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Ecology of coyotes (*Canis latrans*) in Elk Island National Park, Alberta, Canada

by

Shelley D. Pruss ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

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Edmonton, AB
T6C 2S1

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Ecology of coyotes (*Canis latrans*) in Elk Island National Park, Alberta, Canada** submitted by **Shelley D. Pruss** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Wildlife Ecology and Management**.

Dr. R. J. Hudson, Supervisor

Ian Stirling

Dr. I. Stirling

Dr. R. Wein

Dr. F. Robinson

A Lee Foote

Dr. A. L. Foote

Dr. J. Huot, External Reader

Dr. U. Silins, Chair

Dated: 18 Jan 02

For

The Alpha and the Omega

ABSTRACT

I evaluated aspects of the ecology of coyotes (*Canis latrans*) in Elk Island National Park (EINP), Alberta, Canada using radio-telemetry, visual observations, and scat analyses. Coyotes were captured during the winter months. I used diazepam tabs on a modified neck snare to decrease capture injuries and stress. Fifty-one coyotes were caught in this neck snare and 96% of coyotes captured around the neck. Capture mortality was low (<2%). The addition of diazepam tabs reduced the facial and oral lacerations when coyotes chewed and/or removed the tranquilizer. Modified neck snares appear to be a humane technique for capturing coyotes during winter in forested areas without compromising capture efficiency or increasing capture of non-target species. Annual survival of coyotes in EINP was moderately variable and ranged from 0.6 to 0.9 with long-term survival of females averaging 3% compared to 22% for males. The length of time that coyotes survived following collaring was negatively related to the percent of telemetry locations that identified coyotes as being outside EINP and/or the Blackfoot recreation area. Significant variation in home ranges resulted from differences in social organisation rather than gender, and individual home range, core areas, and perimeters decreased with increasing group size. Linear regression analyses showed that home range area typically increased as coyotes spent more time outside of EINP. Coyotes ate at least 36 different food items and displayed a high degree of seasonality in their diet. Small mammals such as mice, voles, and lemmings typically comprised the majority of food items throughout the year. Ungulates were a major (≥ 40% faecal content) food item in 25% of all scats on an annual basis but were highest in winter. The percent of ungulate food as a major diet item was significantly affected by social affiliation in winter when packs had higher proportions of ungulates in their diet compared with solitaires and pairs. For three of four coyotes that changed social affiliation, becoming a member of a pack was associated with a significant increase in the proportion of ungulates in their diet. I estimated a pre-whelping (winter) density of coyotes in EINP of 0.87 – 1.05 coyotes/km^2 which is one of the highest densities recorded. Coyotes establish holes under the perimeter fence in a non-random fashion with disproportionately more holes than expected when lengths of the fence were next to conifer forest and wetlands but dug fewer than expected in areas bordering grasslands and roads.

Keywords: coyote, *Canis latrans*, survival, home range, core area, social affiliation, solitary, pair, pack, diet, scats, density, fence

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CHAPTER ONE

INTRODUCTION

BACKGROUND AND RATIONALE

Interspecific differences in mammalian life history characteristics have been shown to be associated with the three factors of body size, taxonomy, and ecology (Gittleman 1986). Within the order Carnivora, social organization can be strongly affected by the spatial distribution, acquisition, and defense of food resources (Bekoff and Wells 1980, Macdonald 1983, Bekoff and Wells 1986), with the dispersion and richness of these resources determining group and territory size (Bowen 1981, Macdonald 1983). There is often a positive association between the size of the animal and/or social group and the size of their prey (Clutton-Brock and Harvey 1983, Macdonald 1983, Vezina 1985, Gittleman 1989). Increased group size is thought to enable animals to hunt co-operatively to capture larger prey (Nudds 1977, Gese *et al.* 1988). The adaptive value of belonging to a social group has been documented for many species, particularly in terms of resource exploitation and predator avoidance, however other benefits of group living include increased vigilance and territorial boundary patrol, the delay or elimination of the costs of dispersal, increased inclusive fitness, and alloparental behaviour (Geist 1974, Bekoff *et al.* 1981, Messier and Barrette 1982, Gittleman 1989, Bekoff and Wells 1986, Creel 1996, Patterson and Messier 2001). Less well understood are the disadvantages of group living such as being detected by predators, decreases in individual food intake, disease or parasite transmission, and increased potential for injury or aggression (Caraco and Wolf 1975, Underwood 1982, Gittleman 1989).

Canids display a striking degree of intraspecific and to some degree interspecific variation in life history characteristics, social organisation, and foraging behaviours on a population, annual, and seasonal basis (Moehlman 1989). Differences in canid social organization and the use of space are, in part, species-specific adaptations to differences in food resources (*i.e.*, size; temporal and spatial availability) (Bekoff *et al.* 1981, Geffen *et al.* 1996), particularly in species that display a highly flexible social structure (Bekoff and Wells 1986, Moehlman 1989, Gompper and Wayne 1996). For example, when food resources are clumped (*i.e.*, heterogeneously distributed) and defendable, coyotes (*Canis latrans*) (Camenzind 1978, Bekoff and Wells 1982) and golden jackals (*Canis aureus*) (Macdonald 1979) form groups, even if the exploitation of these resources does not require a group foraging effort (Bekoff and Wells 1986). Conversely, when food abundance is low and widely distributed, conspecifics tend to be organised into solitary individuals or mated pairs (Bekoff and Wells 1982).

In the order Carnivora, home range size increases, as a general rule, with metabolic needs (Gittleman and Harvey 1982, Mace *et al.* 1983). As a result, some of the variation in home range size can be explained by diet and the distribution of resources (Grant *et al.* 1992). For example, folivores, frugivores, and insectivores have smaller home ranges than carnivores that depend to a greater extent on meat (Gittleman and Harvey 1982). Intraspecifc variation in home ranges sizes occurs in species with wide geographic distributions that encompass a variety of habitats with food types and dispersion specific to those habitats (Macdonald 1979). Clearly, it is not well understood whether group formation develops as a direct response to prey availability or in reaction to other selective pressures. Although the mechanisms influencing social organisation in animals with flexible sociality are uncertain, social organisation is also related to the use of space (Bowen 1981, Messier and Barrett 1982, Andelt 1985, Mills and Knowlton 1991, Patterson and Messier 2001). For example, solitary, transient, or nomadic coyotes often have large home ranges or living areas that shift both spatially and temporally and often overlap resident pairs or packs (Messier and Barrett 1982, Windberg and Knowlton 1988, Mills and Knowlton 1991).

Territorial defense (as opposed to home range) and the exclusion of con-specific competitors seems to be related to reproduction and the restriction of adult movement when pups are young (Andelt *et al.* 1979). The importance of a core area or territory for social animals with altricial young has been linked to neonatal and juvenile protection as well as a resource base from which to feed offspring (Messier and Barrette 1982, Allen *et al.* 1999). In fact, multi-generational site fidelity has been suggested for coyote packs where sharing and inheritance of home ranges may provide an advantage for offspring, particularly in cases when coyote density is high and dispersal territories are limited (Kitchen *et al.* 2000). Foraging and defense of food resources may also be facilitated by a group effort and core areas may provide shelter, den sites, resting areas or other requirements for survival as well as controlled access to mates, and improved offspring survival (Bekoff and Wells 1980, Bowen 1981, Lamprecht 1981, Laundre and Keller 1981, Messier and Barrett 1982, Gese *et al.* 1988, Person and Hirth 1991, Grant *et al.* 1992). Larger group sizes, particularly in winter, can also result in smaller individual home ranges and territories for pack animals than for solitary or paired coyotes, as the ability to acquire and/or defend large food/prey items may increase net energy gains resulting in more time spent resting and less spent travelling during foraging and hunting

(Bekoff and Wells 1981, Gese *et al.* 1988).

ASPECTS OF THE ECOLOGY OF COYOTES IN ELK ISLAND NATIONAL PARK

Elk Island National Park (EINP) in Alberta, Canada (53° 36' N, 112° 51' W), is small remnant of aspen parkland which provides a unique opportunity to examine the ecology of coyotes in an ecosystem that has one of the highest ungulate densities in North America without major competing carnivores (Blyth and Hudson 1987, Blyth 1995). EINP is surrounded primarily by agricultural lands and acreages except for the southern boundary that borders the Cooking Lake-Blackfoot Grazing, Wildlife, and Provincial Recreation Area. EINP is divided by a four lane highway into a 136 km^2 "Main Park" area located north of Highway 16 and a smaller southern 59 km^2 "Isolation" area (Blyth and Hudson 1987). Both areas of the park are completely fenced with a 2.2 m mesh wire fence and enclose high densities of large ungulates that include bison (*Bos bison*), wapiti (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). Coyotes could utilise the high abundance and biomass of ungulates either through capture of live animals or by consuming ungulate carrion.

Elk Island is situated in the aspen-parkland ecozone that is transitional between prairie to the south and boreal forest to the north. The area around EINP, commonly known as the Beaver Hills, is described as knob and kettle topography that resulted from differential melt of buried remnants of glacial ice, which supports numerous small lakes and wetlands (Blyth 1995).

EINP also provides a level of protection from human-induced mortality, compared to the intensive harvesting of coyotes in the surrounding agricultural and public lands. Coyotes in EINP are thought to be at the northern periphery of their historical range and are the largest remaining predator in this fenced system (Blyth and Hudson 1987). In contrast to many species, the distributional range of coyotes has increased since European settlement (Voight and Berg 1987, Murray and Boutin 1991). This success may be in part due to their opportunistic nature and broad habitat requirements (Macdonald 1983).

GENERAL OBJECTIVES

I evaluated selected aspects of the ecology of coyotes in Elk Island National Park by capturing and radio-collaring 41 coyotes using a modified snaring technique and collecting data on home range use through telemetry incorporated into a Geographical Information System (GIS) (ArcView by ESRI ™). I also assessed survival of collared coyotes and tracked and observed them for indications of their social affiliation (*e.g.* solitary, paired, or in packs). General dietary patterns were determined through monthly scat collection and subsequent analyses, while individual coyote diets were determined through scat analyses combined with telemetry data integrated into GIS. The EINP perimeter fence was inspected for holes dug under it by coyotes and locational and habitat details of these holes were recorded.

The general objectives of the study were:

1) To develop and evaluate a modified locking neck snare for coyotes in an effort to decrease stress, injuries and non-target animal captures (Chapter 2). The modified neck snare consisted of a nine-gauge anchor wire (4mm) anchored to the swivel of

a locking wolf snare and the attachment point was stabilized with a smaller wire. This allowed the snare to be self-supporting. The modified snare also included a diazepam tab and the removal of all sharp edges or protrusions. In Chapter 2, I tested the following hypotheses: 1) diazepam tabs would sedate and calm the captured animals thereby reducing aggression and lacerations; and 2) the modified neck snare would have lower capture mortality and non-target captures while maintaining capture efficiency when compared to published results for padded and nonpadded leghold traps, foot snares, and regular neck snares.

2) To quantify survival rates and home ranges of coyotes in EINP and to determine whether survival and home range were related to gender and social affiliation (Chapter 3). Specifically, I tested the hypotheses that: 1) mean annual coyote survival in EINP is unaffected by gender, and using separate analyses, 2) coyote home range, core area and perimeter size are unaffected by social organisation (*i.e.*, solitary coyotes compared to those belonging to pairs or packs), gender and the interaction of these factors and; 3) coyote home range, core area, and perimeter are unaffected by social organisation time of day (day or night) and season (summer or winter). I also a) determined causes of mortality of radio-collared coyotes and; b) tested for a relationships between: i) coyote survival and pelt price; ii) coyote survival of collared coyotes and total coyote trapping harvest in Alberta and; iii) annual sales of coyote pelts in Alberta with pelt price to understand potential factors affecting coyote survival. For comparative purposes, I contrasted survival rates of coyotes in EINP with that previously published. I

predicted that male and female survival would not differ and there would be a negative relationship between aspects of the Alberta fur harvest and survival of EINP coyotes. I also predicted that home range, core area, and perimeters, per individual coyote would decrease with increasing group size for the three categories of solitaires, pairs and packs and that these areas would be larger at night but that there would not be a seasonal difference.

3) To examine the seasonality of coyote diets in Elk Island National Park and evaluate the differences in diet of solitaires, pairs, packs in summer and winter (Chapter 4). Specifically, I tested the hypotheses that 1) diet is unaffected by seasons (*i.e.* months), and 2) proportion of ungulates in the coyote diet would not differ between social groups during summer and winter. I predicted that coyotes would consume a broad suite of prey and food items consistent with previous studies that have shown them to be highly opportunistic predators. Given large changes in prey abundance and availability at northern latitudes, coyotes should also display a high degree of seasonality in diet. I predicted differences in diets of solitary coyotes compared with those that formed pairs and packs and that such differences would vary between summer and winter months. Specifically, large food items (*i.e.*, ungulates) should increase proportionately as the major food items of individuals that formed packs compared with those that formed pairs and solitary individuals. Finally, EINP provided a unique opportunity to discriminate between the food resource and delayed dispersal / habitat saturation hypotheses regarding pack formation in coyotes.

4) To quantify the density of coyotes in Elk Island National Park and compare this density estimate with those found previously for coyotes occupying a range of habitats in North America. Second, to quantify the number and location of holes in the perimeter fence surrounding Elk Island National Park (Chapter 5). Specifically, I tested the null hypotheses that the density of holes was unaffected by: 1) habitat attributes adjacent to the fence (*i.e.*, agricultural grasslands, forest, wetlands, and roads), 2) season (winter, summer) and 3) adjacency to roads. I predicted that coyotes would create proportionately more holes in vegetation types that would likely provide cover or soils types amenable to digging but disproportionately fewer holes when the perimeter fence was bordered by roads.

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CHAPTER TWO

EVALUATION OF A MODIFIED NECK SNARE TO LIVE-CAPTURE COYOTES

INTRODUCTION

A diversity of live-capture techniques are used to acquire animals for research. These techniques vary in capture efficiency (Novak 1987) and humaneness (Andelt *et al.* 1999). Efforts to improve live capture devices, as well as traps for commercial fur trapping and problem wildlife, have intensified over the last decade (Phillips 1996, Hubert *et al.* 1997, Seddon *et al.* 1999, Shivik *et al.* 2000) and use of traps to capture research animals is becoming more closely scrutinized by Animal Care Committees (Canadian Council on Animal Care 1993). Addressing animal welfare concerns while still maintaining capture efficiency has driven much of the research on humane traps (Linhart and Dasch 1992, Phillips and Mullis 1996, Seddon *et al.* 1999).

For medium sized carnivores such as coyotes (*Canis latrans*), live capture techniques include leg hold traps, foot and neck snares, box traps, and to a lesser extent capture from snowmobiles, darting, and net gunning (Nellis 1968, Baer *et al.* 1978, Gese *et al.* 1987, Novak 1987). In forested areas during winter, there is a high probability of freezing limbs in foot traps or snares. In comparison, neck snares represent a potentially useful method to capture coyotes. However, locking neck snares can also induce stress, injury, or death particularly if set improperly or in inappropriate locations (Van Ballenberghe 1984, Guthery and Beasom 1978). Capture techniques are often determined by habitat or species-specific requirements and no method of live capture is injury free (Kreeger *et al.* 1990, Onderka *et al.* 1990, Mowat *et al.* 1994, Seddon *et al.* 1999).

My preliminary snaring of coyotes in Elk Island National Park (EINP), Alberta, Canada indicated that standard smaller 2.4 mm diameter coyote neck snares without diazepam and a smaller gauge anchor wire caused considerable stress in certain individuals as evidenced by site disturbance (*i.e.* chewed snare cables, broken and chewed vegetation, and trampled snow), aggression (lunging and vocalizations) or catatonia and occasional cutaneous lacerations around the jaw. In addition, this type of set included the only capture mortality and three coyotes escaped by chewing through the smaller snare cable.

These observations served as a basis to evaluate a modified locking neck snare equipped with a diazepam tab for coyotes in an effort to decrease stress, injuries, and non-target animal captures. I tested the following hypotheses: 1) diazepam tabs would sedate and calm the captured animals thereby reducing aggression (as a measure of stress) and lacerations; and 2) the modified neck snare would have lower capture mortality and non-target captures while maintaining capture efficiency when compared to published results for padded and nonpadded leghold traps, foot snares, and regular neck snares.

MATERIALS AND METHODS

Study Area

Research was conducted at EINP, 40 kilometers east of Edmonton, Alberta, Canada (53° 36' N, 112° 51' W). The park is surrounded primarily by agricultural lands and acreages except for the southern boundary, which borders the Cooking Lake-Blackfoot Grazing, Wildlife, and Provincial Recreation Area. EINP is divided by a 4 lane highway into a 134 km^2 Main Park north of the highway and the southern 60 km^2 Isolation Area. Both areas of the park are completely fenced with a 2.2 m paige wire fence and enclose high densities of large ungulates that include bison (*Bos bison*), wapiti (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). Coyotes dominate among large and medium sized carnivores, with occasional reports of black bear (*Ursus americanus*), lynx (*Lynx lynx*), and red fox (*Vulpes vulpes*) (Blyth and Hudson 1987).

EINP is situated in the aspen-parkland ecozone that is transitional between prairie to the south and boreal forest to the north. Trembling aspen (*Populus tremuloides)* and balsam popular (*Populus balsamifera)* are the dominant tree species. The climate is typical of northern mid latitude continental with associated variations in daily and seasonal temperatures. Mean monthly minimum and maximum temperatures vary between – 19.5° C in January and + 23° C in July while annual average precipitation is 48 cm (Blyth 1995).

The snare system

I used a modified neck snare to capture coyotes in EINP during the winter months of 1994-1997 to describe the effects of social affiliation on home range and diet. All research was performed with Animal Policy and Welfare Committee approvals from the Faculty of Science (protocol no.712402) and the Faculty of Agriculture, Forestry and Home Economics (protocol no. 96-53C), University of Alberta.

The control group consisted of 11 coyotes (including one mortality) captured in snares without diazepam attached. These control snares were set for 927 trap nights and 927 trap days during February 1994 and included the three coyotes that escaped.

The modified snare is comprised of a neck snare and supporting anchor wire (Fig. 2-1). Individual wolf snares with a cable diameter of 3.2 mm had a Cam-Loc™ with the lock stop set at 27 cm (reference to trap type or manufacturers does not constitute endorsement by the authors, Parks Canada, or the University of Alberta). Snares were attached to a 4-5 m length of 9-gauge wire that was looped twice through the snare swivel and twisted upon itself to form a doubled anchor. The swivel–anchor wire connection was stabilized with a small 17 gauge wire so that the snare was a self-supporting unit that did not require additional support wires. Sharp edges were cut and filed and the anchor wire ends were turned in on themselves to form an end loop.

Prior to setting, all snares were boiled in a mild detergent to remove contaminants and odors, rinsed in boiling water, and finally boiled in a dark brown commercial trap dye to camouflage the wire. Snares and related equipment were handled with surgical gloves and stored outdoors in an airtight container of spruce boughs to mask any human scent. Snares could be used only once because captured animals damage them. I replaced anchor wires when a snare set did not capture a coyote because I feared that twisting the wire could potentially weaken the anchor and result in a coyote escape.

The modified snare system included a diazepam tab, made by layering two thin strips of sterile cotton batting coated lightly with petroleum jelly on a 6 cm^2 gauze strip (Balser 1965). Forty mg of crushed diazepam tablets were spread on the two layers of cotton and rolled into a 4 cm × 1 cm × 1 cm tab. Rolled tabs were tied with thread and refrigerated in an airtight container until used. Tabs were wired onto the snare swivel

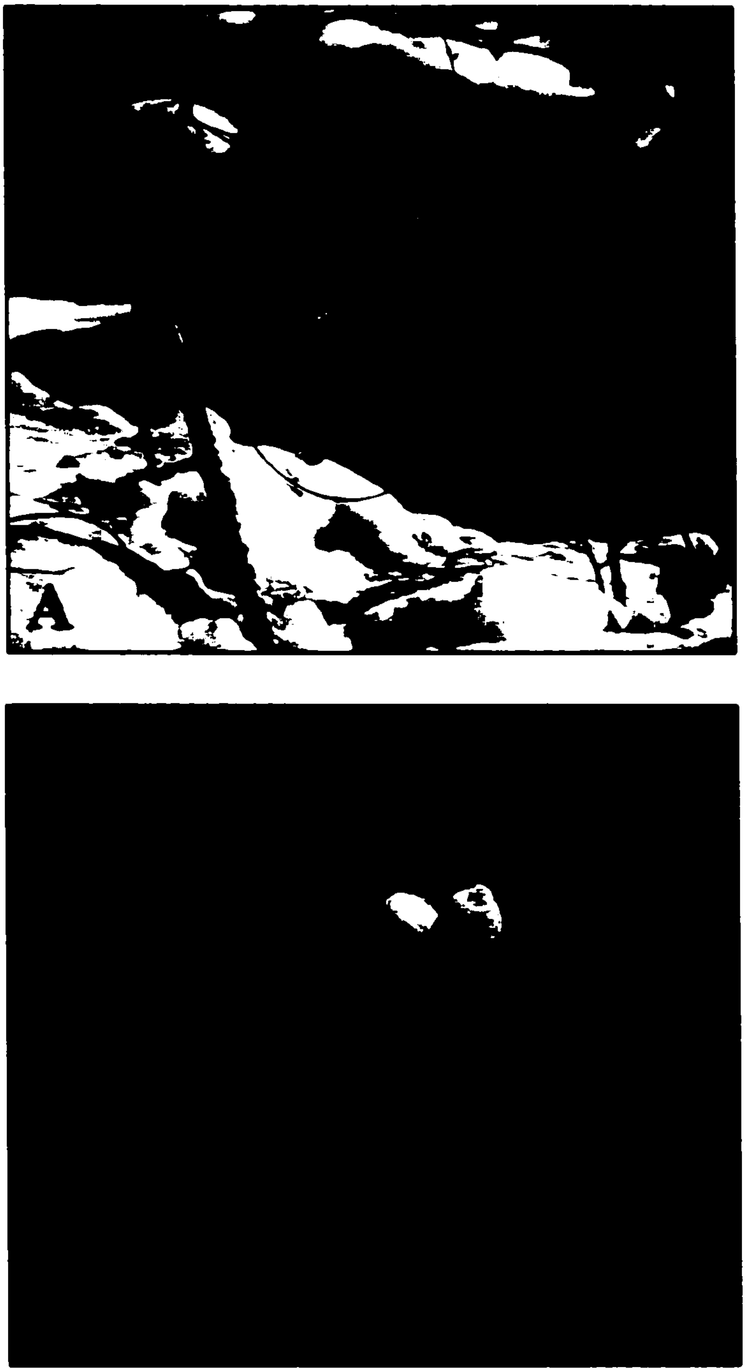

Fig. 2-1 The modified neck snare: (A) camouflaged with vegetation on a coyote run and; (B) details of the snare construction including the attachment of the diazepam tab on the swivel.

immediately before setting the snare. Nellis (1968) emphasized the crucial nature of the snare swivel component for live captures, especially in reducing the risk of inadvertent suffocation. Initial experience indicated that coyotes tended to chew the swivel so it was chosen as the attachment point for the diazepam tab. Diazepam became a controlled drug after the completion of this study. Future use of diazepam would require a researcher to submit a "Request to use controlled substances for research purposes" form to the Drug Strategy and Controlled Substances Programme, Office of Controlled Substances, Ottawa, Canada, or non-research use would require the co-operation of a veterinarian (T. Bayans, Veterinarian, University of Alberta, personal communication).

