers would increase when hares were abundant and more sheep would be killed. Sheep density would be negatively correlated with hare density.

**H2: Apparent mutualism.** Lamb survival would be positively related to hare abundance, because high hare numbers would draw predation away from sheep. Sheep density would be positively correlated with hare density.

In this chapter, we used data on lamb mortality, sheep abundance, and hare abundance to test these hypotheses. We used data on coyote prey selection from Chapter 2 and coyote population dynamics from Chapter 3, as well as additional reproductive data, to determine the mechanisms underlying potential indirect relationships.
Study area

This study was conducted from 1999–2003 in the central Alaska Range (63° 57' N, 147° 18' W). The study area encompassed 1,000 km$^2$ of mountains and foothills on the northern edge of the Alaska Range, approximately 80 km south of Fairbanks. The topography was rugged, with elevation ranging from 600–2100 m. Potential coyote prey species included snowshoe hares (*Lepus americanus*), Dall sheep (*Ovis dalli*), moose (*Alces alces*), caribou (*Rangifer tarandus*), arctic ground squirrels (*Spermophilus parryii*), voles (*Clethrionomys rutilus, Microtus spp.*), red squirrels (*Tamiasciurus hudsonicus*), porcupines (*Erethizon dorsatum*), ptarmigan (*Lagopus spp.*), and grouse (*Dendragapus canadensis* and *Tympanuchus phasianellus*). Other major predators in the area included grey wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), pine martens (*Martes americana*), wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), golden eagles (*Aquila chrysaetos*), northern goshawks (*Accipiter gentilis*), great horned owls (*Bubo virginianus*) and other birds of prey.

Snowshoe hare habitat consisted of willow and alder thickets and closed-canopy white spruce forests, and these cover types made up approximately 43% of the study area. Dall sheep habitat consisted of alpine meadows and bare rock at higher elevations (1,000-2100 m), which made up approximately 41% of the study area. Coyotes moved between high and low elevation habitats on a daily basis (unpublished radio telemetry and snow-tracking data).

Methods

Snowshoe hare abundance

Snowshoe hare density was estimated in our study area using a combination of mark-recapture estimates and fecal pellet counts, and we used hare count data from the nearby Delta Breeding Bird Survey to extend the timeline to a full hare cycle (1995–2003). Hares were counted along a 40 km section of the Richardson Highway while conducting breeding bird surveys in late June or early July. The same observer counted hares each year (Steve Dubois, ADF&G). This census was located approximately 48 km east of our study area (63° 52 N, 145° 45 W). Within our study area, we established a 9.4 ha live-trapping grid with 84 live traps in June of 1999. Traps were set at 2000 h and checked at 0730 h the next morning for five
consecutive nights. Captured hares were marked with numbered ear tags and released. We used model \texttt{M_{HJACK}} in program CAPTURE (Otis et al. 1978) to estimate abundance (Boulanger and Krebs 1996). The trapping grid was surrounded by open habitat inhospitable to hares, so the mark-recapture estimate was converted to a density estimate by dividing the number of hares by the size of the trapping grid.

Hare fecal pellets were counted on 126 plots within the trapping grid to calibrate pellet counts with the mark-recapture estimate. Additional pellet count grids were established throughout the study area \((n = 11)\). At least 50 permanent plots spaced 15 m apart were established on each grid and plots were counted and cleared once per year (for details of the pellet count protocols, see Prugh and Krebs 2004). Pellet counts are an index of hare abundance during the previous year, so there is a lag between changes in hare abundance and changes in pellet counts. To correct for this, we averaged the pellet counts from time \(t\) and time \(t + 1\) when estimating hare abundance at time \(t\).

\textbf{Dall sheep abundance}

Annual estimates of Dall sheep abundance were obtained by aerial surveys in June each year from a Robinson R22 helicopter. Lambs, ewes, rams, and yearlings were counted throughout the study area. Surveys were conducted using the same pilot and observer each year, in similar weather conditions and at the same time of year.

\textbf{Radiocollaring lambs and coyotes}

Coyotes were captured using immobilizing darts fired from low-flying helicopters and immobilized with a mixture of equal parts tiletamine hydrochloride and zolazepam hydrochloride (Telazol\textsuperscript{TM}; Fort Dodge Animal Health, Fort Dodge, IA) administered at dosages of 9.0–10.0 mg/kg. Each coyote was fitted with a radiocollar weighing 0.25 kg (MOD 400, Telonics Inc., Mesa AZ). Lambs were captured by hand after brief pursuit with a helicopter using procedures described by Scotton and Pletcher (1998). Scotton (1998) studied lamb mortality in our study area in 1995 and 1996, and we used these data to extend the timeline of our dataset. Capture and handling procedures followed animal care standards established by the Alaska Department of Fish and Game (unpublished) and the American Society of Mammalogists (Animal Care and Use Committee 1998).

Coyotes and lambs were located by aerial telemetry daily in May (pup-rearing and lambing season), weekly in June, and bi-weekly the remainder of the year. Coyote reproduction
Table 4.1. Causes of juvenile Dall sheep mortality in the Central Alaska Range, 1995–1996 and 1999–2003. Lambs were radio-collared within days of birth and monitored for one year.

<table>
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</tr>
</thead>
<tbody>
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<td>8</td>
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<td>6</td>
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<td>5</td>
</tr>
<tr>
<td><strong>Total mortality</strong></td>
<td>7</td>
<td>16</td>
<td>18</td>
<td>15</td>
<td>16</td>
<td>5</td>
<td>7</td>
<td>61</td>
</tr>
<tr>
<td><strong>n collared</strong></td>
<td>22</td>
<td>34</td>
<td>24</td>
<td>22</td>
<td>20</td>
<td>14</td>
<td>19</td>
<td>99</td>
</tr>
</tbody>
</table>

* Data from (Scotton 1998)
Figure 4.1. Snowshoe hare abundance in the Central Alaska Range study area and in Delta, approximately 48 km east of the study area. Counts in Delta were conducted during annual Breeding Bird Surveys along the Richardson Highway. Alaska Range estimates were obtained from mark-recapture and pellet count techniques, and error bars show 95% confidence limits.
was determined by visual sightings of pups at den sites of radiocollared coyotes. Collars emitted a mortality signal if they remained motionless for ≥6 hours, and we investigated mortalities to determine the cause of death (Scotton 1998). Annual estimates of lamb survival were calculated using the Kaplan-Meier staggered entry method (Pollock et al. 1989).

**Diet of reproductive coyotes**

Reproductive coyotes in our study area gave birth in early May, and they used den sites to raise young for the next two months. We collected scats from a den site in 2001 to examine the diet composition of reproductive coyotes with access to Dall sheep lambs (the Sheep Creek group, Chapter 5). Scats from these coyotes that were collected the preceding winter were identified by fecal genotyping (Chapter 3), and the winter diet was constructed for comparison. Scats were also collected throughout the study area the following summer, but we could not assign scats to social groups because they were not genotyped. All scats were analyzed as described in Chapter 2.

**Results**

A total of 99 lambs and 19 coyotes were radiocollared during the five years of our study. Coyotes were the main predator of Dall sheep lambs, followed by golden eagles (Table 4.1). Coyotes were responsible for 38% of all predation and 21% of all deaths of radiocollared lambs from 1999–2003 (Table 4.1). Hare abundance declined >10-fold during this period, from a peak abundance in 1999 of 2.6 hares/ha to a low of 0.19–0.25 hares/ha in 2002 and 2003 (Figure 4.1). Hare counts from the Delta Breeding Bird Survey showed a trend similar to our hare abundance data (Figure 4.1), and we therefore used the Delta counts to look at a longer time series.

Dall sheep abundance was positively correlated with hare abundance (R = 0.66, P = 0.05; Figure 4.2). Annual estimates of lamb survival varied widely, from 0.12–0.68 (Table 4.2). There was a 1-year time delay between changes in lamb survival and changes in total sheep counts: sheep populations declined following years with low lamb survival (0.12–0.23), and populations increased following years with higher lamb survival (0.36–0.68; Table 4.2).

Lamb survival was negatively related to hare density, with a 2-year time delay when hare numbers were declining (1999–2001) but no evidence of a time delay when hare numbers were increasing (1995–1999; Figure 4.3). Lamb survival increased rapidly while hare numbers were
Figure 4.2. Annual counts of snowshoe hares and Dall sheep, 1995–2003. Hare counts were conducted along the Richardson highway approximately 48 km east of the Central Alaska Range study area. Total sheep counts include all lambs, ewes, rams, and yearlings seen during annual helicopter surveys.
Table 4.2. Annual rates of Dall sheep lamb survival and population counts in the Central Alaska Range, 1995–2003. Lamb mortality was not monitored in 1997 or 1998. Survival rates were calculated using the Kaplan-Meier staggered entry method. Total sheep counts include all lambs, ewes, rams, and yearlings seen during annual helicopter surveys.

<table>
<thead>
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<th>Year</th>
<th>Lamb survival</th>
<th>± 95% CI</th>
<th>Total sheep count</th>
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<tr>
<td>1995*</td>
<td>0.68</td>
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<td>1998</td>
<td></td>
<td></td>
<td>686</td>
</tr>
<tr>
<td>1999</td>
<td>0.12</td>
<td>0.11</td>
<td>690</td>
</tr>
<tr>
<td>2000</td>
<td>0.23</td>
<td>0.16</td>
<td>615</td>
</tr>
<tr>
<td>2001</td>
<td>0.16</td>
<td>0.17</td>
<td>552</td>
</tr>
<tr>
<td>2002</td>
<td>0.36</td>
<td>0.19</td>
<td>496</td>
</tr>
<tr>
<td>2003</td>
<td>0.63</td>
<td>0.22</td>
<td>695</td>
</tr>
</tbody>
</table>

* Data from (Scotton 1998)
Figure 4.3. Relationship between hare abundance and Dall sheep lamb survival. Hare counts were conducted along the Richardson highway approximately 48 km east of the Central Alaska Range study area. Datapoints are labeled by year, and arrows show the year-to-year progression from 1995–2003 (lamb mortality was not monitored in 1997 or 1998).
low (2001–2003; Figure 4.3). The increase in lamb survival was due to a drop in predation by coyotes and golden eagles in 2002 and 2003 (Table 4.1). The total mortality caused by coyotes dropped 3-fold during this period: from 1999–2001, coyotes killed 27% of all radiocollared lambs on average each year versus 9% during 2002–2003. Most radiocollared adult coyotes reproduced during 2000 and 2001 (the hare decline), but reproduction failed in 2002 and 2003 (Table 4.3). Dall sheep made up 17% of the diet of the Sheep Creek coyotes during the denning season in 2001, whereas sheep made up only 2.5% of their diet the preceding winter and 6.7% of the subsequent summer diet (Figure 4.4).