Snare protocols

Coyotes were snared during winter (15 November – 1 April) when capture efficiency is higher, the primary dispersal period is over, and there is no risk of interfering with females nursing their pups. Leg holds and leg snares were not an option because of the potentially high rate (>50%) of freezing limbs, as mean minimum winter temperatures are typically below – 8° C (Onderka *et al.* 1990).

Two types of snare sets, attached to a log or a tree, were used during this study. Snares were set along natural game trails or along trails to carcass sites and were set where trails were confined between trees, passed near trees or through scrub; the latter being preferred for log sets. I avoided risky sites such as areas near deadfall, drop-offs, or fences (risk of hanging) as well as exposed sites (potential risk of hypothermia). The anchor was secured to a tree (diameter >12 cm) or large log and the snare was suspended so the bottom of the loop was 20 - 25 cm above the trail. Natural obstructions (*e.g.* twigs, branches, and grasses) were placed around the snare to direct the animal, to prevent visual detection, and to encourage ungulates to go over or around the set. Snares were checked every 12 hours for the first three years, which indicated all captures occurred at night. Based on these data, the Faculty of Agriculture Animal Policy and Welfare committee allowed trap checks to be conducted every 24 hours.

Handling protocol

Captured coyotes were restrained with a 2 m long "Y" shaped stick placed over the back or side of the neck. The animal was slowly pushed to the ground and maintained in this position while 0.8 - 1.0 cc (100 mg/cc) of the immobilizing anesthetic Telazol® was injected into the flank muscle. When approached, coyotes were categorized as aggressive if they: 1) vocalized (growled and barked); 2) actively attempted to evade the Y-stick; or 3) lunged at, or away, from the researcher.

To avoid heat loss, immobilized coyotes were placed on a plastic covered foam pad and examined for injuries, weighed, measured, and covered with blankets while data were recorded. Blood was collected from the cephalic vein and animals were injected with an antiparasitic agent (ivermectin) and an antibiotic (Penlong XL™) to counter the effects of capture stress. Cuts and abrasions were cleaned and lacerations >1 cm in length were stitched with dissolving sutures to facilitate healing. All relatively fresh cuts on the body were recorded and assumed to be capture-related. Finally, eartags and radio collars were fitted.

In general, recovery from Telazol took several hours (Aveco 1990), and after handling, coyotes were placed in a secluded, sheltered location and left on a 10-cm thick foam pad with their head and body covered with blankets. Care was taken to position the animal's head so that the airway was open and the muzzle tilted down off the foam pad but not resting on the snow or ground. A small (1-2 kg) frozen carrion source was left at the site to mitigate the stress of capture.

Statistical Analyses

A Fisher's exact test (Stokes *et al.* 1995), using a 2 × 3 table design, was used to test the two hypotheses of no association between the presence and absence of cuts or aggressive behavior when: 1) diazepam tab was attached to the snare and subsequently detached (*i.e.* removed and/or eaten by the coyote); 2) diazepam tab was attached to the snare but not removed; and 3) diazepam was not attached to the snare. A one tailed Fisher's exact test, using a 2 × 2 table design, tested an association between the presence or absence of aggression and the presence or absence of cuts.

RESULTS

Capture efficiency

Fifty-one coyotes were captured over the study period (50 different individuals) during 9379 trap nights (dusk to dawn period) and 7421 trap days (dawn to dusk period), *i.e.* 5.4 captures/1000 trap nights. Although capture rate varied 10-fold among years, all captures occurred at night (Table 2-1). Capture mortality was low; 1 out of 51 captures (<2%) and this coyote was found dead in the snare, cause of death unknown. Forty-nine of the captures were made around the neck, one around one foreleg and the neck, and another around the abdomen between the ribs and hips. Inspection of the latter two animals by a veterinary technician did not identify any signs of injury. The latter animal was shot 8 months later by a local farmer and an examination revealed that he was in normal health.

Table 2-1 Capture efficiency (number of coyotes per 1000 trap nights) for locking neck snares used in Elk Island National Park, Alberta, 1994-1997.

Period	Trap days	Day catch	Trap nights	Night catch	Total	Capture Efficiency
Feb.- Mar. 1994	1855	0	1855	20	20	10.8
Nov.- Apr. 1994-95	2926	0	2926	15	15	5.1
Nov.- Apr. 1995-96	2640	0	2640	14	14	5.3
Jan.- Mar. 1997	0[a]	0	1958	2	2	1.0
Total	7421 5.4	0	9379	51	51	

[a] based on previous years' data, permission to change trap checks from every 12 hours to every 24 hours (University of Alberta, Faculty of Agriculture Animal Policy and Welfare Committee).

Effectiveness of diazepam

Coyotes that were held in snares where the diazepam tab was removed and/or ingested by the coyote had a significantly (Fisher's Exact test, $P < 0.05$) lower incidence of cuts compared to those where the diazepam tab was still attached to the snare or those that did not have a diazepam tab (Fig. 2-2a). Of the 17 coyotes that suffered cuts, nine required one or more sutures. Eight of the cuts requiring sutures occurred at the corner of the mouth while one coyote was cut on the top of the head. Two of the injuries requiring stitches occurred during the first 2 weeks of trapping before snare modifications and resulted from sharp protrusions from the snare swivel. Other mouth injuries resulted from chewing on the snare cable. None of the coyotes broke teeth. One coyote had edema around its neck but this was thought to have been due to a puncture from a broken branch. Some coyotes likely experienced bruising around the neck but this could not have been quantified without a necropsy. Aggressive coyotes tended ($P = 0.09$) to have more cuts than non-aggressive animals (Fig. 2-2b). Agression and cuts were not related to gender (Fisher's exact test, $P > 0.05$). Finally, individual responses of snared coyotes to approach from the researcher varied from highly mobile and vocal to catatonic so I was unable to detect a significant association ($P > 0.05$) between the presence or absence of the diazepam tab on the snare and aggression.

Non-target species

The capture of non-target animals was a serious welfare concern. Four non-target animals were captured: two dogs (*Canis familiaris*), one bison cow, and one human

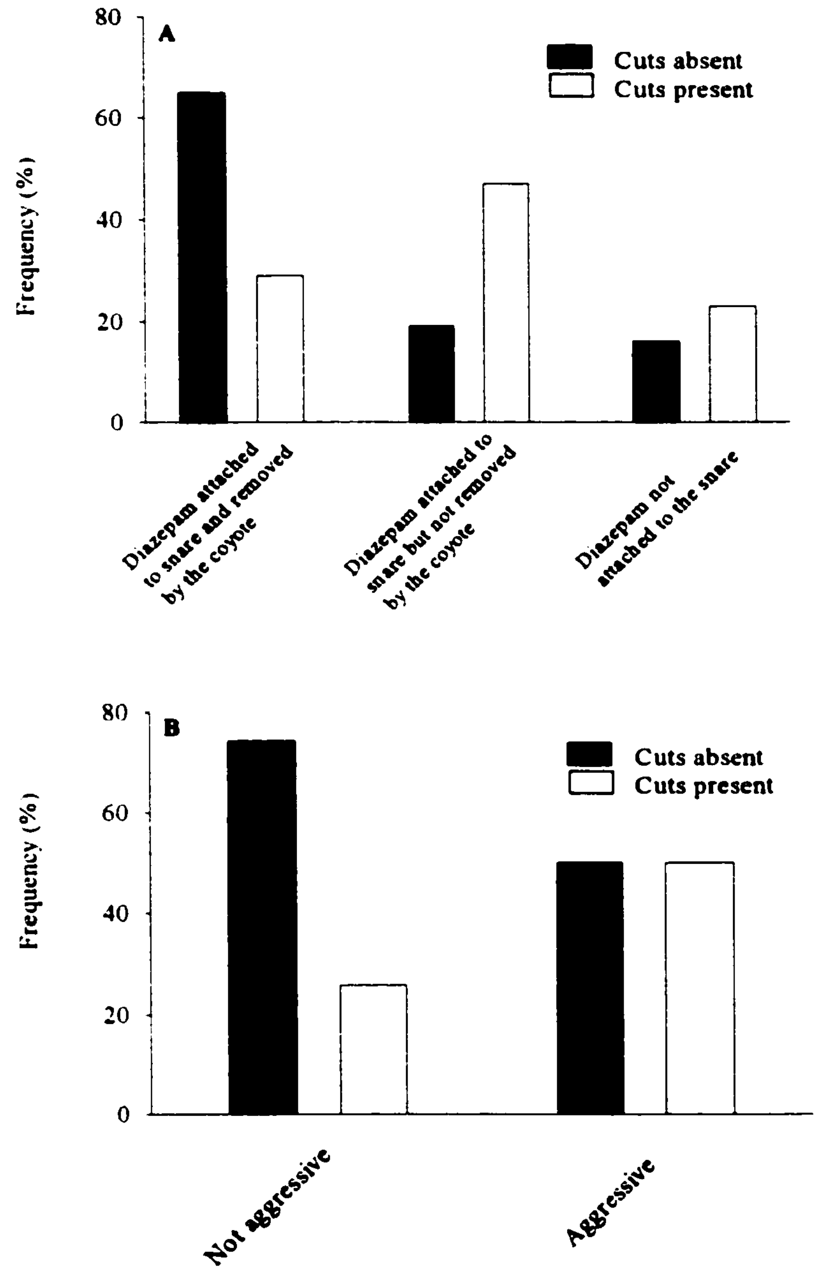

Fig 2-2 Comparison of percent of coyotes with and without cuts: (A) where the diazepam tab was removed and/or ingested by the coyote, where the diazepam tab was attached and remained following capture, and when the diazepam tab was not attached; (B) of aggressive and non-aggressive animals.

(*Homo sapiens*); the latter two caught around the leg. All non-target animals were unhurt. The modified snare was highly specific for capturing coyotes with a non-target species/target species ratio of 7% or 5.5% excluding the human (Table 2-2). Two additional snares were missing and may have been dragged off by bison or destroyed by park visitors. I modified the snares in three ways to increase the selectivity for coyotes. First, I increased the gauge and modified the attachment of the anchor wire to the snare. This increased the strength and stability of the snare unit and also eliminated the need for fragile support wires (Nellis 1968, Baker and Dwyer 1987). This resulted in one less component of the snare that could fail or alter its placement over the trail. Second, I placed obstacles (e.g., branches) over the snare unit to encourage ungulates to go over or around the snare. Third, I incorporated a snare lock that was set at 27 cm to eliminate leg capture of deer, elk, and moose and reduce leg capture of bison.

Table 2-2 Comparisons of capture rate (coyotes/1000 trap nights), capture mortality, and selectivity (non-target animals/coyote) of neck snares, foot snares, and leghold traps.

Location	Trapping Device	Capture rate	Capture mortality	Selectivity	Source
Alberta	necksnare	5.4 (Nov.-Apr.)	< 2%	0.06/1	Pruss (this study)
Texas	necksnare (Collarum 98)	N/A[a]	0%	0/1	Shivik et al. 2000
	necksnare (Collarum 99)	N/A[a]	3%	0/1	
Montana N. and S. Dakota	necksnare (DWRC)	N/A[a] (all year)	N/A	0.35/1[b]	Phillips 1996
	necksnare (Gregerson)	N/A[a]	N/A	0.25/1[c]	
	necksnare (Kelly)	N/A[a]	N/A	0.13/1[c]	
Texas	necksnare	3.2 (Jan.-July)	N/A	0.5/predator	Guthery& Beasom 1978
Alberta	necksnare	4.1 (winter) 1.1 (summer) 9.3 (fall)	16% (no swivel)	N/A	Nellis 1968
Texas	footsnare (Belisle)	N/A[a]	0%	0.2/1	Shivik et al. 2000
	footsnare (WS)	N/A[a]	0%	0.3/1	
Alberta	leghold (unpadded)	4.8	0%	0.72/1[d]	Skinner& Todd 1990
	leghold (padded)	3.8	0%		Onderka et al. 1990
	footsnare (Novak)	1.5	0%		
	footsnare (Freemont)	1.5	0%		
Texas	leghold (unpadded)	2.7 (Feb.-June)	N/A	1.3/predator	Beasom 1974
Colorado, New Mexico and Wyoming	leghold (unpadded)	3.9	N/A	1.4/1	Robinson 1943

[a] Percentage successfully held in snare = no. of coyotes held in snare/no. coyotes held plus those that escaped × 100. Necksnares: Collarum 98= 39%, 99=41%, DWRC=89%, Gregerson=87%, Kelly=97%; Legsnares: Belisle=78%, WS=66%.

[b] total deer and cattle (including escapes)/total coyote captures (including escapes)

[c] total deer (including escapes)/total coyote captures (including escapes)

[d] overall average for four devices

DISCUSSION

Modifications to conventional snares were relatively simple and included: 1) switching to a larger diameter snare cable and removing all sharp edges from the snare by clipping and filing all protrusions; 2) attachment of a 40 mg diazepam tab; 3) and firmly attaching a thicker anchor wire to the snare swivel. This revised design combined with careful site choice resulted in only 4% (2/51) of the coyotes snared improperly and is similar to the 11% reported by Phillips (1996) but is ten-fold lower than that reported by Guthery and Beasom (1978).

Capture efficiency and mortality

In contrast with other techniques such as leg holds, foot snares, box traps, and net gunning, neck snares are used relatively infrequently in live-trapping. Although lethal neck snares are widely used in animal control and commercial fur programs, neither capture efficiency and selectivity (Phillips 1996) nor humane aspects of this technique are well understood. Winter capture efficiency using locking neck snares (5.4/1000 trap nights [TN]) was comparable to other studies (Table 2-2) suggesting that this technique overcame seasonal restrictions for live trapping in EINP without compromising the effort required to capture coyotes. Variation in capture efficiency may be influenced by a variety of factors (Pawlina and Proulx 1999) including the number and choice of appropriate sites to set snares and snow pack conditions. For example, capture efficiency in 1994 was 10 times higher than 1997 and coincided with deep and relatively soft snow compared to 1997 when a hard crust capable of supporting coyotes formed relatively early in the season. Thus, snow conditions may affect capture efficiency by altering the rate at which coyotes use trails and encounter snares.

With the exception of summer, neck snare capture efficiencies are comparable to leg holds but typically higher than foot snares (Table 2-2). Capture efficiency for non-padded legholds, padded leg holds, and foot snares is relatively well documented for a variety of species (*e.g.*, Andelt 1980, Skinner and Todd 1990, Mowat *et al.* 1994, Logan *et al.* 1999). Concern for humane capture has prompted a refinement of these techniques (*e.g.* Skinner and Todd 1990, Mowat *et al.* 1994, Andelt *et al.* 1999) but capture efficiency, rather than humane considerations, continues to be the overriding criteria for trap selection by commercial trappers. For example, more humane padded foothold traps have been commercially available since 1984, but as of 1992 they comprised only 3% of footholds in use in the U.S.A. (Andelt *et al.* 1999). Initially, padded leghold models had lower capture efficiency than padded traps and may explain the lower rates of acceptance by trappers (Linscombe and Wright 1988). Although foot snare capture efficiencies for coyotes tend to be lower (1.5 per 1000 TN) (Skinner and Todd 1990), newer models of padded traps are as efficient as the unpadded traps for capture of coyotes (Skinner and Todd 1990: 3.8/1000 TN and 4.8/1000 TN padded and unpadded respectively).

Capture mortality that occurs while the animal is in the snare can be distinguished from post-release mortality resulting from snaring injury or stress. For coyotes captured in neck snares, capture mortality typically results from strangulation from hanging, hyper- or hypothermia from being snared in an exposed location, or trauma associated with a non-neck capture. With neck snares, capture-related mortality and improper catches (*i.e.*

not around the neck) may be more strongly affected by trapper ability and snare site choice (Guthery and Beasom 1978) than foot or leg restraint techniques.

Effectiveness of diazepam

Initial studies evaluating the utility of diazepam in trapping used doses exceeding 1000 mg and resulted in ataxia (loss or lack of muscular coordination), excessive salivation and incontinence for 2-3 d after ingestion (Nellis 1968). My goal was to reduce stress and struggling by inducing a mild sedative effect while maintaining the animal's ability to behaviorally thermoregulate. Initial dosages of 20 mg per tab were subsequently increased to 40 mg by the second winter to achieve an appropriate sedative effect. This decision was made after observing that the chewed tab was not always completely removed and /or ingested, thus I concluded that an increased dose was necessary especially in cases of partial ingestion. This dosage may have still been too low because full ingestion up to 400 mg of diazepam is still well within the safety range for a canid of coyote size and would produce more effective sedation without inducing compromising ataxia (D. H. Neil and T. F. Bayans, Veterinarians, University of Alberta, personal communication).

While not quantified, subjective observations of the behavioral responses of snared coyotes varied widely both in terms of response to approach by the researcher and site disturbance. When diazepam was ingested, coyotes tended to disturb the site less and tended to chew the surrounding vegetation rather than the snare cable. This propensity conceivably explains the decreased incidence of oral damage. Ingestion by wolves of tranquilizers fixed on legholds resulted in the reduction in the number and severity of limb injuries (Sahr and Knowlton 2000). The lack of aggressive behaviors may not always be a reliable indicator of stress because the absence of aggression can occur when animals are not stressed (*i.e.*, low stress level) or experience extremely high levels of stress (*i.e.*, catatonia). Thus, interpreting the lack of a significant relationship between aggression and the consumption of the diazepam tab is equivocal. Alternatively, the result may have arisen from low sample sizes that may have reduced statistical power of these analyses.

Capture injury rates

Lacerations were the most frequent injury from the modified neck snare. Results from neck snaring of coyotes in EINP showed that the use of diazepam is a promising technique to reduce oral and/or facial cuts, the main (14 of 17) snaring injury. Of these incidents, only one cut involved laceration of subcutaneous muscle and subsequent radio tracking of this individual showed that she survived for 9 months following capture. In fact, with the exception of 2 coyotes that were trapped for fur within 2 weeks of radio-collaring, all coyotes captured using the modified neck snare lived for a minimum of two months following capture. High post-release survival likely resulted from good snare setting protocols, combined with post-snaring procedures that included prevention of hypothermia, cleaning and, if necessary, stitching of lacerations, administering antibiotics and ivermectin, and the practice of leaving a food source (1-2 kg of frozen carrion) near the recovering animal. In addition, frequent (every 12 – 24 hours) checking of snares for captures may have reduced stress and injury by limiting periods that captured animals were held in snares. Lastly, use of the modified neck snare overcomes the problems of appendage injuries (Van Ballenberghe 1984, Kuehn *et al.* 1986, Linhart *et al.* 1986, Olsen *et al.* 1988). Fractures, partial or complete amputation, and maceration of subcutaneous tissues are often associated with foot-hold traps (Kreeger *et al.* 1990, Onderka *et al.* 1990, Phillips *et al.* 1996, Hubert *et al.* 1997). Cold temperatures can also increase the occurrence of frozen appendages in these devices (Onderka *et al.* 1990) that can result in loss of limbs and perhaps reduce a predator's survival.

Non-target species

Trap selectivity is influenced by a variety of factors (*i.e.* trap design, bait type, site location, season and the knowledge-level of the trapper) (Turkowski *et al.* 1984, Novak 1987, Andelt *et al.* 1999). In a review of trap research for a variety of furbearers, Novak (1987) reported selectivity rates (ratio of non-target animals captured to target animals captured) ranging from 0 to 18.1. In many instances, capture of non-target animals resulted in either serious injury or death (Novak 1987, Phillips 1996). In a notable effort to increase selectivity, Phillips (1996) compared three lethal neck snares for coyotes designed to break when a threshold amount of force was applied to the snare lock so that larger non-target animals could escape. While 100% of cattle captured in the snares escaped, 52% of the captured deer died in the snares and the majority of those that escaped were probably caught by the leg.

Use of the modified neck snare to capture coyotes in EINP resulted in only 5.5% non-target captures despite very high ungulate densities (Blyth and Hudson 1987). This is amongst the lowest non-target ratio recorded by Novak (1987) and none of the non-target animals were injured. This low ratio arises, in part, from placement of branches over the snare to encourage ungulates to go around or over the snare set, and the increased stability of the modified snare, which allowed the bottom of the snare loop to remain at 20-26 cm above the trail despite the weight of snowfall or freezing rain, or movement by wind. This also allowed smaller non-target species to use trails without coming into contact with the snare loop. More importantly, the snare stop set at 27 cm effectively allows small mammals and ungulates caught by the legs (with the exception of adult bison) to escape.

I demonstrated that modified neck snares with diazepam tabs reduced the incidence of oral and facial injuries experienced by captured coyotes possibly by decreasing stress and aggression. These modified snares offer a humane, safe, live-capture method with reduced mortality risk for coyotes that can be used during winter months in forested areas without compromising capture efficiency or increasing capture of non-target species.