Discussion

Apparent competition

We found evidence of apparent competition between snowshoe hares and Dall sheep in the Alaska Range and thus support for our first hypothesis (H₁). Dall sheep survival was negatively related to hare density due to the positive effect that hares had on the coyote population. Coyotes were the main predator of lambs, and changes in coyote predation pressure had a large impact on lamb survival rates. Low predation rates were associated with years of failed coyote reproduction, and coyote reproductive failure was associated with low hare abundance. Predation by golden eagles also decreased during the hare low phase, and fewer eagle nests were found during these years (Arthur 2003). Reproductive failure in coyotes, lynx, and great horned owls during times of low hare abundance has been documented in the Yukon (Rohner 1994, Mowat et al. 1996, O'Donoghue et al. 1997), indicating the widespread importance of hares to predator recruitment in northern areas.

Population estimates from 2000–2002 indicated that coyote numbers peaked 1½ years after the snowshoe hare peak and declined nearly 2-fold during the following year (Chapter 3). Coyote survival dropped immediately following the peak of coyote numbers but was high during the hare low phase (Chapter 3). The lack of recruitment during the hare low phase probably caused coyote numbers to continue declining despite high survival. Similar trends in coyote numbers were found in the Yukon: coyote density there changed 6-fold in response to hare density, with a 1-year time delay (O'Donoghue et al. 1997).

Generally, apparent competition operates through a numerical response of predators to prey density (Holt 1977, Holt and Lawton 1994, Chaneton and Bonsall 2000), but the
Table 4.3. Reproduction of radio-collared adult coyote pairs in the Central Alaska Range, 1999–2003. Pairs were considered to have successfully reproduced if pups were seen at their den site. We did not evaluate reproductive success in 1999 because our sample was too small.

<table>
<thead>
<tr>
<th>phase of hare cycle</th>
<th>year</th>
<th># adult pairs</th>
<th>% reproduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>peak</td>
<td>1999</td>
<td>2</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>5</td>
<td>80</td>
</tr>
<tr>
<td>decline</td>
<td>2001</td>
<td>5</td>
<td>60</td>
</tr>
<tr>
<td>low</td>
<td>2002</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>4</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 4.4. Coyote diet composition in 2001, based on the relative occurrence of prey items in scats. Winter and den diets were constructed from scats collected from the Sheep Creek social group, and summer diet was constructed from scats collected throughout the Central Alaska Range study area. Scat sample sizes are shown above bars.
mechanism may not be so straightforward in this case. Although coyotes did respond numerically to hare density, the number of reproductive coyotes, in particular, may have had more influence on lamb survival than total coyote numbers. Scats collected from a coyote den contained approximately four times more sheep occurrences than scats collected in summer and winter. In coyote home ranges that included sheep habitat, all den sites were in sheep habitat rather than snowshoe hare habitat. Coyote pup-rearing season coincides with the lambing season, so it is possible that coyotes were simply responding to a flush of resources and that non-reproductive coyotes may have targeted sheep during this time period as well. We cannot discount this hypothesis because no scats were collected from non-reproductive coyotes during the lambing season. However, coyote predation on lambs did not decline until reproductive failure in 2002, even though coyote numbers were declining the previous year. In addition, coyote predation on lambs appeared to increase without delay when hares increased from 1995–1996. Although we do not have data on coyote populations during these years, hare densities were high enough to facilitate reproduction in 1996. Thus, even if coyote numbers were still low when hares started to increase, predation on lambs may have increased because the existing coyotes were raising pups. Till and Knowlton (1983) found that removing pups from coyote dens dramatically reduced predation on domestic sheep. A growing body of literature suggests that trait-mediated interactions (in this case, coyote reproductive state) can affect communities as strongly as density-mediated interactions (Werner and Peacor 2003, Schmitz et al. 2004).

Time delays and asymmetries

Dall sheep density was positively correlated with hare density, which was a prediction of apparent mutualism (our second hypothesis, H2), not apparent competition. This discrepancy is probably due to time delays. There was a 2-year time delay between hare numbers and lamb survival and a 1-year delay between lamb survival and sheep population trends. Without this 3-year time delay, sheep and hare densities would probably have been negatively correlated, consistent with predictions of apparent competition (H1). Thus, it may not be possible to differentiate between apparent competition and apparent mutualism based on prey densities alone, because time delays complicate the interpretation of correlations.

The relationship between hares and Dall sheep would be more accurately described as "apparent amensalism" than apparent competition (i.e., a "− 0" interaction instead of a "− −" interaction; Begon and Mortimer 1986), because hares negatively affect sheep but sheep probably do not affect hares. Coyote foraging decisions were largely determined by snowshoe
hare density, and Dall sheep was a minor component of the average coyote diet each year (Chapter 2). Although reciprocal predator-mediated negative effects have been documented (e.g., Schmitt 1987), most reported interactions are highly asymmetrical (Chaneton and Bonsall 2000), and theoretical models show that apparent amensalism should be common among non-competing prey (Brassil and Abrams 2004). The species with the higher intrinsic rate of increase tends to negatively affect the species with the lower growth rate (Bonsall and Hassell 1997), as was the case in this study. Unequal preference of predators for different prey types also contributes to asymmetry in indirect interactions (Eubanks and Denno 2000).

**Apparent mutualism**

We did not find support for apparent mutualism between hares and sheep \( (H_2) \), which should have arisen if coyote selection for Dall sheep had increased when hares declined. In Chapter 2, I showed that per-capita coyote predation on sheep was not affected by snowshoe hare or Dall sheep abundance. When hares crashed, coyote per-capita consumption of porcupines increased 25-fold but per-capita consumption of sheep did not change. Thus, short-term apparent mutualism may occur between hares and porcupines. Porcupine occurrences in coyote scats were rare when hares were abundant but common when hares were scarce, so porcupine survival may have been highest when hares were abundant. Given that natural communities support many prey species, and predators do not always selectively prey on the most abundant species (Chapter 2), it can be difficult to predict which species a predator will turn to when its primary prey declines. Thus, it is worthwhile to examine the broader prey community when investigating indirect links among focal prey species.

**Can coyote predation drive sheep to extinction?**

Extinctions, or drastic population reductions, have been documented in several vertebrate communities due to the effects of apparent competition. In Australia and New Zealand, introduced foxes and mustelids are supported by introduced rabbit populations, and incidental predation on native prey has had devastating effects (Pech et al. 1995, Sinclair et al. 1998, Norbury 2001). The prey species that is adversely affected is often consumed opportunistically as the predator searches for primary prey. For example, some rare grassland birds in Maine and rare larks in Spain are imperiled in part due to opportunistic nest predation by canids and mustelids foraging for other prey (Vickery et al. 1992, Yanes and Suarez 1996, Schmidt 2004).
The spatial separation of hares and sheep should have reduced or eliminated the effects of apparent competition (Holt 1984) because coyotes hunting for hares would not incidentally encounter sheep. However, most coyote dens were located in sheep habitat, and most sheep were killed during the denning season (Scotton 1998, Arthur 2003). Coyotes did not restrict their movements to snowshoe hare habitat during peak hare densities (unpublished radio telemetry data), so spatial separation from the primary prey did not provide sheep with “enemy-free space” (Jeffries and Lawton 1984).

The low rates of lamb survival during high hare numbers, which were due primarily to heavy predation by coyotes and golden eagles, led to declining sheep populations. In Chapter 2, I found that the per-capita coyote predation rate on sheep was independent of sheep density. These data indicate that coyote predation could result in sheep extinctions if hare numbers did not regularly crash, but the hare low phase may provide sheep with enough “enemy-free time” to recover from years of high predation. Models have shown that population cycling should reduce the effects of apparent competition (Abrams et al. 1998). Because this study spans only one hare cycle and lacks sufficient data during the hare increase phase, additional research is needed to assess the long-term stability of the interaction. In addition, management practices such as wolf control could increase coyote abundance (Carbyn 1982, Dekker 1989), and changes in weather and habitat due to climate change or other factors could alter the long-term viability of these relationships.

Conclusions

The snowshoe hare cycle affects Dall sheep population dynamics despite the fact that these species occupy non-overlapping habitats. Hares negatively affect Dall sheep by enhancing coyote reproductive activity. The long-term viability of Dall sheep populations may be dependent on the repeated occurrence of low hare numbers, and additional research is needed to determine whether the hare cycle allows sheep populations sufficient recovery time between bouts of high predation.
CHAPTER 5
THE CONSEQUENCES OF RESOURCE HETEROGENEITY: INDIVIDUAL DIET VARIATION AND THE PERSISTENCE OF COYOTES

Introduction

Resource utilization is often studied at the population level, and variation in resource use among individuals is commonly ignored. Each individual may utilize only a subset of the resources exploited by its population, and the degree of individual specialization within a population can have implications for ecology, evolution, and conservation (Bolnick et al. 2003). Individual specialization may reduce intraspecific competition (Kohda 1994), facilitate sympatric speciation (Schluter and McPhail 1992, Wilson 1998), and lead to lags in predator responses to changing prey abundance (Werner et al. 1981). Theoretical models have shown that variation among individuals can lead to outcomes that are not predicted when all individuals are assumed to be “average” (Lomnicki 1978, Huston et al. 1988, Judson 1994). For example, variation in predator dietary preferences can cause bias in which the average population preference is disproportionately affected by individuals that prefer rare prey species (Sherratt and MacDougall 1995). Although complexity is increased when individual variation is considered, this approach provides a direct link between natural selection and population-level processes and thus can help to connect the fields of population biology, behavioral ecology, and evolutionary ecology (Wilson 1998).