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CHAPTER THREE

SURVIVAL AND EFFECTS OF SOCIAL AFFILIATION ON HOME RANGE CHARACTERISTICS OF COYOTES (*Canis latrans*)

INTRODUCTION

Canids display a striking degree of intraspecific variation in foraging behaviours, life history characteristics, and social organisation on a population, seasonal, and annual basis (Moehlman 1989). Social organization of carnivores can be strongly affected by the spatial distribution, acquisition, and defence of food resources (Bekoff and Wells 1980, Macdonald 1983, Bekoff and Wells 1986), with the spatial dispersion and richness of these resources determining group and territory size (Macdonald 1983). The adaptive value of belonging to a social group has been documented for many species, particularly in terms of resource exploitation and predator avoidance (Geist 1974, Messier and Barrette 1982, Bekoff and Wells 1986, Creel 1996).

Differences in canid social organization and the use of space are, in part, species-specific adaptations to differences in food resources (*i.e.*, size; temporal, and spatial availability), particularly in species that display a highly flexible social structure (Bekoff and Wells 1986, Moehlman 1989, Gompper and Wayne 1996). For example, when food resources are clumped (*i.e.* heterogeneously distributed) and defendable, coyotes (*Canis latrans*) (Camenzind 1978, Bekoff and Wells 1982) and golden jackals (*Canis aureus*) (Macdonald 1979) form groups, even if the exploitation of these resources does not require a group foraging effort (Bekoff and Wells 1986). Conversely, when food abundance is low and widely distributed, conspecifics tend to be organized into solitary individuals or mated pairs (Bekoff and Wells 1982). The resulting classification of home-range sizes according to social grouping indicates that individuals that belong to packs have the smallest, least variable home ranges (Bekoff and Wells 1980, Kitchen *et al.* 2000a). Messier and Barrette (1982) suggest that the greatest variation in home ranges is exhibited by solitary coyotes with large, shifting "living areas". Paired coyotes exhibit a higher degree of home range stability than solitaires but home ranges per individual were bigger than those of pack members.

Elk Island National Park (EINP), a small (196 km^2) remnant of aspen parkland, provides a unique opportunity to examine survival and home range characteristics of coyotes in an ecosystem that has one of the highest ungulate densities in North America (Blyth and Hudson 1987). Coyotes could utilise the high abundance and biomass of ungulates either through capture of live animals or by consuming ungulate carrion. Coyotes in EINP are thought to be at the northern periphery of their historical range and are the largest remaining predator in this fenced system (Blyth and Hudson 1987). EINP provides abundant ungulate food resources that include plains bison (*Bos bison bison*) and wood bison (*B. b. athabascae*), wapiti (*Cervus elaphus canadensis*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). EINP also provides a level of protection from human induced mortality, compared to the intensive harvesting of coyotes in the surrounding agricultural and public lands. This remnant of aspen parkland with an intact ungulate guild within the historical range of the coyote without the major competing carnivores provides a unique opportunity to examine the adaptations of coyotes within this system.

In the present study, I sought to determine how survival rates and home range are related to a number of ecological factors. Specifically, I tested the hypotheses that: 1) mean annual coyote survival in EINP is unaffected by gender, and using separate analyses, 2) coyote home range, core area, and perimeter size are unaffected by social organisation (*i.e.*, solitary coyotes compared to those belonging to pairs or packs), gender and the interaction of these factors and; 3) coyote home range, core area, and perimeter are unaffected by social organisation, time of day (day or night), and season (summer or winter). I also a) determined causes of mortality of radio-collared coyotes and; b) tested the relationships between: i) coyote survival and pelt price; ii) coyote survival of collared coyotes and total coyote trapping harvest in Alberta and; iii) annual sales of Alberta coyote pelts with pelt price to understand potential factors affecting coyote survival. To understand the survival rates of coyotes in EINP in a North American context, I compared them with published accounts.

MATERIALS AND METHODS

Study area

Elk Island National Park is situated 40 kilometres east of Edmonton, Alberta, Canada, and is surrounded primarily by agricultural lands, acreages, and a Provincial recreation area that includes grazing leases and traplines. EINP is divided by a four lane highway into a 136 km^2 "Main Park" area located north of Highway 16 and a smaller southern 59 km^2 "Isolation" area (Blyth and Hudson 1987). Both areas of the park are completely fenced with 2.2 m mesh wire while the main park is further bisected by an unfenced highway that travels north and south.

Elk Island is situated within the aspen parkland zone that is bounded by prairie to the south and boreal forest to the north. The area around EINP, known as the Beaver Hills, is described as knob and kettle topography that resulted from differential melt of buried remnants of glacial ice (Jennings 1984). Although it is an undulating terrain, slopes of elevated areas average 3.5% and are typically no longer than 30 m (Blyth and Hudson 1987). The greatest elevational difference in the park is only 45.8 m (754.4 – 708.6 m) and occurs over a distance of about 6 km (Blyth and Hudson 1987). This topography also supports numerous wetlands and small lakes as well as several large, shallow lakes.

Vegetation in the park is dominated by trembling aspen (*Populus tremuloides)* and balsam popular (*Populus balsamifera*) that comprise approximately 70% of vegetated areas of the park. Remaining forest stands include white birch (*Betula papyrifera),* Alaska white birch *(Betula neoalaskana),* white spruce (*Picea glauca),* black spruce (*Picea mariana)* and tamarack (*Larix larricina).* Common shrubs and herbs include hazel *(Corylus cornnuta*), prickly rose (*Rosa acicularis),* willow (*Salix spp),* sedges (*Carex spp.*) and grasses (Gramineae family).

The climate for this region is typical of northern mid-latitude continental with associated variations in daily and seasonal temperatures. Mean minimum temperatures of -20° C typically occur in January while mean maximum temperatures of about +23°C occur in July with 487mm average annual precipitation (Blyth 1995). During the study period, May – October mean daily maximum air temperatures ranged from 11-23^{0}C and November – April mean daily minimum between $^-$2 to $^-$20^{0}C.

With the exception of the coyote, lynx (*Felis lynx*), and red fox (*Vulpes vulpes*), most of the larger carnivores historically present such as grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), wolf (*Canis lupus*), cougar (*Felis concolor*), and wolverine (*Gulo gulo*) have been extirpated from Elk Island National Park. In EINP, lynx and red fox sightings are uncommon and reports of transient wolf, black bear, or cougar are rare. Although currently the coyote is the numerically dominant and largest resident carnivore in EINP, it has been speculated that this area was historically at the northern periphery of its range and that extirpation of wolves and human alteration of the environment has facilitated the subsequent expansion of the coyote's range (Gipson 1978, Blyth and Hudson 1987).

While high densities of large ungulates reside in EINP, elk and bison are intensively managed and consequently numerical abundance for ungulates in EINP is calculated before and after management. Blyth (1995) used Park records from 1906 - 1993, to estimate mean total ungulate (*i.e.* bison, elk, moose, and white-tailed deer) numbers for the main and isolation park areas as follows: Main 1725 ± 128 (before management) and 1497 ± 114 (after); Isolation 517 ± 62 (before) and 470 ± 55 (after). Total ungulate biomass density estimates ranged from 52.9-91.5kg/ha (Blyth 1995). Between 1994-2000, EINP supported 3028 ± 421 (mean annual number ± 1SD) ungulates (Cool 2000, Kaye 2000), equivalent to a density of 15.4 ungulates per km^2.

Coyote capture and radiotelemetry

Estimates of coyote survival, home range areas, cores and perimeters were based on winter live-capture and radio-collaring of 41 coyotes. Coyotes were captured using a modified neck snare described previously (Chapter 2). Briefly, neck snares with a cable diameter of 3.2mm (1/8 in) were fitted with a Cam-Loc^{TM} with the lock stop set at 27 cm and attached to a 4-5 m length of nine-gauge (4 mm) wire that was looped twice through the snare swivel and twisted upon itself to form a doubled anchor wire. The design was sufficiently robust that it did not require additional support wires. The snare was subsequently modified by attaching a diazepam tab (Chapter 2). Snaring was conducted during the winters of 1994-1997 and snares were checked twice (*i.e.* dawn and dusk) per 24-hour period. A maximum of 30 snares were set at any one time during 1994 and 24 snares for the following years.

Captured coyotes were immobilised with Telazol® (tiletamine HCL and zolazepan HCL) and placed on a plastic covered foam pad (1m x 0.5m x 0.1m), covered with blankets, and examined for injuries. Coyotes were weighed, measured and assessed for age by visually analysing tooth wear and development. Cuts were the only type of injury that resulted from snaring and were sutured if required (Chapter 2). Ear tags and radio collars (Telonics, USA and Lotek, Canada) were fitted and all captured coyotes were given antibiotics and ivermectin (anthelminthic) prior to release. Although ear tags were attached for the first three winters, they proved to be of little use for field identification and their use was discontinued. Coyotes in recovery were placed in a secluded, sheltered location and left on a 10-cm thick foam pad with their head and body covered with blankets to prevent hypothermia.

Forty coyotes were fitted with very high frequency (VHF) mortality-sensitive colour coded radio transmitters (Telonics Inc., USA and Lotek Engineering Inc., Ontario. Canada). Collars also included an identification plate that provided a contact phone number and address. Inclusion of this information combined with a reward increased the chance of obtaining mortality information when coyotes were trapped, shot, or hit by cars.

An additional eleven coyotes were fitted with colour collars that had return contact information, but only one was included in the survival analyses. This individual was included because he was shot and returned to me. Typically, identification and tracking of colour collared coyotes was difficult and largely ineffective in contributing to survival estimates.

Human-induced mortality rates outside EINP were investigated by contacting Alberta Fish and Wildlife, local agricultural pest control branches, records from fur harvesters, and the Alberta Ministry of Transportation (*i.e.* road kill data). Assessing numbers of coyotes killed in the Counties surrounding EINP was difficult due to the lack of record keeping for this species. The only source of coyote records was the Alberta Trapper's Association that provided royalty records for the period of 1986 - 2000. These numbers do not take into account road kills, shooting for agricultural or sport reasons, or poisoning.

Survival and causes of mortality

I used the nonparametric Kaplan-Meier survival estimator (Pollock *et al.* 1989) to calculate survival (± 95% confidence intervals) of all radiocollared coyotes and to compare annual and long-term survival estimates for males and females, adults, and juveniles, and among years (1994-2000). The Kaplan-Meier staggered entry design allows for inclusion of animals into survival estimates at any point in time, as well as censoring animals of unknown fates (*i.e.*, animals whose survival status can not be determined because they may have dispersed out of the study area, died without recovery of the collar, carcass, or detection of a mortality signal and/or collars that failed or slipped off the coyote). Assumptions for the survival analyses include: random sampling of age and sex classes; different animals have independent survival times; future survival is not influenced by capture or collaring; previously and newly tagged animals have the same survival function; time of death is known; and finally that the censoring mechanism is random (Pollack *et al.* 1989, Tsai *et al.* 1999).

Causes of coyote mortality were determined either by examining the retrieved carcasses or in the case of human-induced mortality, interviewing the person (*i.e.*, hunter, trapper, or farmer) responsible for the coyote's death. Some coyotes were also placed into an unknown mortality category when the carcasses were too decomposed to determine cause of death. In those cases, death was estimated as the date midway between carcass recovery and the last non-mortality telemetry location. Finally, animals with unknown fates (*i.e.*, dispersal, death without collar or carcass recovery or a mortality signal, collars that failed and/or slipped off the coyote) were censored as well as four animals that were confirmed alive at the endpoint of the survival analyses.

Simple linear regression models were used to test for relationships between 1) coyote survival and previous season's pelt price and 2) coyote survival and total trapping harvest for the same year and 3) total pelts sold annually in Alberta and previous season's pelt price. Previous season's pelt price was used as total numbers and mean annual price for Alberta is typically not widely available until the autumn following winter trapping. In addition, individual survival was related to the percentage of telemetry locations outside of Elk Island National Park and the Blackfoot Recreation area.

Home Range

Radio-collared coyotes were located one to two times per week for the period of May 1994 – December 1997 and bi-weekly thereafter until March 2000 for a total of 3312 locations. Time intervals for telemetry locations were standardised within years. Range roads, township roads and highway 16 outside and between EINP provided year-round access for monitoring. Within the park during the summer the main highway and all service roads provided access for summer monitoring while during winter (November-April) vehicle and foot access was restricted to the main highway and part of Tawayik road due to elk trapping and handling.

Locations were estimated by ground triangulation from compass bearings obtained with a hand held "H" antenna and a Telonics TR2 receiver. Typically, three bearings were used to estimate each location. The error triangle technique (Nams and Boutin 1991) was used in the field to reject locations within triangles that exceeded 500 m on any side. This technique was also used to estimate the coyote's location although the probability of the estimate containing the actual location could not be established (Nams and Boutin 1991). The locational midpoint and area of the triangle were calculated using a program developed specifically for Elk Island National Park by Eric Madsen Programming Ltd. (1994). Procedures to increase accuracy of telemetry locations included using up to 157 geo-referenced universal transverse mercator (UTM) coordinates at landmarks where bearings could be taken. These landmarks were easily identifiable (*i.e.* crossroads, trailheads, bridges, cut lines, fence lines, buildings, or measurable distances from such landmarks) and reduced operator error in determining the UTM from which the compass bearing was taken. If bearings needed to be taken at other points, a handheld Global

Positioning System (GPS) was cross-referenced with a 1:30,000 topographical map. All triangles greater than 0.11 km^2 were eliminated from home range analyses. Accuracy of telemetry locations was investigated with test collars placed at specific locations unknown to the operator. The mean distance between estimated and actual locations was 157 m (Coefficient of Variation = 8%).

Locations gathered through telemetry are typically used to describe home ranges of individual organisms or ranges of populations. The distribution of animal locations throughout a spatial plane has been termed the utilisation distribution (UD) and has become an increasingly popular way of evaluating an animal's use of space (Seaman *et al.* 1999). The UD usually refers to the two dimensional relative frequency distribution of an animal's location over time but can also include the third dimension of the amount of time spent in any given area (Worton 1987, Seaman *et al.* 1999). Both parametric and non-parametric methods of estimating the UD are available. Nonparametric methods, such as the kernel home range estimators used in the present study, have advantages because they make no assumption about the shape of the distribution of the data and can accurately estimate densities (*i.e.* in terms of home range this means an estimate of the amount of time spent in a specified area) of any shape (Seaman and Powell 1996).

Determining the smoothing parameter is an important aspect of implementing a kernel density estimator. Cross validation methods provide approaches to smoothing parameters selection that minimizes the difference between the estimate and true density (Worton 1995). Essentially, the least squares cross validation smoothing parameter is calculated from subsets of each data set to determine the parameter that gives the lowest mean integrated squared error for the density estimate (Seaman and Powell 1996). It allows the home range software program to select the single best bandwidth and the amount of smoothing varies with the structural irregularity of the data set (Seaman and Powell 1996). Computer simulations of real and simulated data, especially when analysing non-normal, multi-modal data suggest that the most accurate kernel estimates with the highest precision resulted from using cross validation and a fixed bandwidth (Worton 1995, Seaman and Powell 1996, Seaman *et al.* 1999).

I used the fixed kernel home range estimator with the least squares cross validation smoothing parameter to estimate the 95 % utilisation distribution (UD) and its perimeter which I will refer to as the home range, and the 50% utilisation distribution and its perimeter which I will refer to as the core area. The 95% UD was chosen as it eliminates most forays or sallies outside of the home range, which, if included, can substantially increase home range estimates (Andelt 1982, Bowen 1982).

Many authors (Reynolds and Laundre 1990, Minta 1992, De Solla *et al.* 1999, Otis and White 1999, Seaman *et al.* 1999) have argued that adequate sample size is more important than independence between points. In particular, Seaman *et al.* (1999) recommend that analyses of home ranges with kernel estimators use a representative minimum sample ≥ 30 locations and preferably ≥ 50. Kernel estimators with larger sample sizes and appropriate smoothing parameters reduce bias and overestimation of the home range size (Seaman *et al.* 1999). For my home range analyses I used data from thirty coyotes that lived and did not disperse for a sufficient amount of time to collect 30 or more telemetry locations (range 30-350). Of these 30 coyotes, 24 had 50 or more telemetry locations.

Coyotes were classified as solitary, members of a pair, or members of a pack. Classification was based on observations combined with areal use. Based on Andelt (1985) coyotes were regarded as together if observed < 100 m apart and if they remained < 100 m apart during subsequent locations (see also Kamler and Gipson 2000). Packs were defined as groupings of adult animals as the parent–pup relationship is an obligate affiliation. Throughout the study, four coyotes changed their social affiliation and as a result 34 coyotes were included in the analysis of social organisation. Ten radio-collared coyotes had insufficient data to include in the analyses due to: dispersal (n=3); slipped radio-collar (n=1); or human induced mortality shortly after collaring (n=6).

Data on the location of coyotes was gathered through telemetry and integrated into a Geographic Information System (ArcView by Esri ™) and overlaid on a UTM map of Elk Island National Park. Individual maps were created for each coyote illustrating complete home ranges and core areas. Where sufficient data were present, maps exhibiting yearly, seasonal, and diurnal/nocturnal home ranges, core areas, and perimeters were also created. The Animal Movement Analysis ARCview Extension (Hooge and Eichenlaub 1997) was then used to analyse the locational point data and calculate a fixed kernel home range utilisation distribution (Worton 1989) for each selected probability (*i.e.* 95% UD and 50%UD). In addition, a polygon shape file for each selected probability, an associated attribute table containing probability and area fields, and the area calculations for each probability were used to create composite and individual home range and core area maps and also provided raw areal data for statistical analyses.

The hypotheses that home range and core areas and perimeters were affected by social organisation (solitaires, pairs, packs), sex (male, female) and the interaction of these factors were tested with a two-factor ANOVA. When the ANOVA model was significant, pairwise comparisons between treatment levels were compared using orthogonal contrasts with Bonferroni's adjusted alphas (Zar 1980).

Preliminary analyses indicated that home range and core areas and perimeters were strongly affected by social organisation. Thus, I tested for differences in home range, core areas, and perimeters observed during the day and night as well as summer and winter separately for social organisation type using paired t-tests. Linear regression was used to test for a relationship between home range area (95% UD) and the percent of telemetry locations outside of EINP.

Prior to analyses, I tested for normality and homogeneity of variances and, where required, data were Log_{10} or Arcsine square root transformed.

RESULTS

Survival and Causes of Mortality

Survival of the 41 collared coyotes, estimated using the Kaplan Meier staggered entry method, indicated that the likelihood of survival decreased throughout the study period (Fig. 3-1). Long-term coyote survival over the 74-month study period was 0.11 (95% C.I. = 0.03 - 0.25) (Fig. 3-1).

Annual (1 Jan.- 31 Dec.) survival probabilities of adult and juvenile coyotes during Feb. 1994 to March 2000 ranged from 0.57 to 0.92 and 0.50 to 0.75 respectively (Table 3-1). For the period when juveniles were collared (1994-1996) adult survival (0.74) was about 10% higher than for juveniles (0.66). Overall combined yearly survival (0.73) was calculated by averaging survival of adults and juveniles (1994-2000) (Table 3-1). When

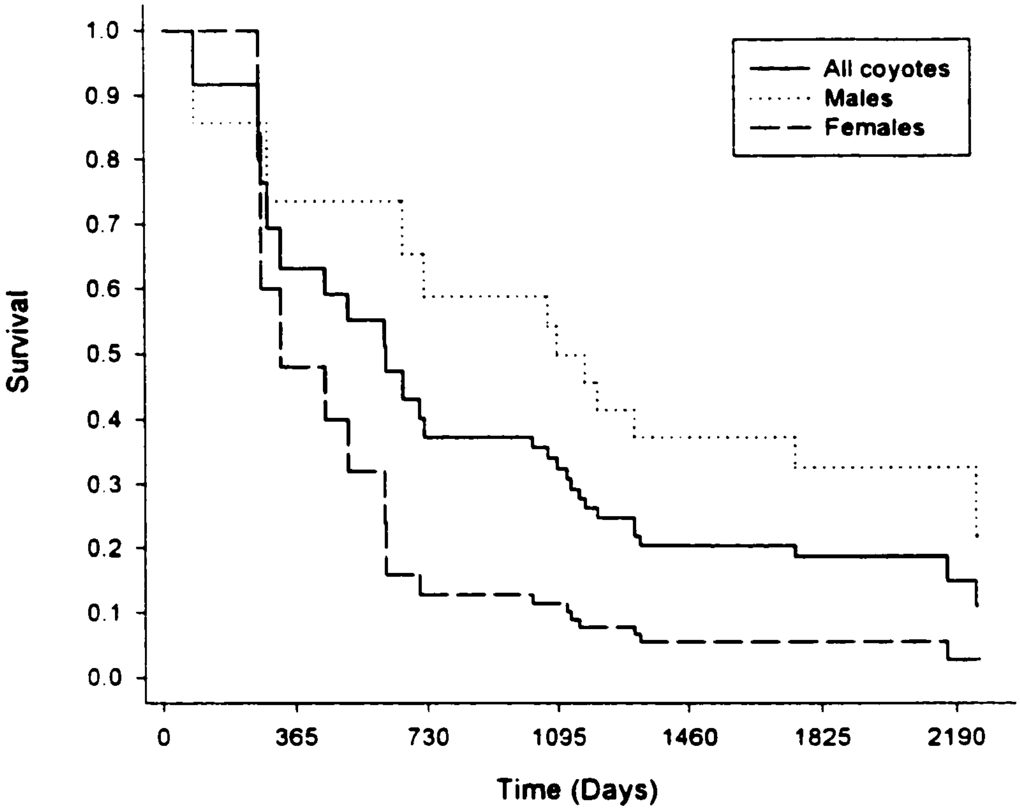

Fig 3-1 Comparative Kaplan-Meier staggered entry survival functions of 41 coyotes captured in Elk Island National Park, Alberta, Canada, for the period of Feb.1994-Mar. 2000.

Table 3-1 Adult, juvenile, and combined survival rates of coyotes from Elk Island National Park, Alberta, 1994-2000.Values in brackets are 95% confidence intervals (C.I.).

Year	Adult Mean	(95% C.I.)	N	Juvenile Mean	(95% C.I.)	N	Combined Mean	(95% C.I.)	N
1994[1]	0.67	(0.29, 0.88)	11	0.60	(0.13, 0.88)	5	0.63	(0.33, 0.83)	16
1995	0.67	(0.34, 0.86)	15	0.75	(0.13, 0.96)	4	0.68	(0.39, 0.85)	19
1996	0.87	(0.58, 0.97)	20	0.50	(0.01, 0.91)	5	0.83	(0.55, 0.94)	25
1997	0.57	(0.35, 0.74)	24	-	- -	-	-	- -	-
1998	0.92	(0.54, 0.99)	14	-	- -	-	-	- -	-
1999-00[2]	0.60	(0.13, 0.88)	11	-	- -	-		- - -	-
Annual Average	0.74	(0.63, 0.82)	-	0.66	(0.31, 0.86)		0.73	(0.62, 0.80)	-

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[1] February 10 – December 31 – overestimation of annual survival

[2] January 01, 1999 – March 31, 2000 - underestimation of annual survival

calculated to include the winter trapping season (1 September – 31 August), coyote survival was more variable and ranged from 0.55-0.92 (Table 3-2).

Comparisons of survival of males and females showed female annual survival (average = 0.61 range 0.33-1.0) was about 20% lower (P>0.05) than that of males (average = 0.80 range 0.63-0.90). In contrast to the relatively minor differences (P>0.05) in annual survival of females and males, differences in sex-specific survival are more pronounced when calculated over the entire study period (Table 3-3). These calculations showed a seven-fold difference. The survival rate is only 3% (*i.e.* study survival = 0.03) for females compared to 22 % for males for the period of 74 months (Fig. 3-1).

Table 3-2 Survival rates of coyotes in Elk Island National Park, Alberta (1994-2000). Data were calculated to include trapping season (1 September – 31 August). Values in brackets are 95% confidence intervals (C.I.).

Trapping Year	**Combined survival** **Mean**	**(95% C.I.)**	**N**
Feb.1994 - Sept 1995[1]	0.55	(0.28, 0.75)	24
September 1995-96	0.68	(0.39, 0.84)	29
September 1996-97	0.66	(0.44, 0.81)	20
September 1997-98	0.81	(0.52, 0.93)	24
September 1998-99	0.92	(0.54, 0.99)	14
Sept.1999- Apr. 2000[2]	0.60	(0.13, 0.88)	11

[1] February 10 – August 31 – underestimation of annual survival

[2] September 01, 1999 – March 31, 2000 - overestimation of annual survival

Table 3-3 Annual and long term survival of male and female coyotes in Elk Island National Park, Alberta, 1994-2000. Values in brackets are 95% confidence intervals (C.I.). Female 1998 C.I. equals 1.0 because all females survived.

Year	Female Mean	(95% C.I.)	N	Male Mean	(95% C.I.)	N
1994[1]	0.48	(0.01, 0.79)	8	0.73	(0.29, 0.93)	8
1995	0.33	(0.05, 0.67)	7	0.89	(0.43, 0.98)	12
1996	0.72	(0.24, 0.93)	11	0.90	(0.47, 0.98)	14
1997	0.49	(0.17, 0.74)	10	0.63	(0.33, 0.82)	14
1998	1.00	(1.00, 1.00)	5	0.87	(0.39, 0.98)	9
1999-00[2]	0.50	(0.01, 0.91)	4	0.67	(0.05, 0.94)	11
Mean annual	0.61	(0.44, 0.75)	-	0.80	(0.66, 0.88)	-
Study Survival	0.03	(0.00, 0.14)	21	0.22	(0.05, 0.47)	20

[1] February 10 – December 31 – overestimation of annual survival

[2] January 01, 1999 – March 31, 2000 - underestimation of annual survival

Sources of mortality were calculated as human induced and unknown. When no confirmation of death was possible, the animals were recorded as having an unknown fate. Of the 26 coyotes whose deaths were confirmed, the majority (77%) of mortalities arose from trapping, snaring, hunting, or collisions with motor vehicles (Table 3-4). Within those categories, 65% of confirmed mortalities resulted from trapping or snaring and shooting (13/20) whereas death resulting from vehicles (7/20) accounted for 35% of the total. In total, only 4 of the 41 collared coyotes in EINP were confirmed alive and remained within or adjacent to EINP at the end of the study period (10 February 1994-31 March 2000).

Annual survival of coyotes in EINP was negatively ($P<0.05$) related to prices paid to trappers for coyote pelts (Fig. 3-2a). This negative relationship between survival of the EINP coyote population coincides with a moderately strong ($P<0.05$, $r^2 = 0.45$) relationship between coyote trapping effort (*i.e.* annual number of pelts sold from Alberta) and pelt prices (Fig. 3-2b). The average number of pelts submitted for sale each year from Alberta was 23,744 (range 10,201 - 35,730 pelts). The moderately weak relationship ($P=0.07$, $r^2 = 0.09$) between coyote survival in EINP and number of Alberta coyote pelts sold (Fig. 3-2c) may reflect the somewhat high and variable proportions of coyotes killed by vehicles, trapped or shot, but not harvested for pelts (Table 3-4).

Table 3-4 Sources of mortality and unknown fate for coyotes within and outside Elk Island National Park, Alberta, March 1994 - March 2000.

Age at capture	N	Human induced mortality (%) Shot	Trap[1]	Road	Unknown death (%)	Unknown fate (%)
Adult (≥1.5 yr)	24	17	17	21	12	33
Juvenile (≤1.5 yr)	13	31	8	15	23	23
Total	37	22	13	19	16	30
Confirmed deaths	26	31	19	27	23	-
Human induced mortality			77			

[1] or snare

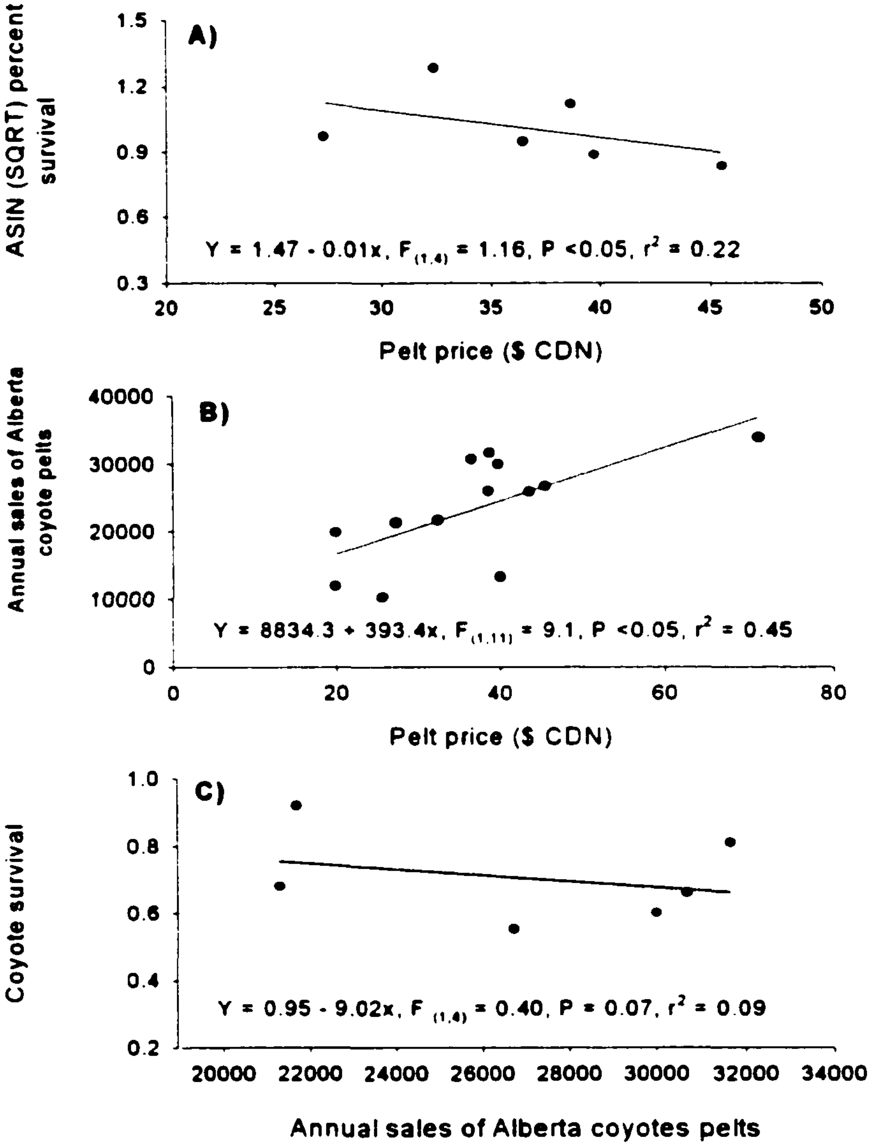

Fig 3-2 Linear regressions of the following: (A) percent survival (asin sqrt) of coyotes in and around Elk Island National Park, Alberta, Canada, with coyote pelt prices in Alberta. (B) number of Alberta coyote pelts sold at public auction with the pelt price. (C) survival of radio-collared coyotes in and around Elk Island National Park with the number of Alberta coyote pelts sold annually.

Lastly, the length of time that coyotes survived following collaring was negatively related to the percent of telemetry locations that identified coyotes as being outside of EINP and/or Blackfoot recreation area (Fig. 3-3). Thus coyotes that spent more time within the relative safety of EINP and to a lesser extent Blackfoot, survived for longer periods of time compared to those that spent a greater proportion of time outside EINP and Blackfoot, although it seems comparatively low for a fully protected park (Table 3-5).

Home Range

Over the course of this study, 18% of radio-collared coyotes were solitary, 26% were members of a pair and 56% belonged to a pack of between three and five members. Two factor analysis of variance tests showed that home range (95% UD) and core (50% UD) areas and perimeters were significantly affected by social organisation ($P<0.001$) but not by sex or the interaction of these terms (Fig. 3-4). Bonferroni adjusted orthogonal contrasts showed that areas occupied by solitaires were significantly greater than that utilised by pairs, which exceeded that occupied by individuals belonging to a pack (Fig. 3-4a). In all other cases, home range and core areas and perimeters occupied by solitaires and pairs exceeded those that formed packs (Fig. 3-4 b-d) which is consistent with other home range studies (Table 3-6).

Paired T-tests for core areas and perimeters used by solitaires, but not by pairs or packs, during the night were significantly greater than those occupied during the day (Fig. 3-5b,d). In contrast, home ranges did not differ significantly between day and night within each social division (Fig. 3-5 a,c). Finally, home ranges, cores, and perimeters did not differ between summer and winter within solitaires, pairs, or packs (Fig. 3-6).

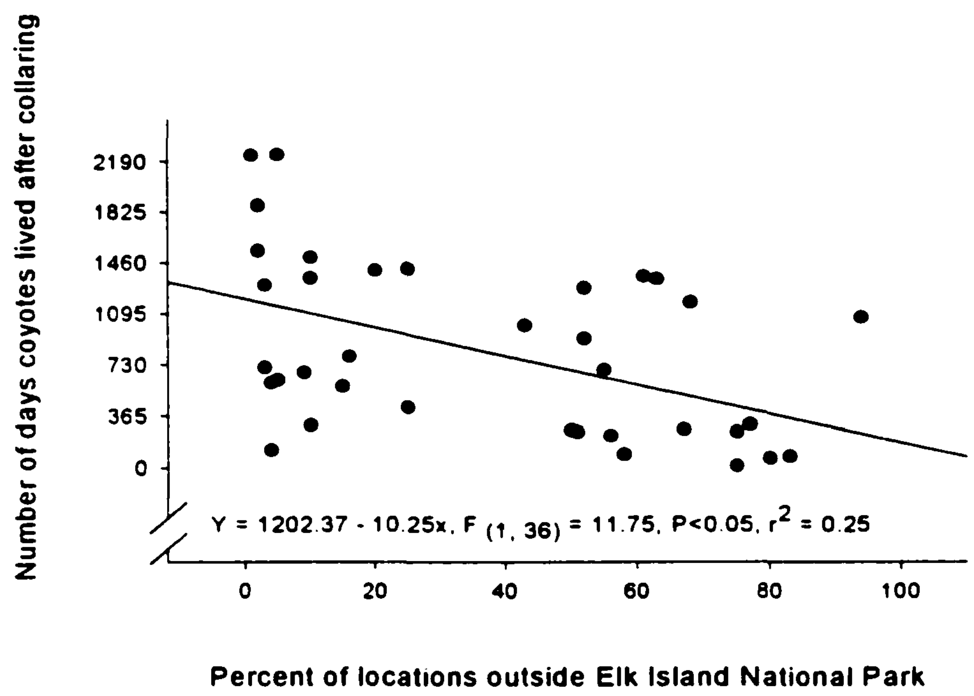

Fig 3-3 Linear regression of number of days coyotes lived with the percent of radio locations outside of Elk Island National Park.

Table 3-5 Comparison of estimates of mean annual coyote survival in North America. R = resident coyotes, T = transient coyotes. – data not published

			Annual survival rate by age class		
Location	**Year**	**Habitat**	**Adult**	**Juvenile**	**Combined**
Texas[1]	1967-69	Grasslands	0.60	-	-
Alberta[2]	1964-68	Grasslands & forest	0.58-0.64	0.29	
Wyoming[3]	1974-76	Forest & grasslands	0.48-0.99	-	-
Iowa[4]	1973-75	Grasslands & forest	0.61	-	-
Alberta[5]	1974-76	Forest & grasslands	-	-	0.55
Northern Utah[6]	1975-78	Shrub desert	0.47	0.23	-
Southern Idaho[6]	1975-78	Shrub desert	0.51	0.45	-
Texas[7]	1974-80	Grasslands	0.70	0.42	-
Alberta[8]	1977-78	Crop & grasslands	-	-	0.38
Southern Texas[9]	1978-79	Grasslands	-	-	0.68
Texas[10]	1976-86	Grasslands	0.69	0.42	-
Colorado[11]	1983-86	Grasslands	0.87	0.52	-
Washington[12]	-	-	0.90	-	-
Kansas[13]	1996-98	Grasslands	-	-	0.85 (R) 0.67 (T)
Alberta[14]	1994-00	Forest & grasslands	0.74	0.66	0.73

[1]Knowlton 1972, [2] Nellis and Keith 1976, [3]Tzilkowski1980, [4]Andrews and Boggess 1978 [5]Bowen 1982, [6]Davison 1980, [7]Windberg *et al.* 1985, [8]Roy and Dorrance 1985, [9]Andelt 1985, [10]Windberg 1995, [11]Gese *et al.* 1989, [12]Crabtree 1988 cited in Windberg 1995, [13]Kamler and Gipson 2000, [14]This study.

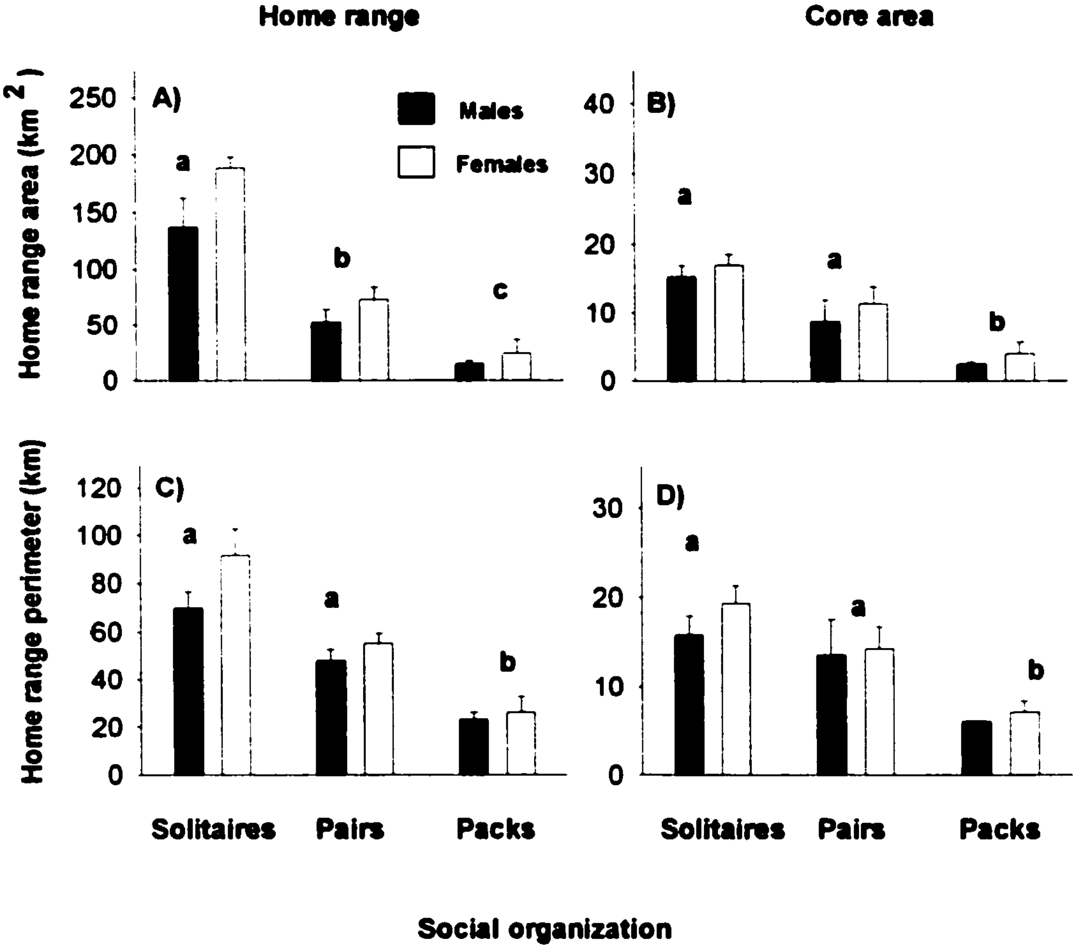

Fig 3-4 Effects of gender and social organisation on mean (± 1 SE) home range area and perimeter for coyotes in Elk Island National Park, Alberta, Canada. Data are shown for both overall home range (i.e. 95% utilisation distributions) and core areas (i.e. 50% utilisation distributions). Letters adjacent to histograms indicate pairwise comparisons for the significant effects of social organisation on home ranges. Histograms sharing the same letter are not significantly different.

Table 3-6 Comparisons of coyote home range sizes (km^2). N/A = not available.

Location	Habitat type	Males Mean	N	Females Mean	N	Sexes Combined Mean	N	Social Organisation
Alaska [1a]	Primarily forest	104.0	3	70.2	6	-	-	N/A
Alberta [2a]	Forest & grasslands	14.4	9	11	13.3	-	-	combined
Alberta [3a]	Crop & grasslands	-	-	-	-	12.1	12	residents
Alberta [4b]	Grasslands	-	-	-	-	90.9	10	N/A
Alberta [5c]	Forest & townsite	22.5	4	24.4	4	-	-	residents
Alberta [6b]	Forest & grasslands	136.9	3	188.5	3	-	-	solitaires
		51.8	4	72.5	5	-	-	pairs
		15.0	13	24.4	6	-	-	packs
California [7a]	Grassland & forest	-	-	-	-	4.6	8	breeders
Colorado [8a]	Grasslands	-	-	-	-	11.3	56	residents
		-	-	-	-	106.5	16	transients
Georgia [9a]	Agricultural & forest	6.9	7	15.6	5	-	-	N/A
Idaho [10d]	Desert grasslands	16.1	3	19.0	2	-	-	N/A
Mexico [4b]	Grasslands	-	-	-	-	90.1	7	N/A
Texas [11a]	Grasslands	4.7	19	4.3	15	-	-	residents
Texas [10d]	Desert grasslands	2.2	2	8.9	7	-	-	N/A
Texas [12c]	Grasslands	N/A	-	2.4	33	-	-	territorial
	Grasslands	-	-	12.4	12	-	-	transient
Vermont [13a]	Agriculture & forest	19.6	3	17.6	3	-	-	breeder
	Agriculture & forest	15.8	4	22.2	1	-	-	associate
	Agriculture & forest	9.2	2	12.4	1	-	-	juvenile
	Agriculture & forest	N/A	-	313.8	-	-	-	transient
Wyoming [14f]	Grassland & forest	-	-	-	-	2.22	18	packs
Kansas [15a]	Grasslands	-	-	-	-	4.1	7	residents
						49.3	6	transients
Quebec [16a]	Forest -	-	-	-	89*	14	N/A	
	Forest -	-	-	-	-	111*	14	N/A
	Forest -	-	-	-	-	27'	10	N/A
	Forest -	-	-	-	-	48'	10	N/A

Source: [1] Thurber *et al.* 1992, [2] Bowen 1982, [3] Roy and Dorrance 1985, [4] Moehrenschalger pers.comm.. 2000, [5] Gibeau 1993, [6] This study, [7] Sacks *et al.* 1999, [8] Gese *et al.* 1988, [9] Holzman *et al.* 1992, [10] Harris 1983, [11] Andelt 1985, [12] Windberg and Knowlton, [13] Person and Hirth 1991, [14] Allen *et al.* 1999, [15] Kamler and Gipson 2000, [16] Crete *et al.* 2001.

Method of deriving home range: [a] Minimum convex polygon, [b] Fixed kernel, [c] Harmonic mean, [d] Grid cell, [e] Adaptive kernel, [f] Scent mark polygons

*+ The same groups of forest (*) and rural (+) coyotes: home range estimated for trapping season (18 October-1 March) and the rest of the year, respectively.