It is often difficult to obtain individual-specific data in wildlife studies, however. Individuals may be hard for observers to distinguish from one another or too elusive to observe directly. Obtaining individual-specific data is particularly difficult when populations are monitored indirectly through examination of animal sign such as feces, a common approach in carnivore diet studies (Putnam 1984). Recent advances in molecular techniques now allow researchers to genotype individuals from small amounts of DNA extracted from feces (Taberlet et al. 1996). When combined with conventional scat analysis, in which prey remains are examined to determine diet, variation in diet among individual predators can be studied without direct observations (Fedriani and Kohn 2001). In this paper, we combine fecal genotyping and diet analysis to examine variation in the winter diets of individual coyotes (Canis latrans) in the Alaska Range from 2000–2002.
Coyotes are known to consume a wide variety of prey items and have long been regarded as a prototypical generalist species (Young and Jackson 1951, Bekoff 1977). However, several studies have shown that, at the population level, coyotes can be selective predators, and changes in resource availability can strongly affect their patterns of resource use (Windberg and Mitchell 1990, O'Donoghue et al. 1998b). In Chapter 2, I examined the average dietary response of coyotes to changes in prey availability and found that diet diversity increased when the staple prey, snowshoe hares (*Lepus americanus*), declined in abundance. In this chapter, I will determine whether the niche breadth expansion of the coyote population was due to the diversification of individual diets or due to divergence as individuals specialized on different prey items.

The diet of an individual can be influenced by characteristics such as age (Sandlin and Willig 1993, Molsher et al. 2000), sex (Ishikawa and Watanuki 2002), size (Zerba and Collins 1992), social status (Gese et al. 1996b), and morphology (Skulason et al. 1993), as well as by external factors such as habitat (Wilson 1998), season (Ben-David et al. 1997), and prey abundance (Zerba and Collins 1992). Because these factors also affect an individual’s chance of survival or reproduction, individual diet and fitness may be linked (Pierotti and Annett 1991, Grant and Grant 1996, Votier et al. 2004). Alternative foraging strategies may differ in risks and payoffs and therefore confer different fitness consequences (Annett and Pierotti 1999).

The goals of this study are to: 1) determine the degree of diet variation among individuals in the coyote population, 2) assess the influence of intrinsic and extrinsic factors on individual diets, and 3) examine potential fitness consequences of diet composition. Snowshoe hare populations in northern boreal forests are characterized by cyclic fluctuations (Hodges 2000), and the decline phase appears to be a period of selection on predators. Many lynx (*Lynx canadensis*) and coyotes die or disperse when hare numbers decline, but individuals that persist through the decline tend to have high survivorship during the low phase (Chapter 3, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 1997). We hypothesized that factors such as age, sex, body size, location, and prey abundance would influence coyote diet and persistence during the snowshoe hare decline, and that alternative dietary strategies would affect persistence directly.
Study area

This study was conducted from May 1999–July 2002 in the central Alaska Range (63° 57’ N, 147° 18’ W; Figure 5.1). The study area encompassed 1,000 km² of mountains and foothills on the northern edge of the Alaska Range, approximately 80 km south of Fairbanks. The topography was rugged, with elevation ranging from 600–2100 m, and the area was not accessible by road. Hunting and trapping were permitted in the area. Major habitat types included willow (Salix spp.) and alder (Alnus spp.) thickets, closed-canopy white spruce (Picea glauca) forests, open-canopy black spruce (P. mariana) forests, moist graminoid meadow (predominantly Eriophorum spp.), and alpine tundra. Potential coyote prey species included snowshoe hares (Lepus americanus), Dall sheep (Ovis dalli), moose (Alces alces), caribou (Rangifer tarandus), ground squirrels (Spermophilus parryii), voles (Clethrionomys rutilus, Microtus spp.), red squirrels (Tamiasciurus hudsonicus), porcupines (Erethizon dorsatum), ptarmigan (Lagopus spp.), and grouse (Dendragapus canadensis and Tymanuchus phasianellus). Other major predators in the area included grey wolves (Canis lupus), red foxes (Vulpes vulpes), pine martens (Martes americana), wolverines (Gulo gulo), lynx (Lynx canadensis), grizzly bears (Ursus arctos), and black bears (Ursus americanus).

Methods

Fecal genotyping

We established >150 km of snowmobile trails along the three major river drainages (Figure 5.1) and collected coyote feces on these trails continuously throughout each winter from 2000–2002. Scats were also collected while following coyote tracks on foot. We recorded the GPS location and estimated maximum age of the scat (based on travel and snowfall history). A total of 1,237 feces were collected, and we selected 834 scats for genetic analysis by random sampling without replacement.

Approximately 100 mg of frozen fecal material was collected from each scat and stored at −80°C in DET storage buffer (Seutin et al. 1991). We extracted DNA from fecal samples using QIAamp DNA Stool Mini-Kits (Qiagen, Valencia, CA) after centrifuging samples for 10 minutes and removing the buffer. DNA isolation and amplification were conducted in separate
Figure 5.1. Central Alaska Range study area (63° 57' N, 147° 18' W), showing coyote home ranges (polygons), rivers (solid lines), connecting trails (dashed lines), and genotyped scats (symbols), 2000–2002. Home ranges of five radiocollared adult pairs (solid polygons) enclosed all radio locations of both coyotes for the study duration. Ranges were estimated for an uncollared pair and an uncollared lone coyote (dashed polygons) based on locations of scats and snow tracks. Locations of genotyped scats collected for these adults and their associated offspring are shown, with a different symbol for each of the seven social groups. Elevation increased to the south and mountain peaks (2000–2600 m) occurred between river drainages south of the connecting trails.
labs to minimize the risk of contaminating stock DNA with post-PCR products. Negative controls were included in each batch of DNA isolation to monitor for contamination.

We screened each fecal DNA sample with a mitochondrial DNA test to ensure that the isolated DNA was from a coyote. Samples that did not amplify or showed non-coyote products were removed from the dataset. For details of the species verification test, see Prugh and Ritland (in press). Nuclear DNA was amplified from confirmed coyote samples at 6 microsatellite loci to establish individual identity. Genotypes obtained from feces can be unreliable (Taberlet et al. 1999) and we therefore assessed the accuracy of our genotyping methods. The probabilities of obtaining identical genotypes for different individuals and creating false individuals through genotyping errors were very low. Coyote sex was determined by amplifying a region of the SRY gene on the Y-chromosome with primers designed specifically for canids. These genetic procedures are detailed in Chapter 3.

**Diet analysis**

After obtaining DNA from each sample, scats were autoclaved to kill *Echinococcus* eggs (Colli and Williams 1972). Sterile samples were washed in nylon mesh bags using a clothes washing machine on gentle cycle, and samples were air-dried before analysis. Dried scats were carefully examined and all food items present were recorded. We compared hairs, teeth, and claws to reference specimens and guide books (Moore et al. 1974) for identification. Hair medulla patterns were examined under a microscope for identification, and scale impressions were made for all moose and caribou hairs, as well as other hairs that were difficult to identify. Occurrences of moose and caribou in scats were assumed to be the result of scavenging and categorized as carrion, because studies of these species in this area did not find coyotes to be a significant source of mortality (Boertje et al. 1996). The number of occurrences of each prey item was divided by the total number of prey occurrences to calculate frequency of occurrence of each prey type.

**Snow-tracking and radio-telemetry**

We followed coyote tracks for 309.5 km during this study and used snow-tracking data to help resolve social group composition. Fresh coyote tracks were located by traveling on snowmobile trails after fresh snowfalls, and they were backtracked on foot. We recorded the number of coyotes traveling together, and individuals were identified by genotyping scats.
collected during the tracking session. We collected and genotyped scats from 61 of the 167 tracking sessions.

Sixteen coyotes were captured using immobilizing darts fired from low-flying helicopters. Coyotes were immobilized with a mixture of equal parts tiletamine hydrochloride and zolazepam hydrochloride (Telazol™; Fort Dodge Animal Health, Fort Dodge, IA) administered at dosages of 9.0–10.0 mg/kg. Each coyote was fitted with a radio collar weighing 0.25 kg (MOD 400, Telonics Inc., Mesa AZ). Ear punches and blood samples were collected for DNA analysis, and samples were genotyped twice to ensure accuracy. Capture and handling procedures followed animal care standards established by the Alaska Department of Fish and Game (unpublished) and the American Society of Mammalogists (Animal Care and Use Committee 1998).

Coyotes were located by aerial telemetry daily in May (pup-rearing and Dall sheep lambing season), weekly in June, and bi-weekly the remainder of the year. Coyote home ranges were determined as the minimum convex polygons enclosing all locations of a particular pair of adult coyotes (Burt 1943). Ten of the collared coyotes were pair-bonded and we therefore had five resident radiocollared pairs. Additionally, the ranges of one uncollared pair and one uncollared lone coyote were inferred from locations of genotyped scats and tracks. These seven groups were named based on their locations: N. Dry Creek, S. Dry Creek, N. West Fork, S. West Fork, Wood River, Sheep Creek, and Lone DC/WF (Figure 5.1). With the exception of the lone coyote, social groups generally consisted of a mated pair and one or more offspring (Table 5.1). Collars emitted a mortality signal if they remained motionless for ≥6 hours, and we investigated mortalities to determine cause of death.