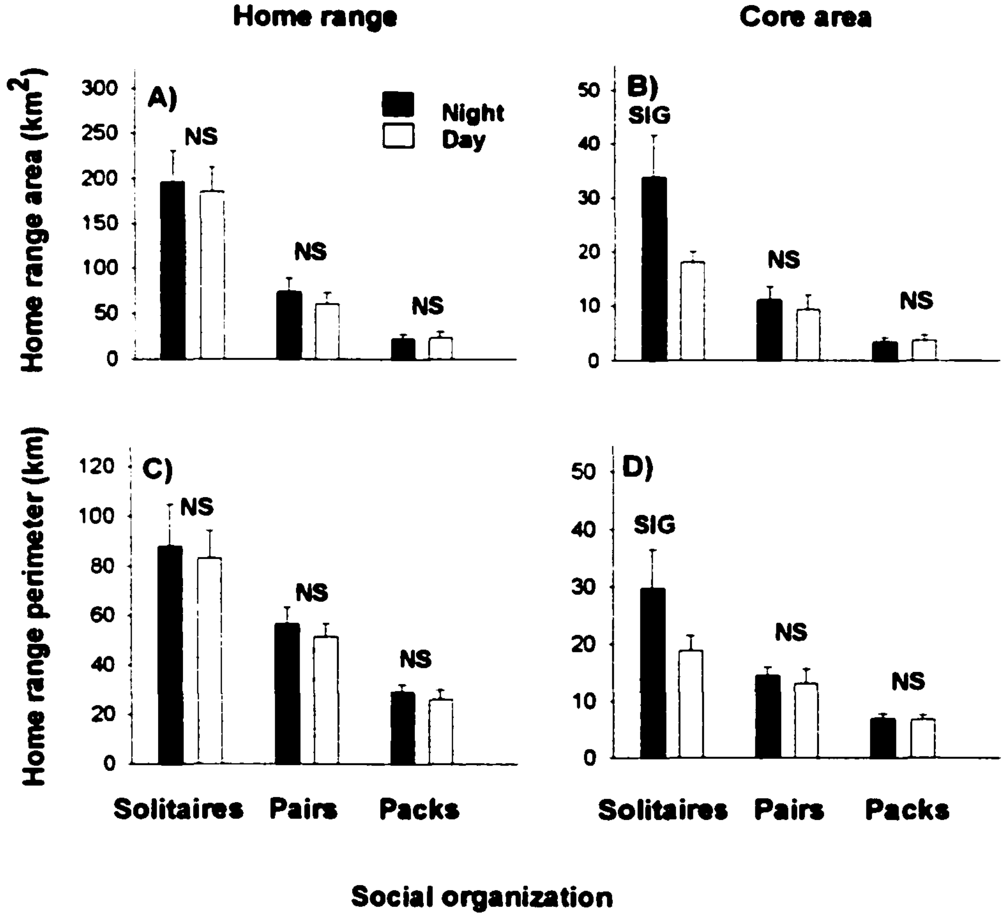

Fig 3-5 Comparison of mean (± 1 SE) home range areas and perimeters of coyotes in Elk Island national Park, Alberta, Canada occupied at night compared with daytime hours. NS= not significant (P> 0.05). Statistical comparisons are based on separate paired t-tests for solitaires, pairs, and packs. Data are shown for home range (95% utilisation distribution) and core areas (50% utilisation distributions).

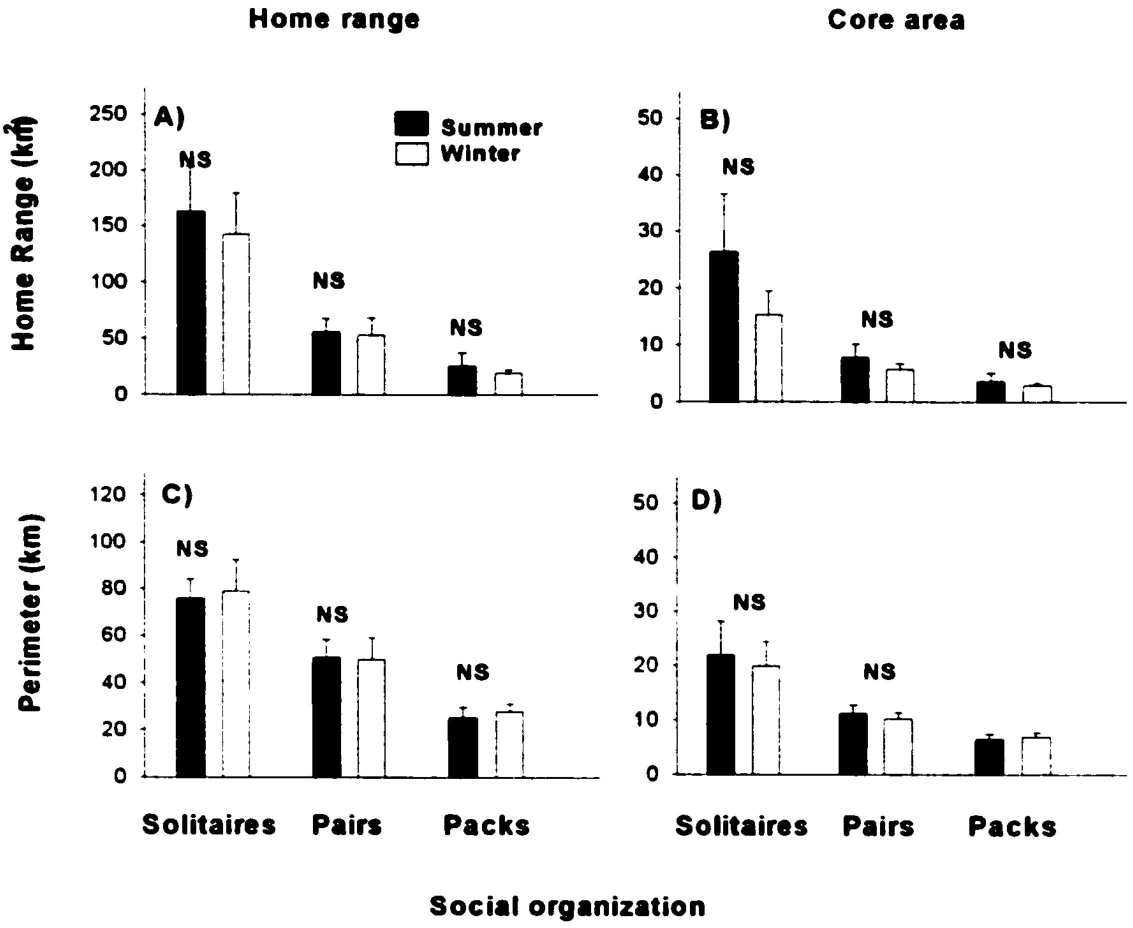

Fig 3-6 Comparisons of mean (± 1 SE) home range areas and perimeters of coyotes in Elk Island National Park, Alberta, Canada during summer and winter. NS= not significant ($P > 0.05$). Statistical comparisons are based on separate paired t-tests for solitaires, pairs, and packs. Data are shown for home range (95% utilisation distribution) and core areas (50% utilisation distributions).

Linear regression showed that home range size (95% UD) was positively ($P<0.05$) related to the percentage of coyote telemetry locations outside of EINP (Fig. 3-7). Lastly, core areas for radio-collared members of neighbouring packs were a single discrete area per animal, stable through time, contiguous and minimally or non-overlapping (Fig. 3-8).

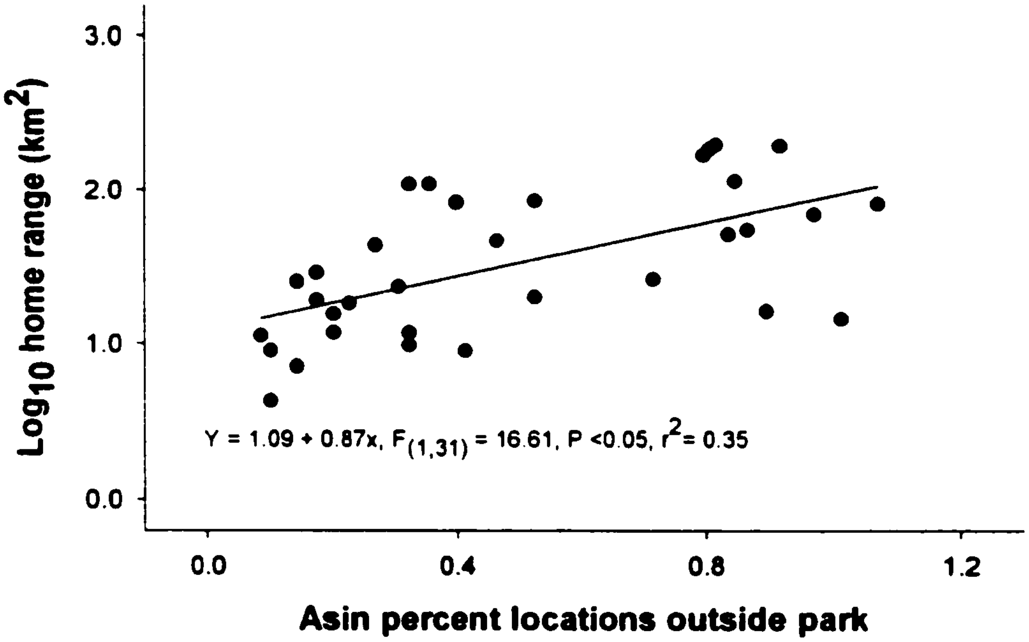

Fig 3-7 Linear regression of home range area (95% utilisation distribution $\log_{10}$ transformed) with percent of home range locations (asin transformed) outside of Elk Island National Park, Alberta, Canada.

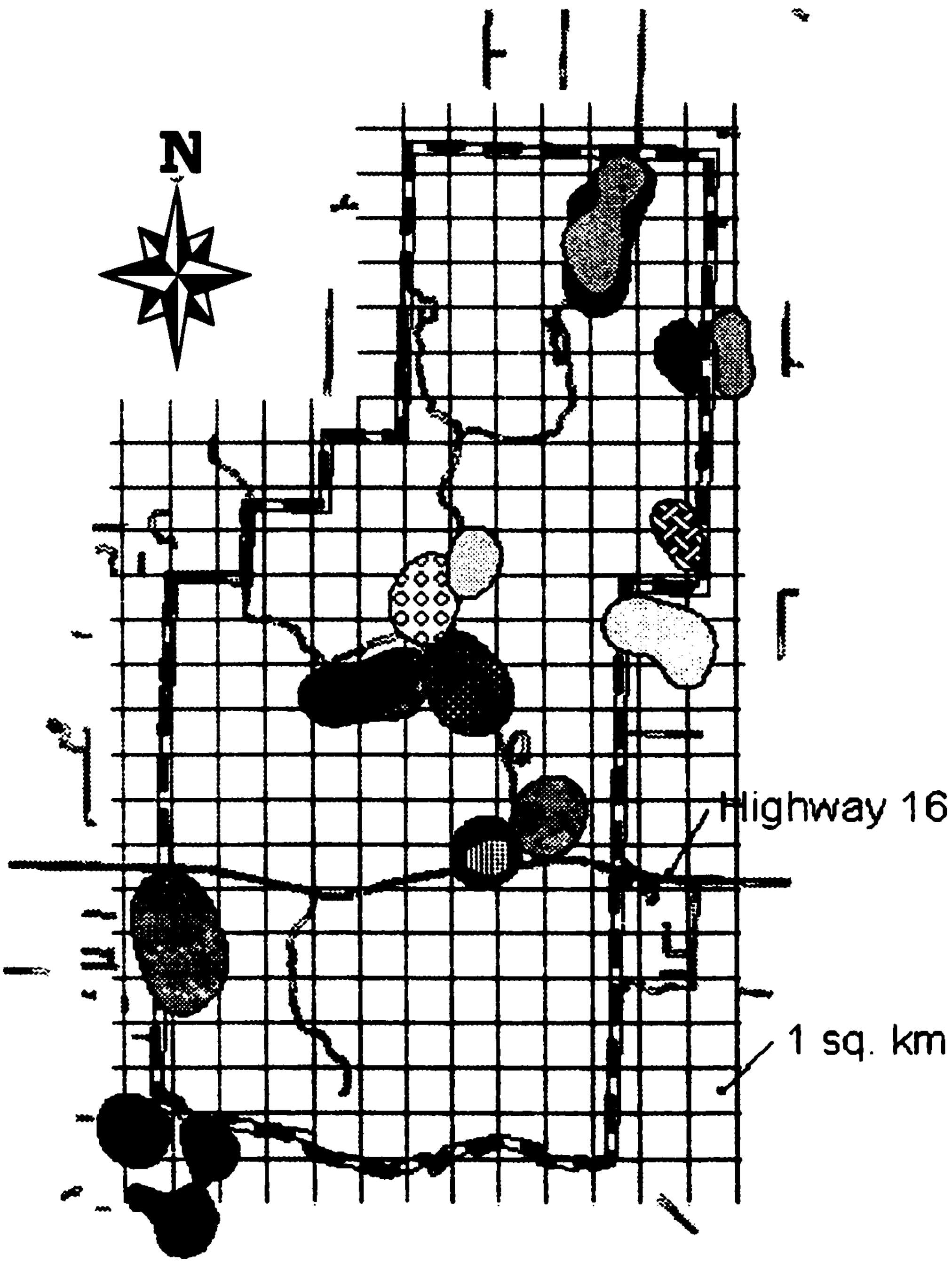

Fig 3-8 An example of contiguous non or minimally overlapping core areas (fixed kernal 50% utilisation distribution) of neighbouring coyote packs in Elk Island National Park, Alberta, Canada. Data have been combined for 1994-1999. Overlaid core areas belong to members of the same pack. Although years are combined, contiguous core areas are for animals alive at the same time.

DISCUSSION

Coyotes in EINP exist at the northern limit of their historical range in a protected remnant of aspen parkland with an intact ungulate guild. In the absence of historically major competing carnivores such as bears, wolverines, and wolves, coyotes remain as the largest predator in the system. However, intense exploitation continues in areas surrounding EINP. Adaptation to these atypical circumstances and food resources within EINP should result in some differences in coyote ecology compared to other studies particularly in terms of survival social and spatial organisation and diet (see Chapter 4 for diet).

Survival and mortality

Annual survival of coyotes in EINP was moderately variable and typically ranged from 0.6 to 0.9. While variation among males and females, juveniles and adults and annual variation throughout the six year study period was evident, my analyses indicated that none of these differences were statistically significant. The lack of detectable differences likely arises from small sample sizes of the different sex and age classes (present study 4 to 25) and is ubiquitous among other non-lethal studies of coyote survival (total n= 10-89) (Roy and Dorrance 1985, Windberg *et al.* 1985, Gese *et al.* 1989, Kamler and Gipson 2000).

The survival of coyotes in Elk Island National Park is in the upper range of survival estimates of coyote populations (Table 3-6). The survival rates I calculated for EINP are however, seemingly low for a population that inhabits a protected national park (adults 0.74 and juveniles 0.66) especially when compared to areas of Colorado and

Washington (0.87 and 0.90 respectively). Nonetheless, the small size of EINP and the ability of the coyotes to move freely beyond boundary fences into agricultural areas markedly increases their risk of human induced sources of mortality. In this regard, my results also suggest that the Blackfoot grazing reserve south of EINP was only a partial refuge from these sources of mortality as registered trap lines, some of which are set to specifically capture coyotes, exist within its boundaries. Additionally, potential exposure to forms of human-mediated causes of mortality other than vehicles (*i.e.*, hunting, trapping, and poisoning) occur without exception, as all radio-collared coyotes were located outside of EINP and Blackfoot perimeter fences at some point during the study period.

Survival and causes of mortality for coyotes and wolves have been reported elsewhere (Knowlton 1972, Nellis and Keith 1976, Andrews and Boggess 1978, Windberg *et al.* 1985, Roy and Dorrance 1985, Fuller 1989, Boitani 1992, Hefner and Geffen 1999). In these studies, the majority of mortalities were human induced, usually resulting from hunting, trapping, or vehicle collisions (Knudson 1976, Tzilkowski 1980, Fritts and Mech 1981, Windberg *et al.* 1985, Gese *et al.* 1989, Boitani 1992, Hefner and Geffen 1999, Kamler and Gipson 2000, Crete *et al.* 2001). This finding is consistent with the results of my study where 77% of confirmed mortalities resulted from hunting, trapping snaring, or collisions with vehicles when the coyotes travelled outside of the Park boundaries. In Jasper National Park, Alberta, collisions with vehicles accounted for the majority of summer (73%) and winter (77%) mortality (Bowen 1978) and suggests that the presence of a national highway through the middle of the park presents a large risk to coyotes. My estimates of the relative importance of human-induced mortality of coyotes are similar to that reported for Utah, Idaho, Wyoming, and Colorado populations that ranged from 78%-100% (Davison 1980, Tzilkowski 1980, Pyrah 1984, Gese *et al.* 1989) but higher than those reported for Texas by Andelt (1985) and Windberg *et al.* (1985) of 38% and 57%, respectively.

Wolves and coyotes are thought to have effective compensatory responses to high levels of human exploitation where the removal of dominant individuals within packs is thought to relax social factors that would otherwise restrict population growth (Camenzind 1978, Packard and Mech 1980, Harrington *et al.* 1982, Windberg 1995). For example Packard *et al.* (1985) observed multiple matings among subordinate wolves when dominant individuals were removed. Population growth may also result from an inverse relationship between litter size as well as juvenile or yearling natality with population density (Knowlton 1972, Camenzind 1978, Andelt 1985). In a high-density coyote population Windberg (1995) reported that practically no juvenile females ovulated and yearlings had low and variable natality. Additionally, only territorial adult females produced viable foetuses (Windberg *et al.* 1985). Ultimately, however, population growth is a complex interaction of food availability, spacing behaviour, and population size (Flowerdew 1987, Windberg 1995, White and Garrott 1999). Lower coyote densities should result in increased food availability and this interaction serves to increase and stabilize population numbers (Keith 1983) by means of various demographic responses including: increased rates of reproduction by subordinate individuals, increased natality and adult and juvenile survival (Eberhardt 1977). Thus, social factors can play an increasingly important role in reducing recruitment as population density increases (Windberg 1995). However, it is unlikely that social factors play a strong role in stabilizing population density of coyotes in EINP because the high levels of coyote mortality probably do not result in long term dominance by older individuals. The lack of social dominance may contribute to the overall resiliency of coyote populations and may partially explain the consistently high trapping harvest numbers that average nearly 25,000 coyotes annually in Alberta.

Home range and social organisation

The concept of a home range as a relatively discrete and stable area occupied by an animal has existed for almost a century (Seton 1909, White and Garrot 1990, Gautestad and Mysterud 1993). The adaptive significance of home range size, shape, and overlap with conspecifics and other species and the causal factors that are thought to determine home ranges (*e.g.* body size, habitat, food availability and social status or organisation) have been the subject of considerable research (Clutton-Brock and Harvey 1983, Bowen 1982, Grant *et al.* 1992, Gautestad and Mysterud 1993, Moorcraft *et al.* 1999, Kitchen *et al.* 2000 a).

Variation in social organization of carnivores is thought to be strongly affected by the spatial distribution, acquisition, and defence of food resources (Macdonald, 1983; Bekoff and Wells, 1980; Bekoff and Wells, 1986). Dispersion and richness of food resources are thought to limit group size and territory size (Bowen 1982, Gittleman and Harvey 1982, Macdonald, 1983, Grant *et al.* 1992) (see also Chapter 4). Intraspecific plasticity in social structure is well illustrated by coyotes (Bekoff and Wells 1982, Andelt 1985) which characteristically exhibit stable pair bonds and may have "helpers" or associates (related non-reproducing conspecifics that contribute to care of offspring) of either sex (Knowlton 1972, Camenzind 1978, Bekoff and Wells 1980, Moehlman 1989, Allen *et al.* 1999). Coyote social organization directly affects spacing patterns as only breeding groups are thought to be territorial (Messier and Barrette 1982, Windberg and Knowlton 1988). However it is probable that an individual coyote may belong to a variety of different social classes within its lifetime (*e.g.* Kamler and Gipson 2000), especially in EINP where high rates of mortality may alter social affiliations (*e.g.* mortality of alpha pack member(s) may disrupt or destroy pack structure and/or membership). Home ranges can be described as areas that are frequented by one or more individuals, but that are not defended against conspecifics. In contrast, territories are considered to be areas that are defended against conspecifics (Burt, 1943). Messier and Barrette (1982) state that territoriality was limited to breeding groups and was evidenced when the core area of one coyote group was limited by the core range of another (*i.e.* contiguous and non overlapping core areas).

Results of my study indicate significant effects of coyote social organisation on home range (delineated using 95% UD), core area (50% UD), and perimeters of solitaires, members of a pair and members of a pack (Fig. 3-4 a-d). Individual home range, core area, and perimeters decreased with increasing group size (*i.e.*, one (solitaires), two (pairs) and three or more (packs)). These findings are consistent with other studies that report solitaires (*i.e.* transients, nomads, wanderers) with comparatively large home ranges with multiple core areas (number of solitaire core areas in this study: mean ± SD = 2.7 ± 1.03) compared to packs or pairs (Camenzind 1978, Bekoff and Wells 1981, Bowen, 1982, Andelt 1985, Gibeau 1993, Sacks *et al.* 1999). Messier and Barrette (1982) also propose that the greatest variation is exhibited by the large, shifting "living areas" of solitaires compared with relatively stable home ranges of individuals that formed pairs or packs (Kitchen *et al.* 2000a).

Solitary coyotes (n=6) were the smallest component of the study population in EINP. Home ranges (95 % UD) of solitaires were almost nine-fold larger than those of individual that belong to packs (Fig. 4-4a) and in all cases, solitaire home ranges overlapped home ranges of other solitaires, pair members, and/or pack members. Large home ranges are thought to result from traveling over large areas in search of breeding opportunities (and possibly access to established groups) as well as exclusion from existing territories (Messier and Barrett 1982, Andelt 1985). While other studies such as Bowen (1978) have divided solitaires into transients and residents, the low number of radio-collared solitaires (n=6) in this study precluded such a division. Although adequate telemetry locations were collected for each individual (range 31 - 77), difficulties arising from low sample sizes were further compounded by the fact that two of the solitary individuals subsequently joined packs and two were shot within a year of collaring.

Home ranges of individual coyotes that belonged to a pack were significantly smaller than those that were members of a pair, which were significantly smaller than solitaire home ranges. Interestingly, for the core area and core perimeter measures, individuals in pairs did not differ from solitaires. However, the mean number of core areas for pairs was 1.5 ± 0.73 SD. Previous studies have often grouped pairs and packs together as "residents" (Table 3-6), which may overwhelm subtle differences in home ranges between pairs and packs.

In my study the home ranges of the majority of coyotes extended to varying degrees beyond the boundaries of EINP. Linear regression showed that home range area typically increased when coyotes spent more time outside of EINP (*i.e.* increased number of locations outside EINP), perhaps because of decreased prey (including carrion) availability outside of EINP.

In contrast to the effects of social organisation on home range dynamics, my observations combined with telemetry of coyotes in Elk Island National Park suggest that with the exception of the use of core areas by solitary coyotes, diurnal and nocturnal home ranges were not significantly different within social groups. The similar diurnal and nocturnal use of space is supported by the Kitchen *et al.* (2000b) study which suggests that activity patterns of coyote populations exploited by humans tend to be predominately nocturnal and crepuscular and reduction in exploitation results in higher levels of diurnal activity. However, Kitchen *et al.* (2000b) did not take into account the influence of social organisation on activity patterns. Solitary animals were the exception to similar nocturnal and diurnal use in my study. Five of six solitaires had multiple core areas (x = 2.7 ± 1.03 SD) and the one exception had a single core area > 17 km^2. Because coyotes are primarily visual hunters (Kavanau and Ramos 1975, Wells and Lehner 1978, Bekoff and Wells 1980, Laundre and Keller 1984), solitary coyotes may be more apt to trespass on established territories and home ranges under the cover of darkness. Additionally, solitary coyotes spend relatively more time in areas outside of EINP, accessed by either digging under fences or using existing holes in fences, where there is intense human persecution of coyotes (Kitchen *et al.* 2000b). Although other studies have documented diurnal and nocturnal movement rates (metres/hour or a linear measure between successive telemetry locations), proximity to roads, and diel habitat use (Woodruff and Keller 1982, Roy and Dorrance 1985, Holzman *et al.* 1992, Gibeau 1992, Grinder and Krausman 2001) there is little information on diurnal and nocturnal patterns in home range or core area use.

In addition, coyotes in EINP did not exhibit seasonal (*i.e.* summer/winter) variation in home ranges within each social group, results that are similar to that reported by Bowen (1982) and Chamberlain *et al.* (2000). Ideally, the calendar year should be divided into four to six biological seasons based on coyote ecology (*i.e.* Andelt and Gipson 1979, Smith *et al.* 1981). However, I was unable to collect a sufficient number of relocations for many of the coyotes in the short time periods involved in this type of temporal division. Thus potential differences in home range or core area size of Elk Island National Park coyotes may be overwhelmed by the pooling of biological seasons into the two seasonal periods of summer and winter.

My review of the literature between 1982-2000 indicated that home range sizes for coyotes in EINP are comparable to those published elsewhere in North America (Table 3-6). For instance, home ranges for male coyotes in EINP (15.0 - 136.9 km^2) are similar but slightly higher than that reported previously (2.4-104 km^2) whereas home ranges for females in EINP (24.4 – 188.5 km^2) fall within the range reported elsewhere (2.4 – 313.8 km^2). My results from EINP, Alberta indicate that variation in home ranges results from differences in social organisation rather than gender. Taken together, those data indicate that home ranges of coyotes are profoundly variable. Significant differences between male and female home range sizes are typically not evident among monogamous canids with a strong pair bond (Kleiman and Eisenberg 1973, Kleiman 1977, Bowen 1982). The extent to which prey and/or food availability and the interaction with social organisation influences home range areas remains poorly understood. Additionally, differences in researcher estimation techniques have also introduced a source of variation (Table 3-6).

Essentially the core area in this study, defined by the 50% utilisation distribution, typically contained >50% of the telemetry locations. The core area for packs in EINP meets the definition of a territory: an area that is definable and stable over time and is contiguous with minimal or non-overlapping boundaries with neighbouring family groups (Fig. 3-8) (Andelt 1985, Windberg and Knowlton 1988, Person and Hirth 1991, Grant *et al.* 1992, Allen *et al.* 1999, Chamberlain *et al.* 2000). This definition violates the behavioural description of territoriality that necessitates the observation of territorial behaviour in the form of display, chasing or fighting (Kaufmann 1983, Windberg and Knowlton 1988). Observation of these behaviours is extremely infrequent and it has been suggested that direct confrontations among neighbouring coyotes are uncommon and territorial maintenance is primarily accomplished through indirect means like scent marking and vocalisations (Camenzind 1978, Allen *et al.* 1999). The rarity of observing these behaviours is consistent with the results of my study where, despite >500 of hours spent tracking coyotes, agonistic behaviour among coyotes was observed only three times. Territoriality is typically inferred through areal analyses (Bowen 1982, Allen *et al.* 1987, Gese *et al.* 1988, Windberg and Knowlton 1988, Kamler and Gipson 2000). Core area size for the pair and pack members in my study were consistent with that reported for resident coyotes in other studies that have regularly been reported as < 10 km^2 (Springer 1982, Windberg and Knowlton 1988, Person and Hirth 1992, Allen *et al.* 1999, Chamberlain *et al.* 2000).

Moehlman (1989) suggests that only when it is difficult for offspring to breed independently (i.e. no dispersal territories or high costs of dispersal/raising offspring) is it worthwhile for a subordinate individual to remain in a group as a non-breeding helper.

The benefits of group or pack membership are thus related to the inability or high costs of dispersal for offspring. The adaptive value of belonging to a social group is thought to be based on improved resource exploitation, parenting (*i.e.* alloparental behaviours) and predator vigilance (Geist 1974, Camenzind 1978, Messier and Barrette 1982, Bekoff and Wells 1986). The importance of a core area or territory for social animals with altricial young has also been linked to neonatal and juvenile protection as well as a resource base from which to feed offspring (Messier and Barrette 1982, Allen *et al.* 1999). In fact, multi-generational site fidelity has been suggested for coyote packs where sharing and inheritance of home ranges may provide an advantage for offspring, particularly in cases when coyote density is high and dispersal territories are limited (Kitchen *et al.* 2000 a). Foraging and defence of food resources may also be facilitated by a group effort and core areas may provide shelter, den sites, resting areas or other requirements for survival (Bekoff and Wells 1980, Bowen 1981, Laundre and Keller 1981, Gese *et al.* 1988, Person and Hirth 1991, Grant *et al.* 1992).

Survival rates and home ranges of coyotes in this study may provide some insight into the effectiveness of a small, protected area like EINP. Determining the ecological effects of habitat fragmentation and connectivity on plant and animal communities are fundamental conservation issues (Wilcove *et al.* 1986, Primack 1993). Studies of animal communities (*e.g.* Redpath 1995, Dyer *et al.* 2001) indicate that fragmentation, in the form of roads for example, can increase mortality, modify behaviour, alter the physical and chemical environment, facilitate the spread of exotics and increase human access and use of areas served by roads (Trombulak and Frissell 2000). In contrast, much less is understood about the effects of protected area size on population viability (Rothley 1999, Gurd *et al.* 2001).

EINP is surrounded primarily by agricultural and private lands and is further fragmented by internal fences and a major highway that divides the Park into two discrete sections (south Isolation area = 59 km^2 and north Main area = 136 km^2). Woodroffe and Ginsberg (1998) suggest that critical carnivore reserve size (*i.e.* carnivore populations persisting with a probability of 50%) should be related to factors that determine the probability of extinction. That is, if extinction is related to population size then critical reserve sizes should be established based on areas required to maintain a sustainable population. Alternately, if extinction is caused by edge effects, home range size should determine critical reserve size. As a result, maintaining viable populations of medium to large carnivores is inherently problematic because they typically occur at low densities and have large home ranges. Additionally, as is well illustrated by coyotes, carnivores often have requirements that conflict with humans (*e.g.* Shivik *et al.* 1996, Sacks *et al.* 1999).

Woodroffe and Ginsberg (1998) compiled 22 studies of large carnivores in protected areas and concluded that 74% of known mortality was human induced and contributed more to the extinctions of large carnivore populations in small reserves than did stochastic processes. My results indicate that 77% of all coyote deaths in EINP were human induced.

Ultimately, Woodroffe and Ginsberg (1998) concluded that for large carnivores, average female home range size was a better predictor of critical reserve size than population density. Although they did not consider coyotes, the nearest canid home range equivalent (using as an example a female in a coyote pair with a home range of 73 km^2) was the dhole (*Cuon alpinus*) (home range size 68.8 km^2) and the critical reserve size was estimated at 723 km^2. This species-specific analyses calculated critical reserve sizes ranging from 36 km^2 for California black bear to 3981 km^2 for the North American brown bear (*Ursus arctos*).

The concept of reserve size changes when considering assemblages of species. Gurd *et al.* (2001) estimated minimum reserve sizes in eastern North America would have to be 5037 km^2 (95% confidence intervals = 2700-13,296 km^2) to ensure that reserves would not lose terrestrial mammals because of insularization. Even for a species at high densities (Chapter 5) and as adaptable as the coyote, long term (*i.e.* 6 years) post-collaring survival for a female coyote in this study was only 3%. The high perimeter:area ratio in EINP (1:2.2) combined with the relatively large home ranges of radio-collared coyotes resulted in 100% of the collared population moving beyond EINP boundaries at some point. Thus, as suggested by Woodroffe and Ginsberg (1998) border areas of reserves can become population sinks when they are surrounded by human use that conflicts with carnivore requirements. Clearly, it would appear that EINP is too small to function as a carnivore conservation area.

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CHAPTER FOUR

SEASONALITY AND EFFECTS OF SOCIAL AFFILIATION ON THE DIET OF A NORTHERN POPULATION OF COYOTES

(Canis latrans)

INTRODUCTION

Predators are strongly affected by the abundance and spatial dispersion of their food resources (Bekoff and Wells 1986, Mills and Knowlton 1990, Patterson and Messier 2001). For instance, home range sizes for species as varied as fish and birds show an inverse relationship to food availability (Slaney and Northcote 1974, Griffin and Buskett 1985). In canids, intraspecific differences in the use of space as well as social organization are also thought to reflect variations in how their prey are distributed (Bekoff and Wells 1986, Moehlman 1989, Geffen *et al.* 1996). For example, when food resources are clumped and defendable, coyotes (*Canis latrans*) (Bekoff and Wells 1982, Camenzind 1978) and golden jackals (*Canis aureus*) (Macdonald 1979) form groups, even if the exploitation of these resources does not require a group foraging effort (Bekoff and Wells 1986). Conversely, when food abundance is low and widely distributed, conspecifics tend to be organized into solitary individuals or mated pairs (Bekoff and Wells, 1982).

There is often a positive correlation in carnivores between the size of the animal and/or social group and the size of the prey they consume (Clutton-Brock and Harvey 1983, Macdonald 1983, Gittleman 1989). Increased group sizes are thought to enable groups of animals to hunt co-operatively to capture larger prey (Nudds 1977). For example, wolves (*Canis lupus*) hunt large ungulates, such as deer or moose, in a cooperative manner whereas foxes are solitary hunters of prey such as mice (Henry 1980, Kunkel and Pletscher 1999). In addition to co-operative hunting and increased foraging efficiency, other benefits of group living include increased predator vigilance and territorial boundary patrol, the delay or elimination of the costs of dispersal, and alloparental behaviour (Messier and Barrette 1982, Macdonald 1983).

Prior to extirpation from the aspen parkland in the Elk Island National Park (EINP) area, group hunters such as wolves, in combination with other large predators (*e.g.* bears, cougars) and ecological dynamics (*i.e.* drought, fire, disease) would have played an important role in regulating the ungulate population (Kunkel and Pletscher 1999, Ballard *et al.* 2001). Today, with an intact ungulate guild, in the absence of large predators, managers in EINP wanted to know whether the largest remaining carnivore, the coyote, had an effect on ungulate dynamics in the park. More specifically, managers wanted to know if seasonal patterns were evident in the coyotes' diet when they used the ungulate resource more heavily (*e.g.* during winter and especially during spring calving and fawning).

Coyotes are medium-sized opportunistic carnivores that are known to consume a diversity of items in their diet including insects, grasses, fruit, reptiles, amphibians, fish and a wide variety of mammal and bird species (Bowen, 1978, Andelt 1987, Hernandez *et al.* 1994, Patterson *et al.* 1998, Kunkel and Pletscher 1999). Social affiliation of coyotes (*i.e.* solitary animals, pairs, or packs) is also thought to have an effect on their diet (Bekoff and Wells 1982, Andelt 1985). Being a pack member can confer an advantage for a coyote by allowing them to kill large prey or defend large carrion while maintaining the advantage of a smaller body size and the resultant efficient use of small prey (Patterson and Messier

2000). Several studies indicate that larger group size and delayed pup dispersal are positively correlated with larger primary food items (*i.e.* elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*)) (Bowen 1981, Bekoff and Wells 1980, 1982).

The objectives of the present study were to use scat analyses to examine: 1) seasonality of diet of coyotes in Elk Island National Park; 2) evaluate differences in diet of solitaires, pairs, packs in summer and winter. I expected that coyotes would consume a broad suite of food items consistent with previous studies that have shown them to be highly opportunistic predators. Given large changes in prey abundance and availability at northern latitudes, coyotes should also display a high degree of seasonality in diet. I predicted differences in diets of solitary coyotes compared with those that formed pairs and packs and that such differences would vary between summer and winter months. Specifically, large food items (*i.e.*, ungulates) should increase proportionately as major food items of individuals that formed packs compared with those that formed pairs and solitary individuals. Finally, EINP provides a unique opportunity to discriminate between the food resource and delayed dispersal / habitat saturation hypotheses (Camenzind 1978, Bekoff and Wells 1980, Bowen 1981, Andelt 1982, Messier and Barrette 1982, Gese 1988, Patterson and Messier 2001) regarding pack formation in coyotes.

MATERIALS AND METHODS

Study Area

Elk Island National Park (EINP) situated 40 kilometres east of Edmonton, Alberta, Canada, is surrounded primarily by agricultural lands and acreages except for the southern boundary that borders the Cooking Lake-Blackfoot Grazing, Wildlife, and Provincial Recreation Area. EINP is divided by the four lane Highway 16 into a 136 km^2 "Main Park" north of the highway and the southern 59 km^2 "Isolation area". Both areas of the park are completely fenced with a 2.2 m mesh wire fence and the main park is bisected by a highway that is oriented north and south.

Elk Island is situated in the aspen-parkland ecozone that is transitional between prairie to the south and boreal forest to the north. The area around EINP is commonly known as the Beaver Hills, described as knob and kettle topography that resulted from differential melt of buried remnants of glacial ice (Blyth 1995). This topography also supports numerous small lakes and wetlands.

Vegetation in the park is dominated primarily by trembling aspen (*Populus tremuloides)* and secondly, balsam popular (*Populus balsamifera*). More restricted forest types include white birch (*Betula papyrifera),* Alaska white birch *(Betula neoalaskana)*, white spruce (*Picea glauca),*black spruce (*Picea mariana)* and tamarack (*Larix laricina)*. Common shrubs and herbs include hazel *(Corylus cornnuta*), prickly rose (*Rosa acicularis),* willow (*Salix spp),* sedges (*Carex spp.*) and grasses (Gramineae family).

The climate for this region is typical of northern mid latitude continental with wide variations in daily and seasonal temperatures. A mean minimum temperature of −16.° C occurs in December while the mean maximum temperature of +23°C occurs in

July while annual average precipitation is 48 cm. (Blyth 1995).

Elk Island National Park supports high densities of large ungulates including plains bison (*Bos bison bison*) and wood bison (*Bos bison athabascae*), wapiti (*Cervus elaphus canadensis*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). With the exception of the coyote, lynx (*Felis lynx*) and red fox (*Vulpes vulpes*), most of the historically resident larger carnivores such as grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), wolf (*Canis lupus*), cougar (*Felis concolor*), and wolverine (*Gulo gulo*) have been extirpated from EINP. Lynx and red fox sightings are uncommon and reports of transient wolf, black bear or cougar are exceptionally rare. Although coyotes are the numerically dominant and largest resident carnivores, it has been speculated that this area was historically at the northern periphery of its range and that extirpation of wolves and human alteration of the environment has facilitated the expansion of coyote's range (Gipson 1974, Blyth and Hudson 1987).

Diet analysis

General protocols

Seasonality and the affect social affiliation has on the diet of coyotes in Elk Island National Park (EINP) were evaluated using scat (*i.e.*, faecal) analyses. Scats were collected at approximately monthly intervals from July 1994 and January 2000 with the majority of scats collected between January 1995 and February 1998 (Table 4-1). Scats were collected in EINP from roads, hiking, and game trails after all areas were cleared of scats 1-2 days before collections to ensure that scats were of known age and thus a reflection of recently consumed food. The location of each scat was quantified using a handheld Garmin™ global positioning system (GPS). Access to interior park roads (other than the main highway and part of Tawayik road) for scat collection and telemetry during November through to mid-April was prohibited due to elk trapping.

Prior to the identification of food items, scats were either sterilized at 121°C for 4h in an autoclave or placed in a drying oven (model Johns Scientific DOE 305685) at 130°C for a minimum of 6 h to kill the ova of *Echinococcus multilocularis*, *Echinococcus granulosa*, and other potential pathogens (Bowen 1978, Margo Pybus, (Alberta Fish and Wildlife) pers. comm. 1996). Following sterilization, scats were washed over sieves to remove fine extraneous detritus, and then oven dried for one hour at 60°C – 100°C (Bowen 1978). Each scat was dissected during the washing process to ensure that small bones and feathers were separated from hair that would otherwise preclude identification (Brillhart and Kaufman 1995, Spaulding *et al.* 2000). Hair was soaked in 70% isopropyl alcohol to remove the layers of oil that often adhere to the hair (Todd and Kennedy 1993). Hairs were then removed, dried and a negative impression taken for identification purposes. Coyote scats from EINP were often comprised of homogenous wads of hair, berries, insect exoskeletons, and/or feathers.

Table 4-1 Number of coyote scats collected from Elk Island National Park, July 1994 and January 2000. – scats not collected.

Year	Month												
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1994	-	-	-	-	-	-	11	90	3	-	-	-	104
1995	18	15	38	51	35	8	71	60	-	30	21	36	383
1996	-	3	-	-	44	19	9	19	30	-	6	-	130
1997	10	12	26	52	102	72	14	-	85	63	41	56	533
1998	24	44	28	-	-	-	-	-	-	-	20	-	116
1999	7	13	-	-	-	-	-	-	-	-	-	-	20
2000	45	-	-	-	-	-	-	-	-	-	-	-	45
Total	104	87	92	103	181	99	105	169	118	93	88	92	1331

Coyote diet analyses was based on macro and microscopic examinations of structures (primarily hair and bony structures) within scats (Gipson 1974, Todd and Kennedy 1993). Using a dissecting microscope, the contents of each scat was sorted according to common macroscopic morphological characteristics of colour, shape and length of primary guard hairs, bones, seed type, insect exoskeletons and feathers (Moore *et al* 1974, Moore 1988). Identification of food items within coyote scats was based on refining techniques from previously described studies (Adorjan and Kolenosky 1969, Spiers 1973, Moore *et al.* 1974, Bowen 1978, Moore 1988, Herandez *et al.* 1992, Lewis *et al.* 1994, Brillhart and Kuafman 1994).

Scat sample hair impressions were made of 3 to 10 randomly selected primary guard hairs with complete basal portions and intact tips (Todd and Kennedy 1993). Acetate strips were put on the glass slides and sample hairs were centred on the slides. When hair samples were longer than the slide the hair was cut and placed on the slide to ensure that the distal and proximal ends of the hair sample were centred on the acetate strip. The prepared slide was covered with another slide, clamped together using small C-clamps, placed on a rack and heated in a drying oven for at least 20 minutes at 100°C (Todd and Kennedy 1993). Hairs were taped next to their negative acetate impressions so both could be examined under a microscope for cuticular scale and medullary patterns. These patterns were compared with photographs, diagrams, and reference slides of known mammals (*e.g.*, Adjoran and Kolenosky 1969, Moore *et al.* 1974, Moore 1988). To reduce identification errors, the majority of the scats were identified by one person combined with occasional independent identification comparisons of the same samples completed by a second qualified individual.

Scat analyses based on hair identification typically overestimate the relative importance (*i.e.* caloric value) of small prey and underestimate the importance larger food items (*e.g.*, Bowen 1978, Andelt 1982). Food abundance categories (*e.g.*, Bowen 1978) have been used to partially correct for this bias (Bowen 1981, Andelt 1985). In the present study, I identified three levels of prey or food abundance: 1) major food item (≥ 40% of faecal volume); 2) minor food item (5 - 39 % faecal volume.) and; 3) trace item (< 5% faecal volume). One percent of scats contained two major food items and in these cases, each item was recorded as 0.5 occurrence to maintain original sample size. Two percent of the scats had multiple items that each contributed less than 40 % of faecal volume and these scats were recorded as "no major food item". Seasonality of coyote diet and differences in diet among the three social affiliations were completed using the major food item classification. Seasons were divided into summer and winter based on the mean minimum monthly temperature being above 0° C (summer = May - October) or below 0° C (*i.e.* winter = November – April) (Environment Canada 1998). October mean minimum temperatures for weather stations around Edmonton varied above and below 0° C so to equally divide these data, October was put into the above 0 category.

Identification of food items varied from species-level to familial level descriptions. Mammals were generally identified to species and included bison, moose, wapiti, mule deer, white tailed deer, domesticated cattle (*Bos taurus*), horses (*Equus caballus*), and goats (*Capra hircus*), badger (*Taxidea taxus*), beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), porcupine (*Erethizon dorsatum*), Richardson's ground squirrel (*Spermophilus richardsonii*), red squirrel (*Tamiascuirus hudsonicus*), snowshoe hare (*Lepus americanus*), skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), least chipmunk

(*Eutimias minimus*), shrews (*Sorex* spp.), pocket gopher (*Thomomys talpoides*), and domestic cats (*Felix domestica*) and dogs (*Canis familiaris*). Trace amounts of coyote hair were occasionally found among scats and were possibly due to grooming. Identification of individual mice, voles, and lemmings to species was not completed because species level identifications are difficult due to minor differences in hair structure and cuticular patterns among these species. Thus, while our analyses indicated the presence of 6 species of Cricetidae (*i.e.*, meadow vole (*Microtus pennsylvanicus)*, heather vole (*Phenacomys intermedius)*, red backed vole (*Clethrionomys gapperi)*, northern bog lemming (*Synaptomys borealis)*, western jumping mouse (*Zapus principes*), deer mouse (*Peromyscus maniculatus*) and house mouse (*Mus musculus*), these species were subsequently grouped together and referred to as Cricetidae.

In contrast, birds, insects, grasses and species of vascular plants, typically using berries (Alwyne Beaudoin (Provincial Museum of Alberta) pers. comm. 1997, Martin and Barkley 1961) were identified to only coarse levels. The spur-throated grasshopper (*Schistocerca americana*) was the only abundant insect identified in the scats.