Coyote age at time of first detection (i.e., capture or first genotyped scat) was categorized as juvenile (<1 year old), adult (>1 year old), or unknown. The age of each captured coyote was determined by subjectively assessing tooth wear and body condition. Uncollared coyotes were categorized as juvenile if their genotype indicated that they were the offspring of a known adult pair; otherwise age was recorded as unknown. Because the probability of detecting coyotes present in the area for ≥1 year was close to 100% (Chapter 3), we believe we were correct in categorizing the offspring of resident coyotes as juveniles during the first year they were found in the area. Only one juvenile (S3) remained in the study area for >1 year, and this coyote was categorized as a juvenile during both years because he remained in his natal territory and his diet was more similar to juveniles than adults.
Table 5.1. Characteristics of coyotes included in this study. Scats were collected in the Alaska Range from 2000–2002 and genotyped to establish individual identity.

<table>
<thead>
<tr>
<th>coyote ID</th>
<th>social group</th>
<th>n scats</th>
<th>sex</th>
<th>age</th>
<th>years scats collected</th>
<th>years radio-collared</th>
<th>fate</th>
<th>cause of death</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1</td>
<td>Lone DC/WF</td>
<td>18</td>
<td>F</td>
<td>unknown</td>
<td>2000-2</td>
<td>none</td>
<td>died</td>
<td>fur trapping</td>
</tr>
<tr>
<td>ND1</td>
<td>N. Dry Cr.</td>
<td>11</td>
<td>M</td>
<td>adult</td>
<td>2000-1</td>
<td>2000-1</td>
<td>dispersed</td>
<td></td>
</tr>
<tr>
<td>ND2</td>
<td>N. Dry Cr.</td>
<td>3</td>
<td>F</td>
<td>adult</td>
<td>2000-1</td>
<td>2000-1</td>
<td>died</td>
<td></td>
</tr>
<tr>
<td>ND3</td>
<td>N. Dry Cr.</td>
<td>13</td>
<td>M</td>
<td>juvenile</td>
<td>2000</td>
<td>none</td>
<td>dispersed</td>
<td>porcupine quills</td>
</tr>
<tr>
<td>ND4</td>
<td>N. Dry Cr.</td>
<td>7</td>
<td>F</td>
<td>adult</td>
<td>2000</td>
<td>none</td>
<td>died</td>
<td></td>
</tr>
<tr>
<td>ND5</td>
<td>N. Dry Cr.</td>
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<td>M</td>
<td>juvenile</td>
<td>2000</td>
<td>none</td>
<td>died</td>
<td></td>
</tr>
<tr>
<td>ND6</td>
<td>N. Dry Cr.</td>
<td>2</td>
<td>F</td>
<td>juvenile</td>
<td>2001</td>
<td>none</td>
<td>dispersed</td>
<td></td>
</tr>
<tr>
<td>NW1</td>
<td>N. W. Fork</td>
<td>11</td>
<td>F</td>
<td>adult</td>
<td>2001-2</td>
<td>2002-2003^2</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
<td>NW2</td>
<td>N. W. Fork</td>
<td>25</td>
<td>M</td>
<td>unknown</td>
<td>2001-2</td>
<td>none</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
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<td>Sheep Cr.</td>
<td>49</td>
<td>M</td>
<td>adult</td>
<td>2000-2</td>
<td>1999-2002^1</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
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<td>Sheep Cr.</td>
<td>36</td>
<td>F</td>
<td>adult</td>
<td>2000-2</td>
<td>1999-2002^1</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
<td>S3</td>
<td>Sheep Cr.</td>
<td>40</td>
<td>M</td>
<td>juvenile</td>
<td>2001-2</td>
<td>none</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
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<td>S. Dry Cr.</td>
<td>10</td>
<td>M</td>
<td>adult</td>
<td>2000</td>
<td>1998-2000</td>
<td>died</td>
<td>wolves</td>
</tr>
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<td>2000-1</td>
<td>1999-2001</td>
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<td>porcupine</td>
</tr>
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<td>35</td>
<td>M</td>
<td>adult</td>
<td>2000-1</td>
<td>2000-2001</td>
<td>died</td>
<td>wolves</td>
</tr>
<tr>
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<td>S. Dry Cr.</td>
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<td>M</td>
<td>juvenile</td>
<td>2001</td>
<td>none</td>
<td>died/dispers ed</td>
<td></td>
</tr>
<tr>
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<td>S. W. Fork</td>
<td>18</td>
<td>F</td>
<td>adult</td>
<td>2000-2</td>
<td>1998-2002^1</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
<td>SW2</td>
<td>S. W. Fork</td>
<td>17</td>
<td>M</td>
<td>adult</td>
<td>2000-2</td>
<td>2000-2002^1</td>
<td>persisted</td>
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<td>S. W. Fork</td>
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<td>F</td>
<td>juvenile</td>
<td>2002</td>
<td>none</td>
<td>persisted</td>
<td></td>
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<tr>
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<td>S. W. Fork</td>
<td>6</td>
<td>F</td>
<td>juvenile</td>
<td>2000</td>
<td>2000</td>
<td>died</td>
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<tr>
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<td>adult</td>
<td>2000-2</td>
<td>2000-2002^1</td>
<td>persisted</td>
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</tr>
<tr>
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<td>Wood R.</td>
<td>15</td>
<td>M</td>
<td>unknown</td>
<td>2000-2</td>
<td>none</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
<td>W3</td>
<td>Wood R.</td>
<td>24</td>
<td>M</td>
<td>unknown</td>
<td>2000-2</td>
<td>none</td>
<td>persisted</td>
<td></td>
</tr>
<tr>
<td>W4</td>
<td>Wood R.</td>
<td>15</td>
<td>F</td>
<td>unknown</td>
<td>2000-2</td>
<td>none</td>
<td>persisted</td>
<td></td>
</tr>
</tbody>
</table>

1 Coyote was still present in study area as of September 2004
2 Coyote was not radiocollared during scat collection
Hare abundance

We used a combination of mark-recapture estimates from live-trapping and fecal pellet counts to estimate snowshoe hare abundance. A 9.4 ha live-trapping grid with 84 live traps was established in June of 1999. Traps were set at 2000 h and checked at 0730 h the next morning for 5 consecutive nights. Captured hares were marked with numbered ear tags and released. We used model $M_{HJACKKNIFE}$ in program CAPTURE (Otis et al. 1978) to estimate abundance (Boulanger and Krebs 1996). The trapping grid was surrounded by open habitat inhospitable to hares, so the mark-recapture estimate was converted to a density estimate by dividing the number of hares by the area of the trapping grid.

Hare fecal pellets were counted on 126 plots within the trapping grid to calibrate pellet counts with the mark-recapture estimate. Eleven additional pellet count grids of ≥50 plots were established throughout the study area, for a total of 12 grids in the study area. Each grid was within or adjacent to the home range of a resident coyote pair. Plots were counted and cleared once per year (for details of the pellet count protocols, see Prugh and Krebs 2004).

Data analysis

Sample size requirements. We examined the effect of scat sample size on the estimation of diet breadth by drawing random subsamples of increasing size (starting from $n = 1$) from the 2 largest samples of individually-identified scats (40 and 49 scats each), and we constructed diets from each subsample as the frequency of prey occurrence in scats. We also subsampled from the pooled scat sample ($n = 544$) to determine the minimum sample size required to accurately estimate the average diet of the coyote population.

Individual specialization. We used two measures of resource use variation detailed in Bolnick et al. (2002) to examine diet specialization by individuals and social groups. First, we used the total niche width (TNW) to quantify the dietary niche breadth of the coyote population each year (Roughgarden 1972, 1979). The TNW can be broken into within-individual and between-individual variance components to examine the degree of specialization within the population (Roughgarden 1972). However, this method is prone to bias when sample sizes and resource availability are uneven (Bolnick et al. 2002). We therefore used Petraitis’ $W$, a robust maximum-likelihood index, to examine niche breadths of individuals and social groups (Petraitis 1979, Bolnick et al. 2002). This method calculates the likelihood that an individual has the same resource use distribution as the population:
\[
\lambda_i = \prod_j \left( \frac{q_j}{p_j} \right)^{n_{ij}}
\]

where \( n_{ij} \) is the number of occurrences of resource \( j \) in individual \( i \)'s diet, \( p_j \) is the proportion resource \( j \) in individual \( i \)'s diet, and \( q_j \) is the proportion of resource \( j \) in the population diet. \( \lambda_i \) can vary from \( q_j \) to 1, where \( q_j \) indicates complete specialization on resource \( j \) and 1 indicates an individual whose diet exactly matches the population diet. Petraitis' \( W \) is a standardization of \( \lambda_i \):

\[
W_i = (\lambda_i)^{1/n_{ix}}
\]

where \( n_{ix} \) is the total number of prey occurrences in individual \( i \)'s diet. We tested whether each individual or social group's diet significantly differed from the population diet. The value 

\[ -2 \ln(\lambda_i) \]

has an approximately chi-square distribution with \( (r-1) \) degrees of freedom, where \( r \) is the number of resource categories (Petraitis 1979, Bolnick et al. 2002). The population diet was calculated as the average frequency of prey occurrences in each category for the individuals or groups included in the analysis. Alternatively, population diet can be calculated by summing prey occurrences in each category for all individuals, but this method can be biased because it gives more weight to individuals with larger sample sizes. It is worth noting that the latter method must be used in carnivore diet studies when individual identities are unknown.

Scats were pooled across years when examining individual diet in order to maintain adequate sample size. To examine changes in niche breadth across years, scats of coyotes within each social group were pooled each year. Although diets may vary among individuals within a group, coyotes in social groups often hunt together and may not represent independent datapoints. Resource categories were: snowshoe hares, Sciuridae (marmots and squirrels), small mammals (voles and shrews), porcupine, carrion (moose or caribou), Dall sheep, birds, vegetation, and carnivores. We used the program IndSpec1 (Bolnick et al. 2002) for these analyses. We also used chi-square contingency tables to test for dietary differences among individuals and groups as an alternative approach. Sciuridae, birds, shrews, vegetation, and carnivores were lumped into an "other" category because they occurred infrequently.