Determining the diet differences between solitaires, pairs, and packs

Locations of retrieved scats were recorded using a global positioning system (GPS). Assigning the origin of scats to known coyote home ranges based on scat collection information has been validated by Bowen (1978) who compared known scats with scats collected on specific pack ranges during the same time period from populations in Jasper National Park. Proportional estimate for species comprising 90% of food remains were almost identical. In EINP, scat locations were overlaid with core areas (see

Chapter 3) of each coyote using ARCVIEW geographical information systems (ESRI ™). Scats were selected that were collected during the life span of each individual coyote and then assigned to the representative social affiliation. Food items were divided into two categories representing ungulate food and non-ungulate food. This division was based on size greater than 30 kg where cooperation is generally necessary for capture of prey and/or defence of food that is shared (after Bowen 1978). Neonatal and juvenile ungulates were excluded from the comparisons and ungulate weights were taken from Geist (1998).

Statistical Analyses

I evaluated patterns in diet of coyotes using both qualitative and quantitative analyses. Monthly patterns in, a) frequency of occurrence and b) percent as a major food item (*i.e.*, ≥40% faecal volume), were evaluated qualitatively.

Differences in the percentage of ungulates as the major food items among the three social affiliations (*i.e.*, solitaires, pairs, and packs) were evaluated using single factor ANOVA. This analysis was completed separately for data grouped into summer and winter periods. When the ANOVA model was significant, differences among social affiliations were tested using Bonferroni adjusted, orthogonal contrasts (Zar 1984). Prior to analyses, percent data were arcsine square root transformed to satisfy assumptions of normality and homogeneity of variances.

In addition to the ANOVA tests, I was also interested in evaluating differences in diets of individual coyotes whose social affiliations changed during the study period. Thus, I evaluated changes in diet of a) two solitaires that subsequently joined packs and b) two animals that were members of a pair and that subsequently joined packs. Due to small sample sizes, changes in the proportion of ungulate food were evaluated using a one tailed Fisher's exact test (Stokes *et al.* 1995) with a 2 × 2 table design. These tests were completed separately for scats collected during the summer and winter periods. These analyses were used to test for associations between social group and the proportion of ungulate and non-ungulate food items in scats.

RESULTS

Dietary Trends

Fieldwork completed between July 1994 and January 2000 resulted in the collection of 1331 scats. In total, 36 different foods, including identifiable species in Cricetidae (*i.e.* mice, voles, and lemmings), were recorded as major (*i.e.* ≥40% faecal volume) items. Twenty-eight species of mammal, birds (which were grouped together), four fruits, two insect species, and grass species (grouped together) were identified. In addition, two other mammal species (horse (*Equus caballus* and coyote) appeared as minor or trace items.

Although a wide variety of food items were discovered in coyote scats, comparisons of frequency of occurrence indicated that Cricetidae (mice, voles, and lemmings) typically comprised the majority of prey items throughout the year. The occurrence of Cricetidae was lowest in May followed by a steady increase until September (Fig. 4-1). Muskrat and beaver occurred in coyote scats throughout the year, but occurred most frequently in May (44%) and June (22%), respectively. Muskrat were also frequently observed in scats between September and December (Fig. 4-1). Monthly trends in the occurrence of other food items were also observed including fruit, grasshoppers and birds which were most frequently observed in July-August (fruit) and July-October (grasshoppers, birds) compared to other months (Fig. 4-1).

Classification of scat components into major food items (≥ 40 % faecal volume) was used to correct the bias of overestimating the caloric contribution of small food items and underestimating that of large items. My analyses of overall trends in coyote diet indicated that mice and voles were the dominant major prey items consumed by coyotes in Elk Island National Park for nine of the 12 months whereas elk, muskrat, and muskrat were the predominant major food items in March, May, and June (Fig. 4-2). When combined with muskrats, elk, beaver, white tailed deer, and fruit these food groups were the dominant food items in greater than 85% of all scats collected (Table 4-2).

On average, mammals contributed 82.2 ± 12.2 % (x ± 1SD) and 95.3 ± 2.3 % of all major food items found in summer and winter coyote scats, respectively (Fig. 4-2). The remainder of the summer diet consisted of fruit (11.3 ± 10.4%), birds (3.2 ± 1.8%), grasshoppers (2.2 ± 2.6 %), and grasses (1.2 ± 1.3 %). In the winter, the non-mammal portion of the diet consisted of fruit (2.1 ±1.9 %), grasses (1.8 ± 0.9%), birds (0.3 ± 0.5%), and grasshoppers (0.2 ± 0.5%) (Fig. 4-2).

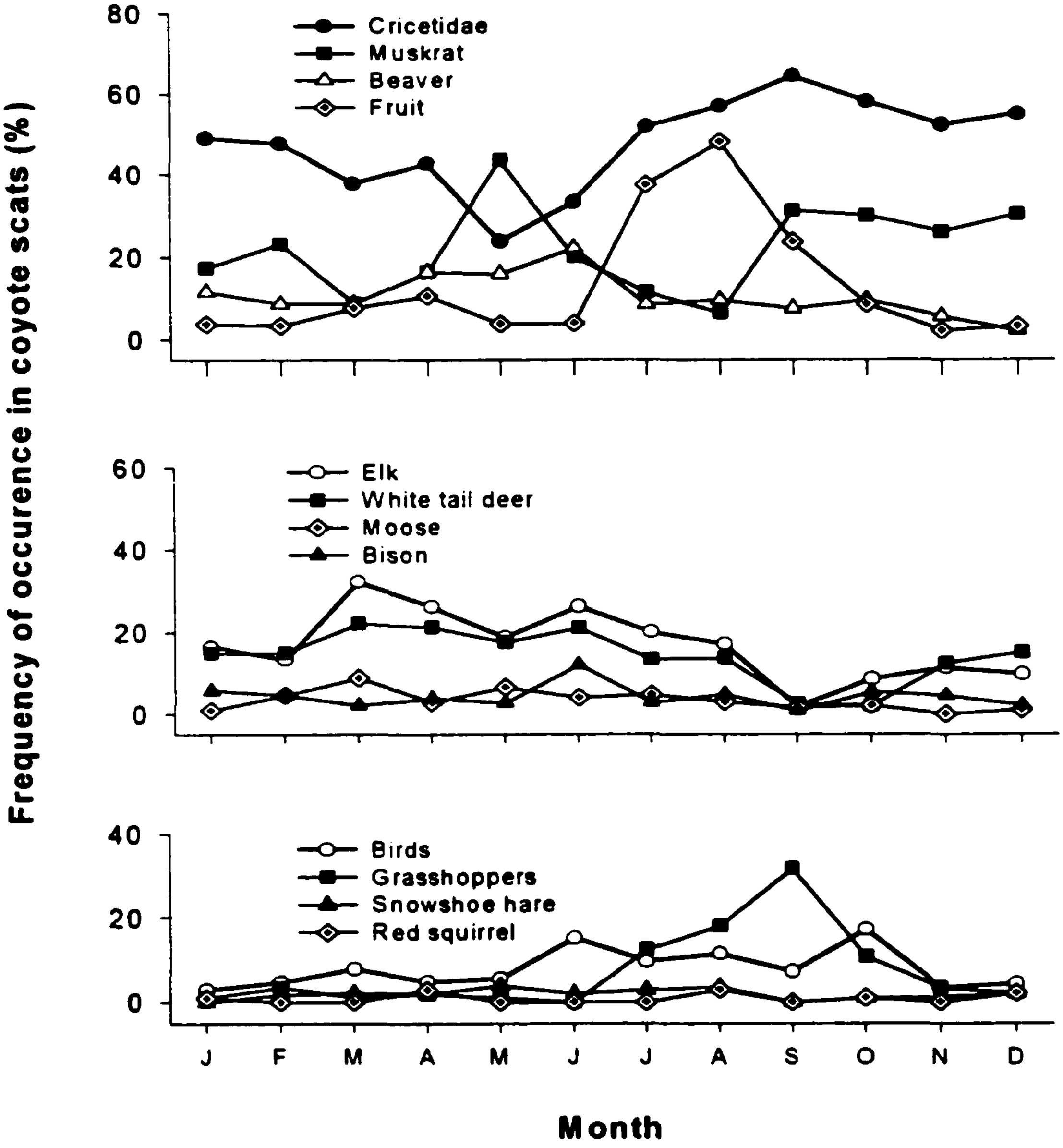

Fig 4-1 Monthly comparison of frequency of occurrence of the most abundant items in coyote scats from Elk Island National Park. Data from 1994-2000 have been combined. Cricetidae are comprised of mice, voles, and lemmings. The categories of fruit and birds are comprised of multiple species.

Similar to comparisons of scats using frequency of occurrence data, the dominance of major food items also varied on a monthly basis (Fig. 4-2). Comparisons of scats among months (with birds and Cricetidae (i.e. mice, voles, and lemmings) forming single groups in each month), showed that scats contained 11.8 ± 2.9 (x ± 1SD) food items in the winter compared to 14.3 ± 5.4 in the summer (May – October) with the greatest variation in food species occurring in August with 22 different food categories. The maximum percentage individual ungulate species contributed to the monthly diet occurs in March for elk (24.4% as major food item), white-tailed deer (13.3%), and moose (7.8%) however, the peak for bison (7.7 %) and mule deer (3.3%) occur in June (Fig. 4-2). Strong seasonal patterns in food items were found for grasshoppers and berries that were most often major items in July, August, and September (Fig. 4-2.). The preponderance of non-mammalian food occurring as major items was also highest (34% of all scats) in August.

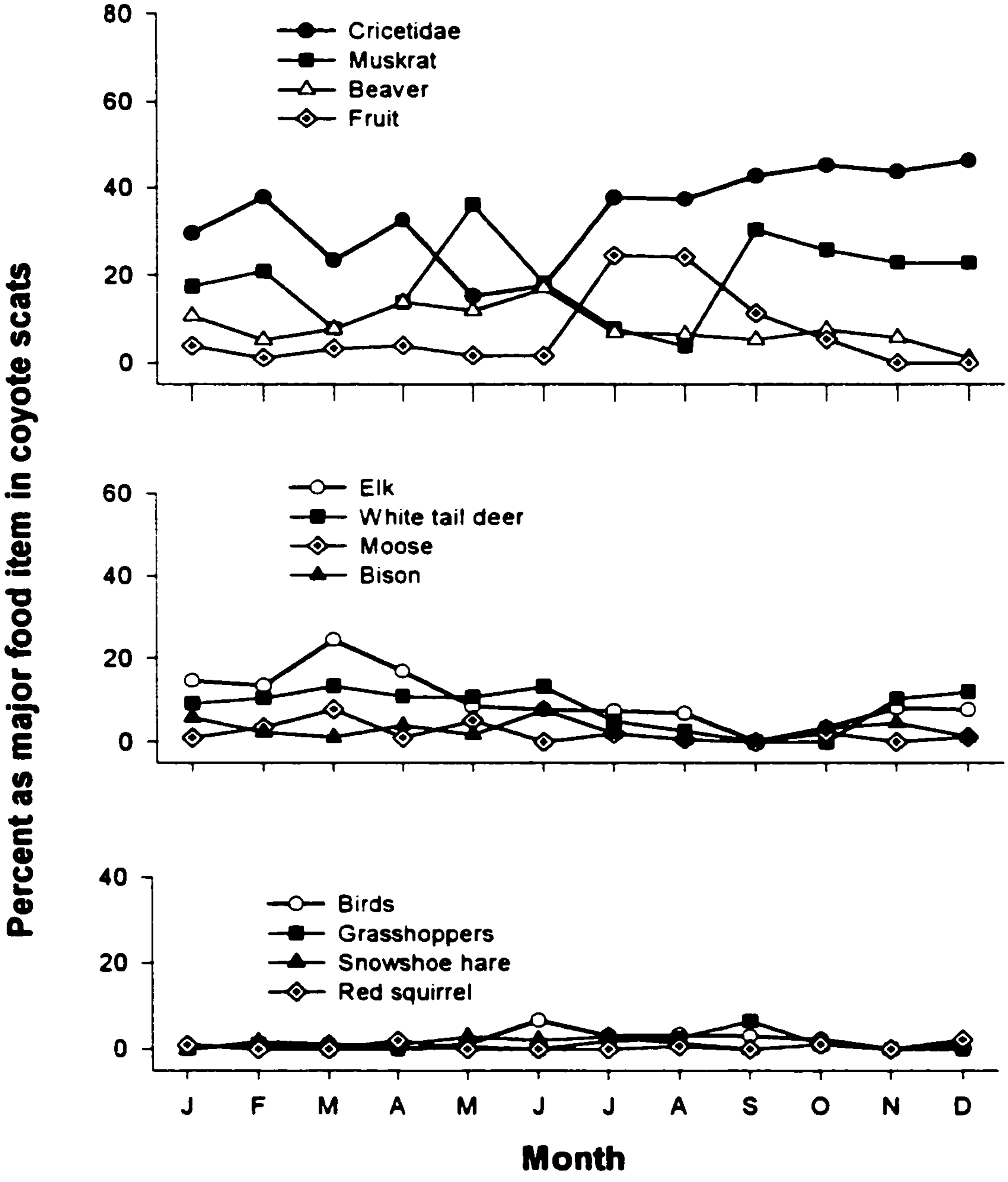

Fig 4-2 Monthly comprisons of percent of major food items (≥ 40% of faecal volume) of the most abundant foods in coyote scats from Elk Island National Park. Data from 1994-2000 have been combined. Cricetidae are comprised of mice, voles, and lemmings. The categories of fruit and birds are comprised of multiple species.

Table 4-2 Percent as a dominant food item and percent occurrence of food items in coyote scats from Elk Island National Park, July 1994 – January 2000. Data are ranked from high to low based on percentage as major food item. Genus and species are provided for individual species. Major items = groups comprising ≥40.0% scat volume. Ground squirrel = Richardson's ground squirrel.

Common name	Order, Family, or Genus and species	Percent as dominant item	Percent occurrence
Mice, voles, lemmings	Cricetidae	32.82	46.06
Muskrat	*Ondatra zibethicus*	19.43	23.29
Elk	*Cervus elaphus*	9.39	16.53
Beaver	*Castor canadensis*	8.54	11.12
White tailed deer	*Odocoileus virginianus*	8.03	14.50
Fruit	-	7.45	14.88
Bison	*Bos bison*	2.68	4.43
Moose	*Alces alces*	2.09	3.38
Birds	Aves	1.71	7.89
Grass	Gramineae	1.47	4.13
Grasshoppers	*Schistocerca americana*	1.28	8.04
Snowshoe hare	*Lepus americanus*	1.16	2.10
Domestic cattle	*Bos taurus*	0.66	2.70
Red squirrel	*Tamiascuirus hudsonicus*	0.54	0.98
Mule deer	*Odocoileus hemionus*	0.54	0.98
Goat	*Capra hircus*	0.39	0.45
Unidentified bones	-	0.35	0.53
Ground squirrels	*Spermophilus richardsonii*	0.31	0.60
Skunk	*Mephitis mephitis*	0.16	0.15
Pocket gopher	*Thomomys talpoides*	0.16	0.30
Domestic cat	*Felix domestica*	0.16	0.53
Least chipmunk	*Eutimias minimus*	0.16	0.22
Woody matter	-	0.08	0.08
Badger	*Taxidea taxus*	0.08	0.08
Beetles	Coleoptera	0.08	0.15
Domestic dog	*Canis familiaris*	0.08	0.15
Porcupine	*Erethizon dorsatum*	0.08	0.45
Raccoon	*Procyon lotor*	0.08	0.08
Shrew	*Sorex* spp.	0.08	0.15

Interestingly, the lowest variation in food items (7 groups) occurred in September when the second peak in muskrats and an increased reliance on grasshoppers is recorded.

Monthly comparisons of ungulates and non-ungulates as major food items in scats showed that non-ungulates comprised between 50 and 100% of coyote diet and was the highest in the late summer months (July through October) (Fig. 4-3). Monthly fluctuations in ungulate remains were highest in March (50%) and lowest in September (Fig. 4-3).

The extent to which neonatal and juvenile ungulates comprise important food for coyotes is unclear. Overall, only 1.8% of total scats were determined to be fawns or calves and the majority of these were collected in June. However, cervid remains are difficult to classify as adult or fawns. Nevertheless, the occurrence of white-tailed deer as a major food item in summer scats was second highest in June (13.2%) (after March) compared with April (10.9%), May (10.7%), July (4.9%) and August (3%) and coincided with the production of fawns.

Social affiliation and diet

ANOVA comparisons indicated that the percent ungulates as the major food item were significantly affected by social affiliation in winter ($F_{(2,23)}$=19.5, P=0.001) but not in the summer ($F_{(2,23)}$=2.9, P=0.07). In winter, the percentage of ungulates as a major food item in packs was significantly higher than that of solitaires and pairs (Bonferroni adjusted means comparisons) (Fig. 4-4).

Changes in the social affiliation of four coyotes over the course of the study provided an opportunity to further evaluate the effects of social organisation on coyote

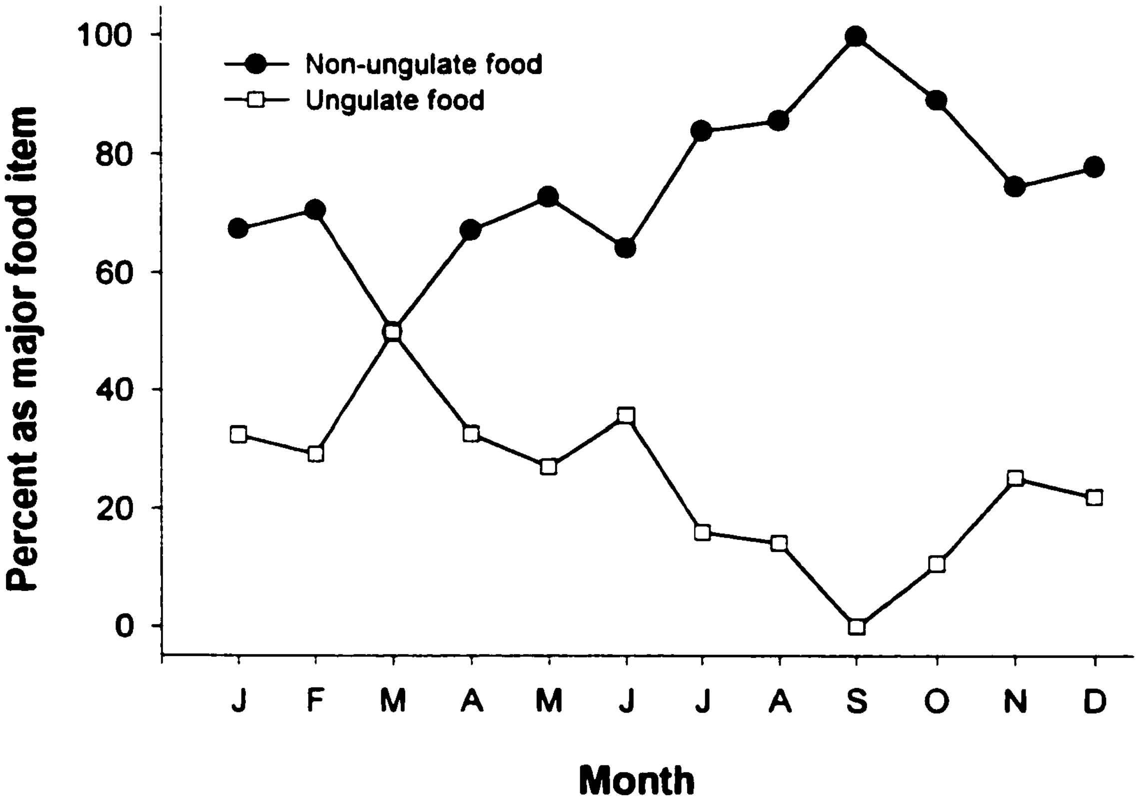

Fig 4-3 Monthly proportions of ungulate and non-ungulate foods occurring as major (≥ 40% of faecal volume) food items in coyote scats in Elk Island National Park.

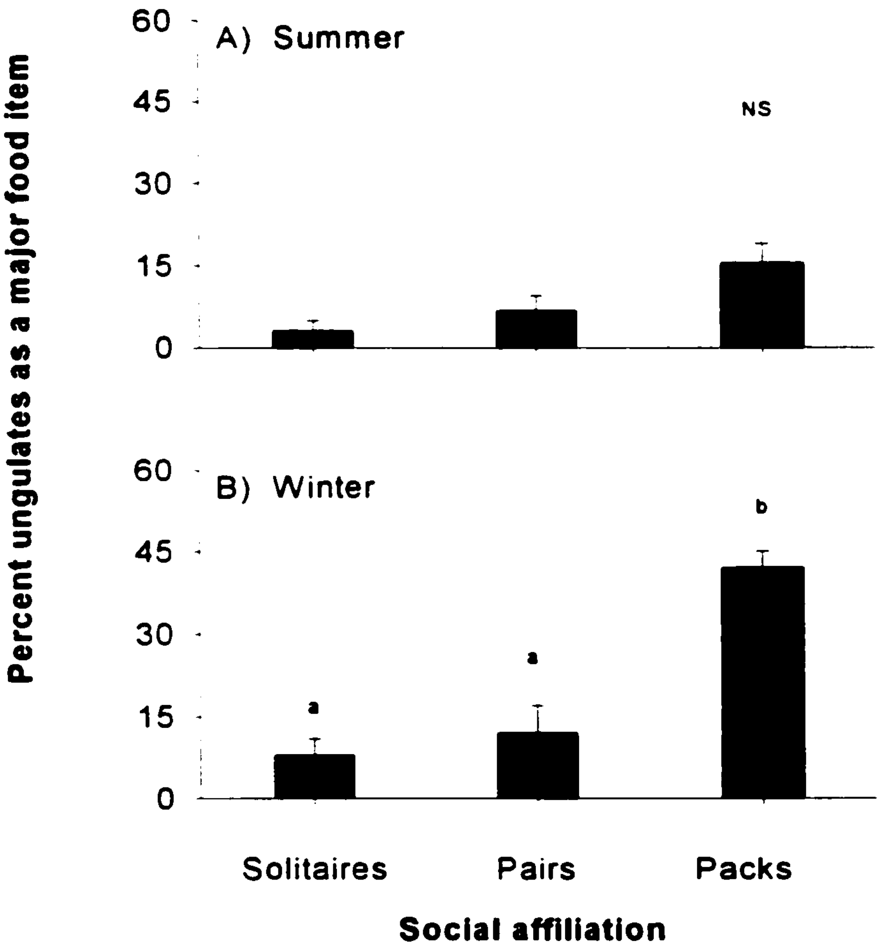

Fig 4-4 Effects of social affiliation on mean (± 1 SE) proportion of ungulates as a major food item in diets of coyotes in EINP. Histograms sharing the same letter are not significantly different. NS=not significant (P>0.05).

diet (Fig. 4-5). Fisher's exact tests showed that changes in social organisation from a solitaire to a pack resulted in a significant ($P< 0.05$) increase in the percent of ungulate food in scats for both individuals (Fig. 4-5). In contrast, dietary changes resulting from a switch in social organisation from a pair to a pack were more equivocal. Significant differences in the percent of ungulates as a major food item increased for only one of the two individuals (Fig. 4-5). Sample sizes were too small to make seasonal comparisons.