Factors affecting diet. A 2-way analysis of variance was used to determine whether social group or sex of coyotes explained variation in diet among individuals. The seven social groups were distributed among three river drainages, so dietary differences among social groups may have been caused by differences in prey abundance among drainages. These data were too limited to include "location" (i.e., river drainage) and "social group" as factors in the same
ANOVA, so we compared diets among locations separately, controlling for the effect of sex in a 2-way ANOVA. We used arcsine square-root transformed proportions (frequency of occurrence of prey types in scats) as the response variables. Prey types were categorized as: snowshoe hare, carrion, Dall sheep, porcupine, or vole. Sciuridae, birds, shrews, vegetation, and predators were excluded. Because we had only three known juveniles with ≥10 scats (Table 5.1), we could not include age as a factor in the ANOVA. We therefore used a chi-square contingency test to compare juvenile and adult diets, pooling scats by age class for eight juveniles and 11 adults (Table 5.1).

Factors affecting persistence. Coyote fate was categorized as either persistence or death/dispersal. Uncollared coyotes were assumed to have survived and remained in the area (i.e., persisted) if scats were collected through the end of study and to have died or dispersed if scats were not collected during the final 2 months of the study. We used logistic regression to determine whether coyote body weight influenced persistence. Fisher’s exact tests were used to determine if persistence differed among sex and age classes. Coyote diet was compared among adults of differing fates during the period of highest mortality and emigration (2001) using a chi-square contingency test. Analyses were conducted using JMP-IN (SAS Institute 2000).

Results

Sample size requirements

The frequency of hare occurrences in coyote diets was highly variable when <10 scats were used to construct the diet, but the frequency stabilized when ≥10 scats were used (Figure 5.2a). The frequency of other prey types also showed this pattern (data not shown). In contrast, diets constructed from subsamples of the pooled scats did not stabilize until the sample size was ≥45 (Figure 5.2b). Thus, we included only individuals or social groups with ≥10 scats in our diet analyses. The average number of prey occurrences per scat was 1.8 (±0.09 SE), so 10 scats equaled approximately 18 prey occurrences.

Diet specialization

Individual diet with years pooled. We had ≥10 genotyped scats for 18 coyotes (Table 5.1), and diets varied significantly among these individuals (Figure 5.3, $\chi^2_{85} = 218.2$, $P < 0.001$). Petraitis’ W ranged from 0.60–0.92, and the diets of six coyotes were significantly different from
Figure 5.2. Effect of sample size on the estimated percent occurrence of snowshoe hare in diets constructed from (a) individually-identified scats (b) and scats from all coyotes. Subsamples of increasing size were randomly drawn with replacement from (a) each individual’s full sample \((n = 40 \text{ and } 49 \text{ scats each})\) and (b) from the pooled sample \((n = 544)\). The frequency of snowshoe hare occurrence in the scats is shown, and other prey items showed a similar pattern.
Figure 5.3. Winter diet composition of 18 coyotes for which ≥10 genotyped scats were collected in the Alaska Range, 2000–2002. Diet is shown as the relative frequency of prey occurrences in scats (n scats shown above bars). Asterisks indicate diets that were significantly different from the average population diet. The “other” category consisted mainly of birds and vegetation.
the average population diet (Table 5.2). Thus, most coyotes had fairly generalized diets, but a third of the coyotes were more specialized.

**Hare abundance and niche width across years.** Snowshoe hare abundance declined approximately 10-fold from 2000–2002 in all three river drainages, and the total niche width of the coyote population expanded during this period from 1.15–1.78. Dietary differences among social groups were examined across years. Average values of Petraitis’ W were fairly high each year (0.83–0.89; Table 5.3), indicating that most variation in the total niche width was due to within-group variation rather than between-group variation each winter. However, social group diets appeared to diverge as hares declined. Few social group diets were significantly different from average population diets in 2000 and 2001, but most group diets diverged from the average diet in 2002 (Table 5.3). However, the significance of the tests seemed to be more related to sample size than the actual value of Petraitis’ W, as evidenced by the obvious association between high sample sizes and low p-values in Table 5.3. Groups with high Petraitis’ W values (close to 1) should have diets that are most similar to the population average, but in many cases, groups with significantly different diets had higher Petraitis’ W values (>0.9) than groups that did not differ significantly from the population (Table 5.3). Thus, it is unclear whether these significance tests provided biologically meaningful results.

Looking instead at the average values of Petraitis’ W each year, social group diets appear to have been most divergent in 2001 rather than 2002 (Table 5.3). However, chi-square contingency tests indicate that diets may indeed have been most divergent in 2002. Based on these tests, diet did not differ among social groups in 2000, when all diets were dominated by snowshoe hare (Figure 5.4a; $\chi^2_{25} = 19.4$, $P = 0.25$). Social group diets diverged as hares declined in 2001 (Figure 5.4b; $\chi^2_{25} = 45.6$, $P = 0.007$), and diets were highly divergent in 2002 (Figure 5.4c; $\chi^2_{15} = 60.4$, $P < 0.001$). In 2002, the S. West Fork coyotes included Dall sheep as an important alternative prey in their winter diet, whereas the N. West Fork coyotes favored carrion and the Wood River and Sheep Creek coyotes favored porcupine (Figure 5.4c). Although the different tests of diet specialization provided slightly conflicting results, they all indicate that diets of social groups diverged in response to lower hare abundance.

**Factors affecting diet**

Hare abundance differed markedly among drainages each year but declined approximately 10-fold in all areas (Figure 5.5a). Hares were more abundant in the West Fork
Table 5.2. Frequency of diet specialization among individual coyotes in the Alaska Range, from scats collected winters 2000–2002. The total number of prey occurrences is shown for each individual. Petraitis' W is a likelihood measure of the degree of diet specialization, with a value of 1 indicating a diet that exactly matches the average population diet. The probability that the individual’s diet originated from the population diet distribution is shown, and significant differences (P ≤ 0.05) are in bold.

<table>
<thead>
<tr>
<th>Individual ID</th>
<th>n occurrences</th>
<th>Petraitis's W</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>W2</td>
<td>31</td>
<td>0.92</td>
<td>0.76</td>
</tr>
<tr>
<td>W3</td>
<td>40</td>
<td>0.89</td>
<td>0.34</td>
</tr>
<tr>
<td>L1</td>
<td>38</td>
<td>0.79</td>
<td>0.02</td>
</tr>
<tr>
<td>W4</td>
<td>26</td>
<td>0.81</td>
<td>0.20</td>
</tr>
<tr>
<td>S3</td>
<td>102</td>
<td>0.86</td>
<td>0.000</td>
</tr>
<tr>
<td>NW2</td>
<td>55</td>
<td>0.78</td>
<td>0.001</td>
</tr>
<tr>
<td>W1</td>
<td>37</td>
<td>0.74</td>
<td>0.004</td>
</tr>
<tr>
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<td>0.35</td>
</tr>
<tr>
<td>SD4</td>
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<td>0.46</td>
</tr>
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</tr>
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<tr>
<td>NW1</td>
<td>23</td>
<td>0.79</td>
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</tr>
</tbody>
</table>

Average 42 0.82
Table 5.3. Diet specialization among coyote social groups in the Alaska Range, 2000–2002. The total number of prey occurrences is shown for each group each year. Petraitis’ W is a likelihood measure of the degree of diet specialization, with a value of 1 indicating a diet that exactly matches the average population diet. The probability that the group’s diet originated from the population diet distribution is shown, and significant differences (P ≤ 0.05) are in bold.

<table>
<thead>
<tr>
<th>Social Group</th>
<th>n occurrences</th>
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<th>2001</th>
<th>2002</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>Petraitis’ W</td>
<td>P</td>
<td>n occurrences</td>
</tr>
<tr>
<td>N. Dry Creek</td>
<td>54</td>
<td>0.88</td>
<td>0.03</td>
<td>19</td>
</tr>
<tr>
<td>N. West Fork</td>
<td>47</td>
<td>0.87</td>
<td>0.04</td>
<td>19</td>
</tr>
<tr>
<td>S. Dry Creek</td>
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<td>0.87</td>
<td>0.04</td>
<td>113</td>
</tr>
<tr>
<td>S. West Fork</td>
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<td>19</td>
</tr>
<tr>
<td>Sheep Creek</td>
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<td>0.84</td>
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<td>40</td>
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<tr>
<td>Wood River</td>
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</tr>
<tr>
<td>Average</td>
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<tr>
<td></td>
<td></td>
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</table>
Figure 5.4. Winter diet composition of coyote social groups in (a) 2000, (b) 2001, and (c) 2002 in the Alaska Range. Diet is shown as the relative frequency of prey occurrences in scats (n scats shown above bars). Asterisks indicate diets that were significantly different from the average population diet. The “other” category consisted mainly of birds and vegetation.
and Wood River/Sheep Creek than in Dry Creek during 2000 and 2001 (2000: $F_{2,529} = 54.7$, $P < 0.001$; 2001: $F_{2,435} = 68.0$, $P < 0.001$). In 2002, hare abundance in the West Fork dropped to the level of Dry Creek, and both drainages had lower hare density than the Wood River ($F_{2,385} = 6.77$, $P = 0.001$). Consumption of hares by coyote social groups largely mirrored the pattern of hare abundance in space and time, except that Dry Creek coyotes ate more hare and West Fork coyotes ate less hare than expected based on hare abundance in 2000 (Figure 5.5b). A 2-factor ANOVA showed that location and year significantly affected hare occurrence in the diet of social groups ($F_{4,14} = 6.77$, $P = 0.007$).

We hypothesized that age, sex, and social group might explain some of the dietary variation among individuals when years were pooled. We were not able to account for differences among years in this analysis due to the limitations of the dataset. Adult and juvenile diets differed significantly ($\chi^2 = 27.6$, $P < 0.001$): adults ate more porcupine than juveniles (15.1 vs. 5.6 % of diet, respectively), more Dall sheep (3.4 vs. 0.5% of diet), and less vole (5.9 vs. 11.6% of diet). Coyote diet did not differ among sexes, but social group affiliation explained 72% of the variation in Dall sheep occurrences and 58% of the variation in vole occurrences among individuals (Table 5.4a). The Lone DC/WF female and the S. West Fork group consumed 2½–3 times more Dall sheep than the five other social groups (7.9–9.9% of diet vs. 0–3.1%, respectively), and the N. West Fork group consumed approximately twice the amount of voles as other groups (20.3% of diet vs. 0–12.1%, respectively). Differences in Dall sheep and vole consumption among groups were partially explained by the location of groups within the study area (Table 5.4b). In general, Dry Creek coyotes consumed fewer voles than West Fork and Wood River coyotes (1.7% of diet vs. 11–14%, respectively), and West Fork coyotes consumed more Dall sheep than coyotes in other drainages (6.5% of diet vs. 0.6–1.5%).

**Factors affecting persistence**

Half of the coyotes died or dispersed during this study (12 of 24; Table 5.1). Males weighed more than females ($R^2 = 0.75$, $F_{1,9} = 27.7$, $P < 0.001$), but persistence was not affected by sex ($n = 24$, Fisher’s Exact Test $P = 1.00$) or body weight (logistic regression $\chi^2 = 0.07$, $P = 0.79$). Although the disappearance rate of known adults (45%) was lower than the rate of known juveniles (75%), the difference was not statistically significant, perhaps due to low sample size ($n = 19$, Fisher’s Exact Test $P = 0.35$).

Low prey abundance and high predator numbers may have caused the most intense hardship for coyotes in 2001. Coyotes experienced the highest rate of mortality and emigration
Figure 5.5. (a) Snowshoe hare abundance and (b) frequency of hare occurrences in scats of coyote social groups in the three main river drainages from 2000–2002. Error bars show 95% confidence intervals in (a) and standard error of the mean in (b).
Table 4. ANOVA tables showing the effect of (a) sex and social group and (b) sex and location (river drainage) on the frequency of prey occurrences in scats of individual coyotes. Five prey types were analyzed: snowshoe hare, carrion, porcupine, Dall sheep, and vole. Significant effects (P ≤ 0.05) are shown in bold.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Snowshoe hare</th>
<th>Snowshoe hare</th>
</tr>
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<tbody>
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<td>SS</td>
<td>DF</td>
</tr>
<tr>
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</tr>
<tr>
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<tr>
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<tr>
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<tr>
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<tr>
<td>Total</td>
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</tr>
</tbody>
</table>
during this period: 50% of deaths and dispersals occurred in 2001. Moreover, five of the six radiocollared coyotes that were alive in the study area at the end of 2001 were still present as of September 2004. Diet composition during 2001 may therefore have influenced coyote persistence during the hare decline. We compared the diets between 10 adults that persisted and four adults that died or dispersed in 2001 (Table 5.1). We excluded juveniles because differences among adult and juvenile diets, survival, and dispersal rates could have confounded results. The overall diet differed among adults that persisted and those that died or dispersed in 2001 (Figure 5.6; $\chi^2_5 = 17.0, P = 0.005$). Compared to adults that died or dispersed, persisting adults consumed more hare (50% vs. 37% of diet), more vole (5% vs. 0), less carrion (15% vs. 29%), and less porcupine (5% vs. 13%). Of the three coyotes that were known to have died during 2001, two died from porcupine-induced injuries and one was killed by wolves (Table 5.1).

All coyotes in the Dry Creek drainage died or dispersed, whereas all coyotes in the Wood River/Sheep Creek drainage survived and remained in the area, and only 1 coyote died in the West Fork ($\chi^2_2 = 20.7, P < 0.001$). The ratio of juveniles:adults did not differ among drainages ($\chi^2_2 = 0.75, P = 0.69$), so possible differences in juvenile and adult persistence do not explain this pattern. None of the 56 coyotes identified in our study area lived exclusively in the Dry Creek drainage for all three years.

Discussion

Individual specialization

As the niche width of the coyote population expanded during this study, the diets of coyote social groups diverged from one another, indicating that different groups “specialized” on different prey species to some degree. However, the diet of most individual coyotes did not differ significantly from the average population diet, and the high average values of Petraitis’ W each year (0.60–0.92, Table 5.2) indicated that within-individual diet variation substantially outweighed between-individual variation. The majority of cases documented in a recent review reported similar values of diet specialization in a variety of taxa (Bolnick et al. 2003). The relatively low abundance of each alternative prey type may have constrained the ability of coyotes to specialize on particular items when hares declined, thus resulting in wide niche widths among most coyotes. Although coyotes consumed a wide variety of prey, individuals and groups
Figure 5.6. Comparison of winter diet composition among adults that survived ($n = 10$) or died/dispersed ($n = 4$) in the Alaska Range during 2001. Diet is shown as the relative frequency of prey occurrences in scats ($n$ scats shown above bars). The “other” category consisted of vegetation, birds, flying squirrel (*Glaucomys sabrinus*), hoary marmot (*Marmota caligata*), and lynx.
relied on different prey items to varying degrees, and the causes and consequences of these differences will be the focus of the following discussion.

**Factors affecting diet**

When different prey items require different foraging tactics, specializing on one prey type can greatly increase foraging efficiency (Werner et al. 1981, Serra et al. 1997). Several prey species consumed by coyotes, such as porcupine and Dall sheep, inhabit non-overlapping habitat types and require specialized hunting tactics. Juvenile coyotes were less likely to consume porcupine and Dall sheep than adults. During the process of killing a porcupine, the coyote risks incurring injury or death from the porcupine’s quills, and an individual’s skill and experience level may influence the outcome of this battle. Dall sheep can be difficult to capture due to the steep terrain they inhabit and high level of vigilance within bands of sheep (Geist 1971), so it also may take time for coyotes to learn how to hunt mountain sheep effectively.

When hares were scarce in 2002, one coyote social group targeted Dall sheep as an important alternative prey source, whereas two groups preferred porcupine and one group preferred carrion. As the staple prey of coyotes declined, it may have benefited coyotes to master the technique required to exploit the most profitable alternative prey item. Why, then, did social groups target different alternative prey types? The social groups occupied relatively exclusive ranges (Figure 5.1), so targeting different prey would not have reduced intraspecific competition appreciably. However, differences in prey distribution and coyote learning experiences may explain most of this variation.

Alternative prey availability may have differed among social group home ranges, resulting in corresponding differences in prey profitability. We did not have spatially-explicit abundance data for alternative prey, but the pattern of hare abundance in space and time was an important factor influencing coyote diet. Coyotes consumed proportionally more hares in areas where hares were most abundant, and hare consumption declined as hare numbers fell. Similarly, the location of social groups within the study area influenced the frequency of vole and sheep occurrences in the diet. The N. Dry Creek and Wood River coyotes, which had no sheep in their diet, occupied lower-elevation home ranges where they were unlikely to encounter sheep (Figure 5.1). Coyotes in the other five groups could readily access sheep, but the S. West Fork and Unknown DC/WF coyotes ate $2\frac{1}{2}$–3 times more sheep than the other groups. Thus, prey distribution may have been the dominant factor affecting coyote diet, but it probably does not explain all of the variation among groups.
Random differences in the learning experiences of coyotes in different groups could have contributed to the divergence in foraging strategies. Murdoch (1969) found that predators with weak prey preferences could be trained to prefer specific prey. When hares were abundant, coyotes may not have developed strong preferences among the alternative prey types. Thus, when hares crashed, initial experiences subsisting on alternative prey could have strongly influenced future foraging patterns. Previous experience has been shown to influence dietary preferences of foragers (Ramos and Tennessen 1992, Sandlin and Willig 1993, Persons and Rypstra 2000), and social animals can develop preferences by learning from conspecifics (Morgan et al. 2003).

Regardless of the cause, these varying strategies may have caused predation pressure on alternative prey to be patchy, which could have resulted in localized prey population declines in the home ranges of certain coyotes. For example, a single cougar killed 26% of the lambs and 9% of the ewes in a bighorn sheep population during one winter in Alberta, whereas other cougars nearby rarely killed sheep (Ross et al. 1997). Individual variation in predation on sheep nicely illustrates the “fallacy of averages” (Sherratt and MacDougall 1995): ineffective management strategies may result from assuming all coyotes kill equal numbers of sheep, because removal of “problem” individuals can be much more effective at reducing depredation than indiscriminate culling (Blejwas et al. 2002).

Factors affecting coyote survival

Eleven of the 24 coyotes included in this study died or dispersed during the first two years, whereas only one coyote died during the third year (2002) and five of six radiocollared coyotes that survived the snowshoe hare decline were present in the study area as of September 2004 (Table 5.1). Thus, coyotes that survived the initial hare crash fared well in the subsequent lean years, indicating that the early hare decline was a period of selection on coyotes. Adults had higher rates of persistence than juveniles, and although this difference was not statistically significant, several studies have shown that juvenile coyotes have higher mortality and emigration rates than adults (Windberg 1995, Crete et al. 2001). Age differences in persistence rates may have been accentuated during the hare decline but are of little interest from an evolutionary perspective because age is not a heritable trait. We therefore examined factors affecting the persistence of individuals in the reproductive age class.

The winter diet of adults that persisted differed significantly from the winter diet of adults that died or dispersed during the early hare decline. Dispersal rates of radiocollared adults were
low during this study (Chapter 3), so persistence was nearly equal to true survival in this analysis. Adult coyotes that ate relatively more hares and voles were more likely to survive and remain in the area than adults that ate more porcupine and carrion. Furthermore, most deaths were due to factors directly related to feeding strategies: wolves, which killed two coyotes during this study, may have been encountered by coyotes scavenging wolf-killed carrion, and injuries from porcupine quills killed two coyotes. The coyote population in Yellowstone National Park declined by 50% after the reintroduction of wolves (Smith et al. 2003), and most coyotes were killed while scavenging in areas of high wolf activity (Switalski 2003). In contrast, preying on snowshoe hares and voles has little, if any, intrinsic danger. Thus, coyotes that could obtain more hares and voles may have had a fitness advantage over coyotes that consumed more carrion and porcupine during the early decline. Variation in risk-taking behavior has been shown to have fitness consequences in taxa as varied as bighorn sheep (Reale and Festa-Bianchet 2003) and sunfish (Wilson 1998), and it is generally thought to be an important component of predator-prey interactions (McNamara and Houston 1992).

Individuals may alter their risk-taking behavior due to perceived changes in their environment (Bateson 2002), and this may have occurred for coyotes that survived the hardship period of 2001. The coyotes that ate relatively little porcupine and carrion in 2001 ate substantial amounts of these risky food items in 2002 (Figure 5.4). Hare densities were much lower throughout the study area in 2002, so increased risk-taking may have been necessary for survival as hare densities continued to fall. The fact that the “risk-prone” strategy incurred high mortality costs in 2001 but not in 2002 suggests that coyotes that survived the early decline may have been more skilled at hunting and consuming these risky prey items.

Ninety-two percent of coyote deaths and dispersals occurred in the Dry Creek drainage, which had much lower hare densities in 2000 and 2001 than the West Fork and Wood River/Sheep Creek drainages. Several researchers have proposed that hares retreat to areas with the densest cover during decline periods, and that these areas serve as refugia for remnant hare populations during the low phase (Keith 1966, Wolff 1980). We did not measure vegetative characteristics, but Dry Creek was smaller and narrower than the other drainages and may have had poorer-quality hare habitat. Coyotes that adopted risk-prone foraging tactics in 2001 may have been prompted to do so by excessively low hare abundance. In fact, Dry Creek may have been a coyote population sink during this study. The neighboring drainages, in which coyote persistence was higher, may have served as coyote sources for Dry Creek. For example, the
Sheep Creek juvenile (S3) made repeated forays into the Dry Creek drainage in 2002 (Figure 5.1), and these explorations may have been precursors to dispersal (Harrison 1992).

Although low hare abundance in Dry Creek may partially explain the high mortality and dispersal rates in 2001, hare abundance was even lower throughout the study area in 2002, and coyote persistence remained high in the Wood River and West Fork. Thus, other characteristics of Dry Creek may have contributed to coyote deaths and emigration. Trappers were active in Dry Creek during 2002 only, so trapping was not responsible for the high mortality and emigration in 2000 and 2001. However, there were 50% more wolf tracks per km in Dry Creek than the other drainages each winter (unpublished track count data). Coyotes tend to avoid areas of high wolf activity, and individuals that do not avoid these areas can have increased mortality rates (Carbyn 1982, Paquet 1992, Arjo 1999).

In conclusion, results from this study suggest that territory quality may be the most important factor influencing which predators survive periods of prey scarcity. The decline phase of the hare cycle may therefore have selected for coyotes with traits that enabled them to secure high-quality territories, such as aggression or social dominance (Gese et al. 1996a). This selection should be relaxed during cyclic hare peaks and probably does not result in long-term evolutionary changes in northern coyote populations. However, in areas that experience sustained periods of prey scarcity (due to human disturbance or other factors; Both and Visser 2001), selection may favor those predators that are better able to secure patches of higher prey abundance or are more efficient at exploiting the remaining prey items.

**Fecal genotyping as a tool for the study of individual diet**

Although the genetic analysis of feces was proposed as a method of studying individual diet in the 1990s (Kohn and Wayne 1997), only one other study has used this technique to date (Fedriani and Kohn 2001). The most likely reason for this paucity is the large sample size of scats required to obtain meaningful results. In conventional diet studies, approximately 30–70 scats are needed to accurately estimate the average diet of a predator population (Windberg and Mitchell 1990, Mukherjee et al. 1994). Our data indicate that at least 45 scats were needed to construct an accurate winter diet when scats were pooled across individuals. However, only 10 scats were needed to construct accurate diets of individuals, most likely because the between-individual variation had been removed. Fedriani and Kohn (2001) genotyped 115 scats and constructed individual diets of coyotes with as few as three scats per individual (mean = 5.7, max = 11). Conclusions drawn from such data may be invalid, because our subsampling tests showed
that diets constructed with fewer than 10 scats could be highly inaccurate. Researchers seeking to use fecal genotyping to study individual diet may need substantially larger datasets than is needed for applications such as population size estimation, but valuable information can be obtained by taking this approach.
CHAPTER 6
GENERAL CONCLUSIONS

Overview of thesis

The primary objective of this thesis was to examine the response of coyotes to the snowshoe hare population decline in central Alaska and to evaluate the subsequent impact on other species in the vertebrate prey community. Coyotes responded to the decline in snowshoe hare numbers both behaviorally and numerically, and these responses affected alternative prey species in the Alaska Range. Dall sheep were relatively unimportant prey for coyotes, but coyotes were major predators of lambs and the numerical response of coyotes to hares substantially affected lamb survival. However, coyotes did not increase selection for Dall sheep when hares declined, so the coyote per-capita predation rate on sheep was not affected by hare numbers. Conversely, coyote per-capita consumption of porcupine increased 25-fold when hares declined, indicating that porcupine populations may have been affected by the prey-switching behavior of coyotes. Thus, coyotes may have mediated apparent competition between hares and sheep (due to their numerical response) while simultaneously mediating apparent mutualism between hares and porcupines (due to their behavioral response). Because coyote foraging behavior and population dynamics were driven by the absolute abundance of snowshoe hares, I have concluded that coyote predation may be a destabilizing influence on the prey community, perhaps triggering population cycles in alternative prey species. These results highlight the importance of indirect interactions among species and demonstrate the utility of monitoring the broader community when examining focal species interactions. In addition, heterogeneity in prey availability and differences in diet choice among coyotes can affect which individuals survive prey scarcity and may lead to localized differences in predation pressure on various prey species.

The four major findings of this thesis are:

1) Coyote predation is not a stabilizing influence on prey populations in the Alaska Range.

The absolute abundance of snowshoe hares had a strong effect on coyote diet composition. Coyotes were relatively insensitive to changes in the abundance of alternative
prey, and the absolute biomass of hares was a good predictor of the amount of carrion, voles, porcupine, and hare in the diet of coyotes. Because coyote predation on alternative prey was not dependent on alternative prey density, coyote predation was not a stabilizing influence on this vertebrate prey community (Sinclair and Pech 1996). Coyotes therefore did not function as “keystone” predators that mediate prey coexistence by selectively preying upon the most abundant species (Crowley 1979), so prey diversity in northern boreal forests would probably not decline if coyotes were removed. This finding may be community-specific, however, because coyote removal led to lower levels of rodent diversity in Texas (Henke and Bryant 1999). The relative profitability of prey items is influenced by many factors other than abundance, such as prey size, vulnerability, nutritional content, and risk of injury (Stephens and Krebs 1986). In addition, switching amongst prey can reduce foraging efficiency (Werner et al. 1981, Serra et al. 1997), so it may benefit a predator to continue targeting a particular prey item even if a different prey becomes more abundant. When prey profitability is determined primarily by factors other than abundance, which may be common in communities with prey species that vary greatly in size, predation rates should often be independent of prey density.

2) Coyote populations declined in response to the snowshoe hare decline with a 1 ½ year time lag.

Snowshoe hare populations were at peak abundance in 1999/2000, and the coyote population peaked in 2001, with approximately 35 individuals in the study area. By March 2002, the coyote population had declined to approximately 20 individuals. A pulse of high mortality and emigration occurred immediately following the peak in coyote numbers, but survival and site fidelity were high in subsequent years. Although coyote survival was high during the low phase of the hare cycle, reproduction did not occur during these years. Thus, coyote numbers probably continued to decline due to a lack of recruitment. These results are consistent with findings from the Yukon (O'Donoghue et al. 1997), but the magnitude of the coyote decline was lower in the Alaska Range, perhaps due to a higher diversity and abundance of alternative prey.

Applying open population models to fecal genotyping data provided accurate information about coyote population dynamics, but the precision of population estimates was low. Several factors influenced the success of fecal genotyping, such as DNA storage method, extract color, and storage time. I conclude that fecal genotyping can be a useful tool for the long-term monitoring of elusive animals like coyotes.
3) Coyotes mediate apparent competition between snowshoe hares and Dall sheep.

The numerical response of coyotes to snowshoe hares, and in particular their reproductive response, had a large impact on Dall sheep recruitment. Coyotes were the main predator of Dall sheep lambs from 1999–2003, and predation on lambs declined 3-fold during years when coyote reproduction failed. Coyote reproductive failure occurred during years of low hare abundance, and lamb survival was therefore negatively related to hare abundance. Coyotes may kill lambs primarily to raise pups, in which case the number of reproductive coyotes should influence lamb survival more strongly than the total number of coyotes in the population. Due to multiple time delays, Dall sheep abundance was positively correlated with hare abundance despite the negative effect of hares on lamb survival. Although spatial separation of hares and sheep does not appear to provide sheep with “enemy-free space” (Holt 1984), repeated hare crashes due to the population cycle may provide sheep with enough “enemy-free time” to recover from years of high predation.

4) The diets of coyote social groups diverged as hares declined, and diet composition affected the chance that an adult coyote would survive the decline.

The niche breadths of coyote social groups were relatively wide during all years, but niches diverged when hare abundance declined because different groups favored different alternative prey types. The pattern of snowshoe hare consumption by social groups largely mirrored the pattern of hare abundance in space and time, indicating that patchiness in prey abundance may have been the main cause of diet variation among coyote groups. Adult coyotes with higher proportions of hare and vole in their diets and lower proportions of porcupine and carrion had increased chances of surviving the hare decline and remaining in the study area. The main causes of coyote death (n = 4) were wolf attacks and porcupine-induced injuries, suggesting that preying on hares and voles was less risky than preying on wolf-killed carrion and porcupines. Patchiness in prey abundance and enemy activity may interact with characteristics such as risk-taking behavior to determine which predators survive periods of prey scarcity. In addition, variation in diet choice among predators could lead to source-sink dynamics among prey species in the community, possibly causing localized extinctions or declines within the home ranges of certain predators.
Future directions

*Predator behavior, prey characteristics, and stability.* In Chapter 2, I hypothesized that predators choosing among similar-sized prey would be more likely to exert a stabilizing influence than predators choosing among prey with large size differences. This hypothesis could be examined with a meta-analysis or perhaps a controlled field or laboratory study. Sinclair et al. (2003) found that prey body size in an African ungulate community moderated the impact of predation on prey populations. Many studies of stability in population ecology have involved measuring functional responses (e.g., Oaten and Murdoch 1975a, O'Donoghue et al. 1998b, Sinclair et al. 1998, Hayes and Harestad 2000), while community ecologists have focused on interpreting broad trends along productivity and diversity gradients (e.g., May 1973, Murdoch 1975, Menge and Sutherland 1976, Oksanen et al. 1981, Chase 2003). Although evaluating broad-scale trends can help to focus research in relevant directions, this approach does not address the mechanisms producing these patterns. Likewise, measuring the functional responses of predators has been criticized as an approach that is not furthering our understanding of population and community processes (Krebs 1995). Understanding mechanisms requires studying individual organisms. Studies that examine the behavior of predators in relation to characteristics of their prey could lead to useful new insights relevant to community ecology.

*Porcupine population dynamics.* There is currently no research being conducted on porcupines in Alaska or the Yukon. Previous research has focused on the impact of porcupines on commercial timber harvests (Eglitis and Hennon 1997, Zimmerling 2001), and little is known about porcupines in the boreal forest. Emerging results from Quebec indicate that populations cycle with minor peaks every 11 years and major peaks every 22 years (Berteaux et al. 2004). Fishers (*Martes pennanti*) are considered to be the primary predator of porcupines in areas where they co-occur (Woods 1973, Powell 1980), but fishers are not present in Alaska or the Yukon. Predation by other species can affect porcupines, however. For example, prey-switching by cougars in response to a deer population decline led to the near-extinction of porcupines in the Great Basin Desert region of California (Sweitzer et al. 1997). My results suggest that coyote predation could destabilize porcupine populations, and snowshoe hare dynamics may indirectly affect porcupines via prey-switching by shared predators. A study of porcupine demography in
relation to the snowshoe hare cycle would provide valuable new information about this long-neglected resident of northern boreal forests.

**Dall sheep population dynamics.** This study suggests that coyote predation could lead to declines or localized extinctions of Dall sheep but that repeated crashes in hare populations may provide enough recovery time to ensure the long-term viability of the sheep- coyote-hare interaction. A stage-specific Leslie matrix model of Dall sheep populations would provide a useful tool for predicting long-term population trends and investigating alternative scenarios (Caswell 1989). For example, the Leslie model could be used to determine the number of years of low predation during the hare cycle that are necessary to compensate for the years of high predation during hare peaks. The Alaska Department of Fish and Game has collected a total of eight years of data on the causes and rates of adult and juvenile sheep mortality, pregnancy rates, and population trends of Dall sheep in the Alaska Range that could be used in the model. The relative sensitivity of sheep populations to changes in juvenile versus adult mortality could be examined with such a model. Our data show that wolves are the main predators of adult sheep, whereas coyotes are the main predator of lambs. Wolf control has been used as a management tool in the Alaska Range (Boertje et al. 1996), and this practice may lead to increased coyote populations since wolves are a major source of coyote mortality in this area. The model could be used to investigate the impact of wolf control on Dall sheep, because adult survival may increase due to fewer wolves but juvenile survival may decline due to more coyotes.

**Intraguild interactions among predators.** This thesis focused on the relationships between coyotes and their prey, but my study area supported an abundance of carnivore species that also interact with coyotes. These intraguild interactions could have substantial impacts on food web structure via direct and indirect competition, predation, and direct and indirect effects on the prey community. During this study, we documented interactions among coyotes and the following predators: wolves (*Canis lupus*), wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), otters (*Lutra canadensis*), and northern goshawks (*Accipiter gentilis*). Two radiocollared coyotes were killed by wolves; a pair of coyotes was observed circling a wolverine; lynx, otter, and goshawk remains were found in several coyote scats. Coyotes also compete with and often kill red foxes, *Vulpes vulpes* (Polis et al. 1982, Dekker 1989), which were common in the study area. The diet of coyotes overlaps with smaller mustelids that also resided in the study area such as pine marten (*Martes americana*) and weasels (*Mustela spp.*), as well as other birds of prey.
such as golden eagles (*Aquila chrysaetos*), great horned owls (*Bubo virginianus*), and hawk owls (*Surnia ulula*). I found that hare density had a large effect on coyote population dynamics, but interactions with other carnivores may also have strong effects. Predation by wolves and bears (*Ursus arctos* and *U. americanus*) may limit coyote populations during hare peaks, and risk of predation could influence their choice of denning habitat and movement patterns (Switalski 2003). Alternatively, food subsidies in the form of partially consumed carcasses may benefit coyotes (Paquet 1992). A study of the interactions among predators would add greatly to our understanding of top-down effects in this system.

**Development of new open population models.** My study showed that fecal genotyping can be a promising tool for monitoring elusive species, but I had to use population estimation techniques that were designed for data collected during discrete time intervals. Because animals defecate continuously, I argue that fecal surveys are continuous regardless of the researcher’s collection schedule. Discrete sampling is possible if researchers can determine the age of deposited scats, but limiting collection to short time intervals could lead to inadequate sample sizes, particularly since carnivore densities are often low. Arbitrarily subdividing continuous data into discrete intervals, as I did in this study, could affect estimates, and information is lost because multiple captures during the intervals are ignored. Mark-recapture models for continuously-collected data have been developed for closed populations using maximum likelihood approaches (Hwang et al. 2002, Wang and Yip 2002), and extending these models to open populations seems feasible.

**Optimization of laboratory techniques for fecal DNA.** This study was the first to show that extract color can strongly influence the genotyping success of fecal samples. My suggestion that darker extracts contain higher levels of PCR inhibitors needs to be tested, and the relative impact of inhibitors versus DNA quantity on genotyping success should be evaluated. I speculate that PCR inhibitors in feces pose a larger challenge to fecal genotyping than limited DNA quantity or poor DNA quality. If this is the case, laboratory optimization research should focus on ways to reduce the presence of PCR inhibitors while maintaining adequate DNA yield.
General implications

The predictable and dramatic variation in the density of snowshoe hares in northern forests creates an ideal opportunity to explore food web dynamics in a system of substantial human interest. The northern boreal forest represents approximately 1/3 of the world’s remaining forested areas, and boreal vertebrate communities will be increasingly affected by global climate change and resource exploitation in the coming years. In order to predict the impact of these changes on boreal vertebrate communities, detailed knowledge of species interactions, both direct and indirect, is needed. This thesis represents a small contribution to our growing knowledge base about the nature of predator-prey interactions, and I hope it will be useful for sound science-based conservation and management in northern regions.

My study highlighted the importance of considering indirect interactions when studying food web dynamics. Recent research indicates that, in comparison to direct interactions, indirect interactions may be equally or more important in structuring communities (Abrams 1987, Menge 1997, Bolker et al. 2003, Dill et al. 2003, Schmitz et al. 2004). When building models and designing empirical research, community ecologists should include indirect interactions whenever possible, because failing to do so may compromise the usefulness of results. Likewise, ignoring variation among individuals when modeling population dynamics can lead to inaccurate predictions (Sherratt and MacDougall 1995, Fryxell and Lundberg 1998). My results show that investigating the causes and consequences of individual variation can provide insights that are useful for conservation and management.
LITERATURE CITED


Alaska Department of Fish and Game. 2003. Alaska Hunting Regulations No. 43, July 2002-June 2003. Alaska Department of Fish and Game, Juneau, AK.


Dejean, A., Schatz, B., Orivel, J., and Beugnon, G. 1999. Prey capture behavior of
Psalidomyrmex procerus (Formicidae: Ponerinae), a specialist predator of earthworms
(Annelida). Sociobiology 34: 545-554.

Dekker, D. 1989. Population fluctuations and spatial relationships among wolves (Canis lupus),
coyotes (Canis latrans), and red foxes (Vulpes vulpes) in central Alberta 1972-1981.
Canadian Field-Naturalist 97: 303-306.


Dukas, R., and Ellner, S. 1993. Information-processing and prey detection. Ecology 74: 1337-
1346.

animals: the forest elephants of Kakum National Park, Ghana. Molecular Ecology 12:
1389-1402.

conifer stands of central Southeast Alaska. Western Journal of Applied Forestry 12: 115-
121.

Elton, C., and Nicholson, M. 1942. The ten year cycle in numbers of lynx in Canada. Journal of

Erlinge, S., Goransson, G., Hansson, L., Hogstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T.,
Vonschantz, T., and Sylven, M. 1983. Predation as a regulating factor on small rodent
populations in southern Sweden. Oikos 40: 36-52.

Naturalist 123: 125-133.

tracking of mountain lions in the Yosemite Valley region in California: genetic analysis
using microsatellites and faecal DNA. Molecular Ecology 9: 433-441.

Eubanks, M. D., and Denno, R. F. 2000. Health food versus fast food: the effects of prey quality
and mobility on prey selection by a generalist predator and indirect interactions among
prey species. Ecological Entomology 25: 140-146.


Finerty, J. P. 1980. The population ecology of cycles in small mammals. Yale University Press,
New Haven, Connecticut, USA.


Menge, B. A. 1997. Detection of direct versus indirect effects: were experiments long enough? American Naturalist 149: 801-823.


Young, S. P., and Jackson, H. H. T. 1951. The clever coyote. University of Nebraska Press, Lincoln, Nebraska, USA.

Appendix I. Genotypes of the 56 coyotes identified in a sample of 544 genotyped feces collected in the Alaska Range, 2000–2002. Allele sizes are shown for each loci, with “0” recorded for missing data. For each individual, the sex, number of scats collected, number of years present, and whether or not it was radiocollared were recorded.

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