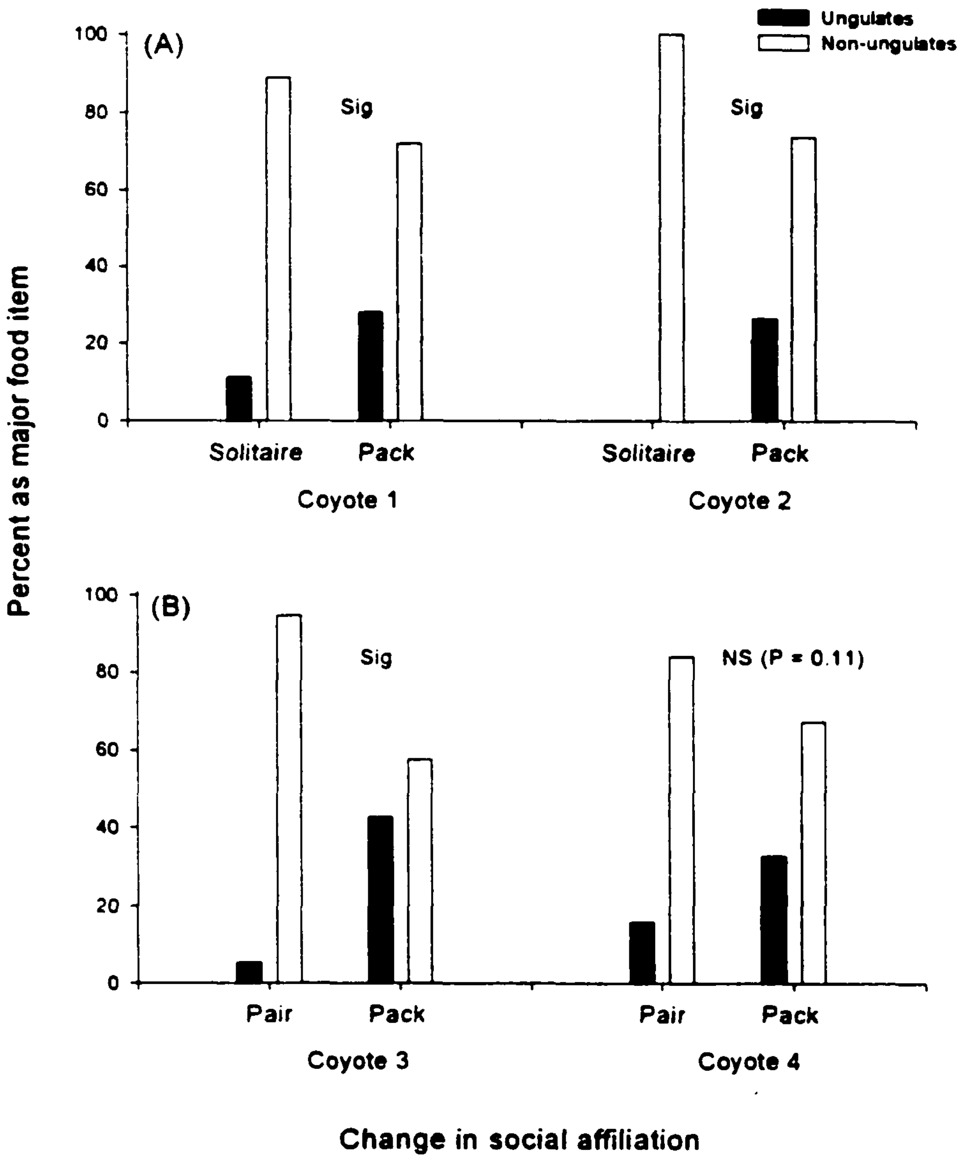

Fig 4-5 Comparisons of percent of ungulates and non-ungulates as major food items for four coyotes in Elk Island National Park that changed social affiliation from (A) solitaires to packs (coyotes 1 and 2) and from (B) pairs to packs (coyotes 3 and 4). Sig.=significant ($P<0.05$), NS=not significant ($P>0.05$).

DISCUSSION

Elk Island National Park provides a unique opportunity to examine diet of coyotes in an ecosystem that supports one of the highest ungulate densities in North America (Blyth and Hudson 1987). Because EINP is completely fenced, it provides protection for coyotes within its boundaries, as well as a unique and discrete source of ungulate food resources either in the form of potential prey or as carrion. Coyotes however are able to move freely in and out of the Park by digging or using existing spaces under the fences and intense coyote exploitation occurs in areas surrounding EINP. Between 1994-2000, EINP supported 3028 ± 421 (mean annual number ± 1SD) ungulates (Cool 2000, Kaye 2000), equivalent to a density of 15.4 ungulates per km^2. Areas adjacent to EINP support reduced densities of moose and elk whereas bison do not exist unless they are farmed. Deer are not managed in EINP but to some extent are able to go over or under the boundary fences (Canadian Heritage 1997). The objectives of the present study were to: 1) describe the composition of coyote diets; 2) describe temporal variations and; 3) evaluate whether coyote diet differed with social affiliation. Diet was examined using scat (faecal) analyses.

Coyotes are opportunistic carnivores that consume a broad diversity of food items including insects, grasses, fruit, reptiles, amphibians, fish and a wide array of mammal and bird species (Bowen1978, Hernandez *et al.* 1994, Andelt 1985, Patterson *et al.* 1998, Kunkel and Pletscher 1999, Dumond *et al.* 2001). Coyotes in EINP ate at least 36 identifiable food items although this is an underestimate because birds, which comprised one category, likely contained several species. Secondly, I am not confident that all Cricetidae species were identified because of the difficulties in distinguishing hair samples

(Table 4-2).

Despite different methods used to analyse scats, (*i.e.* frequency of occurrence, division into major food categories, relative volume of each food type) my results are consistent with that found in other studies. For example, many studies have reported mammals to be a predominant (>80%) food item of coyotes (Gipson 1974, Bowen 1978, MacCracken 1984, Andelt 1985, Toweill and Anthony 1988, Windberg and Mitchell 1990, Brillhart and Kaufman 1994, 1995, Lewis *et al.* 1994, Patterson *et al.* 1998, Lingle 2000, Dumond *et al.* 2001). My study showed that, on average, mammals accounted for 89 ± 11% (mean ± 1SD)(range 66-98 %) of the major food items in the annual coyote diet in EINP. Similarly, several studies have reported the importance of birds, fruit, and insects in coyote diets (Bowen 1981, Andelt 1985, Toweill and Anthony 1988, Windberg and Mitchell 1990, Dumond *et al.* 2001).

Temporal variation in the coyote diet

Seasonal variation in coyote diets often results from changes in abundance, vulnerability, and activity of their prey. My comparisons of coyote scats in EINP showed that on average mammals contributed 82% and 95% of all major food items found in coyote scats during summer and winter, respectively. These data are similar to that reported by Bowen (1981) for coyotes in Jasper National Park located approximately 450 km west of EINP, but differ from that described by Andelt (1985) who recorded that mammals comprised only 28% of the summer diet and 87% of the winter diet of coyotes in Texas.

Small mammals, particularly rodents, are typically a primary food source for coyotes on a year round basis (*e.g.* Bowen 1981, Andelt 1982, Toweill and Anthony 1988, Elliott and Guetig 1990, Windberg and Mitchell 1990, Crete *et al.* 2001). For example, Brillhart and Kaufman (1995) in Kansas report 86% frequency of occurrence for rodents in coyote scats. Given favourable conditions, many species of mice and voles can reproduce throughout the year (Stoddart 1993). The peak of usage as a major food item for coyotes in EINP occurred in December (46%) (Fig. 4-2), and is similar to that found by Bowen (1981) in Jasper where the midwinter peak was 57%.

Although muskrats and beaver are found throughout North America (Boutin and Birkenholz 1987, Novak 1987) they are not commonly found in coyote diets (*e.g.* Elliot and Guetig 1990, Windberg and Mitchell 1990, Brillhart and Kaufman 1995) and are often combined to form a composite food category with other species, such as beaver (*e.g.* Bowen 1981, Messier *et al.* 1986, Toweill and Anthony 1988, Patterson *et al.* 1998, Dumond *et al.* 2001, Crete *et al.* 2001). My results showed that on an annual basis muskrat and beaver alone were a major food in 28% of all scats collected (Table 4-1). The knob and kettle topography of EINP supports numerous wetlands, small lakes, and several large shallow lakes that provide good habitat for muskrat and beaver (Blyth and Hudson 1987).

After mice and voles, muskrats were the most important food source (19% of major food items) for coyotes in EINP (Table 4-1). High use of muskrat by coyotes in May (36%) and September-December (range 23%- 30%) (Fig. 4-1) coincide with the main muskrat dispersal periods. Juvenile muskrat may disperse during the autumn in search of overwintering habitat or, more commonly, may overwinter on the parental home range and disperse in spring in search of breeding territories (Boutin and Birkenholz

1987). Annually, each breeding muskrat pair can produce two to three litters of up to nine young at a time (Danell 1978) potentially resulting in high, biannual juvenile dispersal events. Because the muskrat social unit is the breeding pair with an exclusive home range, animals that do not secure a breeding territory in the spring when the ice melts are forced to disperse, which would make them susceptible to predation (Errington 1963, Proulx and Gilbert 1983).

Although beaver are not as common as muskrats in the diet of EINP coyotes, they still occurred as major food items throughout the year (1%-17%). Increased consumption of beaver by coyotes in June coincides with subadult (≤ 2 years) dispersal just prior to the birth of the annual litter of kits (Novak 1987). The importance of beaver as a food source for EINP coyotes should not be underestimated because yearling and adult (≥ 2 yrs) beavers in Alberta weigh about 9.6 and 15.8 kg., respectively (Novak 1987).

My results also indicate seasonality in the importance of fruits and insects in coyote diets in EINP as has been reported elsewhere (Andelt 1985, Smith 1990, Brillhart and Kaufman 1995, Samson and Crete 1997, Dumond *et al.* 2001). Andelt *et al.* (1987) and Brillhart and Kaufman (1994) found 20% and 10% mean annual use of fruit as a major food (≥ 40% scat volume) for coyotes in Texas and Kansas, respectively.

In EINP, fruits contributed 24% of the major food items in coyote diets in July and August (Fig. 4-2) (38% and 48% frequency of occurrence respectively), (Fig. 4-1) when the frequency of mammals as major food was the lowest (71% and 66 % respectively). Blueberries (*Vaccinium* spp), sarsaparilla berries (*Aralia nudicaulis*), and saskatoons (*Amelanchier alnifolia*) were the predominant fruit species eaten by coyotes in EINP. The occurrence of fruit, often as a sole major food item, suggests that fruits are actively consumed rather than being consumed incidental to other foods. Changes in the importance of fruit and insects in coyote diets could be related to: overall scarcity of alternative food items during late summer and early fall (Samson and Crete 1997); abundance of fruit and insects during these times (Brillhart and Kaufman 1995); or the inexperience of juveniles as hunters. Consumption of fruit by other canids has also been reported and may be an important factor influencing deposition of body fat (Lindstrom 1983) and may result in coyotes actively searching for carbohydrate rich fruit (Dumond *et al.* 2001).

The proportion of ungulate food in the diet of coyotes has been shown to vary considerably throughout North America (Bowen 1981, MacCracken 1984). However, direct comparisons of the importance of ungulates in coyote diets are difficult because of differences in measures used to describe diet (Windberg and Mitchell 1990, Patterson *et al.* 1998). Based on frequency of occurrence, ungulates are often present in 26% to 47% of coyote scats (Toweill and Anthony 1988, Brillhart and Kaufman 1994) and is similar to my observations in EINP (frequency of occurrence = 43%). Comparisons based on frequency as a major food item (≥ 40% of faecal volume) also suggest that ungulates are important food for EINP coyotes. Windberg and Mitchell (1990) reported that white-tailed deer were a major food item in 4-17% of winter coyote scats in Texas, whereas Lingle (2000) found that white-tailed and mule deer comprised 17% of coyote diets in southern Alberta.

Seasonal and annual variability in the use of ungulates as a food item for coyotes is thought to reflect variations in climatic conditions, habitat types, availability of alternate food sources, and coyote social organisation (Bowen 1981, Samson and Crete 1997, Lingle 2000, Dumond *et al.* 2001). My results from EINP indicated that ungulates were a major food item in 25% of all scats collected on an annual basis but was highest in winter (Fig. 4-3). Increased use of ungulates in March coincides with the highest rates of ungulate "winter kill" in EINP (W. Olson, EINP Warden Service, pers. comm. 2000). A secondary peak was observed in June (36%) and may be related to the consumption of young ungulates, particularly bison and white-tailed deer. Although the difference in ungulate percentage in scats between June and the highest months in winter (excluding March) is only 3%.

The role of social organisation in the diets of coyotes

Prey abundance and distribution strongly affect the spatial and social organisation of most medium to large carnivores (Bekoff and Wells 1980, Bowen 1981, Patterson and Messier 2001). In many cases, there is a positive correlation between the size of the animal and/or social group and prey size (Clutton-Brock and Harvey 1983, Macdonald 1983, Moehlman 1987, Gittleman 1989, Carbone et.al 1999).

The general relationship of increased carnivore size with cooperative hunting for larger prey does not always explain differences in group size (Carr and Macdonald 1986, Carbone 1999). For example, jackals hunt small prey in a co-operative manner, whereas individual swift foxes (*Vulpes velox*) and kit foxes (*Vulpes macrotis*) may hunt jackrabbits almost twice their own body weight (Macdonald 1983, Cameron 1984). The resource dispersion hypothesis also suggests that some groups are formed for species like badgers not because of any particular benefits of group membership but rather as a passive result of food distribution (Johnson *et al.* 2001).

I predicted differences in coyote diets in EINP based on their social affiliation (*i.e.* solitaires, pairs, and packs). I tested this prediction by comparing: 1) diets of solitaires, pairs and packs and 2) diets of individuals that changed social affiliation during the study period. These comparisons indicated that the percentage of ungulates as a major diet item was significantly affected by social affiliation in winter (P=0.001) when packs had significantly higher proportions of ungulates in their diet compared with solitaires and pairs (Fig. 4-4). Although the difference is not statistically significant (P=0.07), packs tended to consume higher numbers of ungulates compared with pairs and solitaires in the summer.

Significant effects of social affiliation on winter diet could arise from increased winter carrion and the superior ability of packs (versus pairs or solitaires) to defend this food resource (Bowen 1981, Gese *et al.* 1988, Patterson and Messier 2000). Differences could also result from improved efficacies of coyote packs to hunt or kill large prey such as deer and elk when deep snow is present (Gese *et al.* 1988, Parker and Maxwell 1989, Gese and Grothe 1995, Patterson and Messier 2001).

The lack of a statistically significant effect of social affiliation on coyote diets in the summer is contrary to my initial prediction. However, my comparisons between different social groups does not take into account differences in pack size. In fact, with the exception of Lingle (2000), numerous studies report smaller pack sizes in summer compared to winter (*e.g.* Camenzind 1978, Bowen 1981, Gese *et al.* 1988). Thus, lack of significant differences in summer may reflect reductions in pack size. Alternately, increased adult ungulate survival during the summer (versus annual winter kill) and an abundance of smaller food items during the summer could reduce group cohesion. Finally, group cohesion and large packs could be related more to increased winter carrion availability than predation by coyotes.

Changes in the social affiliation by four coyotes during the study period allowed me to confirm whether differences on an individual level were consistent with population trends. These comparisons confirmed that in three of four coyotes, becoming a member of a pack was associated with a significant increase in the proportion of ungulates as a food item in their diet. Animals that formed packs either from solitary existence or from pairs also became older in the process. The extent to which age, and perhaps experience, accounts for shifts in diet compared with cooperative hunting is not well understood (Gese and Grothe 1995, Patterson and Messier 2000).

Two hypotheses have been posed to explain variation in the social organization of coyotes. The food resource hypothesis states that group size is determined by the size and distribution of their prey (Camenzind 1978, Bekoff and Wells 1980, Bowen 1981). Under this hypothesis, group size increases, whereas individual territory and home range sizes decreases when food resources are abundant, clumped and defendable. Other benefits accrued from group living include: increased predator vigilance, defence of territories and carcasses, increased inclusive fitness, delay or deferral of dispersal, alloparental behaviour, and the possibility of inheriting the familial territory (Bekoff and Wells 1980, Messier and Barrette 1982, Macdonald, 1983, Carr and Macdonald 1986, Moehlman 1981, 1989, Patterson and Messier 2001). In contrast, the competing delayed dispersal / habitat saturation hypothesis (Andelt 1982, Messier and Barrette 1982, Gese 1988, Patterson and Messier 2001) contends that group living in coyotes is a result of delayed or unsuccessful dispersal that can result from late sexual maturity of offspring or high coyote density and habitat saturation resulting in a scarcity of unoccupied territories or home ranges.

In Jasper, Alberta, Bowen (1978) maintained that differences in the size of prey consumed by coyotes explained much of the variation in social organisation whereas Andelt (1982) showed that coyotes in Texas that formed large groups consumed predominately small prey items. Because coyotes in Texas were also present at high densities, large group sizes may have resulted from high habitat saturation and low exploitation by humans. Gese *et al.* (1988) suggested that group size in coyotes influenced prey selection and that 71% of the variation in the volume of ungulate remains in coyote scats was explained by group size but increased group sizes were caused primarily by increased sociality during the breeding season. Clearly, it is not well understood whether group formation develops as a direct response to prey/food availability or in reaction to other selective pressures. Messier and Barrette (1982) have suggested that perhaps prey size only facilitates the unity of groups formed for other reasons. Thus, although it is difficult to determine the mechanism that causes grouping behaviour, coyotes that take advantage of large, clumped, defendable food resources should exhibit larger more cohesive groups than coyotes that do not utilize large prey or carrion (Patterson and Messier 2001).

Elk Island provides a unique opportunity to discriminate between these two hypotheses. Elk Island National Park supports one of the highest ungulate densities in North America, whereas intensive coyote exploitation in areas surrounding EINP likely results in available vacant territories (Blyth and Hudson 1987). Because coyotes are able to move freely from EINP into adjacent habitats, pack formation likely results from or is facilitated by an abundance of large, clumped, defendable food resources, consistent with predictions of the food resource hypothesis. Given the high levels of human exploitation around EINP (Chapter 3), delayed dispersal because of habitat saturation due to high coyote densities in the areas surrounding EINP, is unlikely (Messier and Barrett 1982).

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CHAPTER FIVE

COYOTE DENSITY AND FENCE PERMEABILITY IN ELK ISLAND NATIONAL PARK

INTRODUCTION

Industrial activities such as forestry, oil and gas, and agriculture as well as increased urbanisation and road development have heightened landscape fragmentation. While fragmentation can benefit some species by increasing edge habitat, it often results in overall habitat loss and isolation (Forman 1995). For many animals, habitat patches may be interspersed with, or bounded by, unsuitable environments, and under certain conditions, patch size may affect the local population density (Bender *et al.* 1998). The extent to which boundaries and corridors affect the spatial distribution of a species is dependent on the boundary or corridor scale, its structural form and the spatial and temporal scales at which an animal moves (Lidicker 1999, Puth and Wilson 2001). While both boundaries and corridors modify ecological flows, some structures such as fences and the gaps underneath can serve as both a boundary and a corridor depending on the species in question (Puth and Wilson 2001).

Research on the effects of fences on wildlife has typically focussed on controlling predation on livestock (*e.g.* the dingo barrier fence, Allen and Sparkes 2001), or disease and parasite transmission from wildlife to livestock (*e.g.* veterinary fences in Zimbabwe, Taylor and Martin 1987), and the extent to which fences reduce wildlife collisions with vehicles (Feldhammer *et al.* 1986, Woods 1990, Clevenger *et al.* 2001). In contrast to research on the ecological effects of roads (Haugen 1944, Trombulak and Frissell 2000, Clevenger *et al.* 2001), relatively little work has assessed the extent to which fences affect movements of wildlife (Taylor and Martin 1987) or whether permeability of fences is affected by habitat attributes such as vegetation cover and adjacency to roads (Puth and Wilson 2001). For coyotes, the boundary fence in Elk Island National Park (EINP) is a sharp gradient (Foreman 1995) that redirects the movement of coyotes to areas where they have dug routes to adjacent habitat in or out of EINP (*i.e.* corridors).

Coyotes are the dominant predator in EINP and are thought to attain moderately high densities in the Park, in part because of the abundance of prey like ungulates and muskrats in addition to the absence of large predators such as wolves (*i.e.* mesopredator release). I have shown previously that home ranges of coyotes extend beyond the perimeter fence of Elk Island National Park. However, the extent to which coyotes establish holes in the perimeter fence based on habitat attributes including the adjacency of roads and forest cover types is unknown. Coyotes might be expected to establish holes in a non-random fashion under the perimeter fence if habitat attributes adjacent to the fence vary in the extent to which they provide cover for coyotes, or in soil conditions that are more amenable to digging.

The objectives of the present study were two-fold. First, I quantified the density of coyotes in Elk Island National Park and compared this density estimate with those found previously for coyotes occupying a range of habitats in North America. Second, I quantified the number and location of holes in the perimeter fence surrounding Elk Island National Park. Specifically, I tested the null hypotheses that the density of holes is unaffected by: 1) habitat attributes adjacent to the fence (*i.e.*, agricultural grasslands, forest, wetlands, and roads), 2) season (winter, summer) and 3) adjacency to roads. I predicted that coyotes would create proportionately more holes in vegetation types that would likely provide cover, or soils types amenable to digging, but disproportionately fewer holes when the perimeter fence was bordered by roads.

MATERIALS AND METHODS

Study Area

Elk Island National Park (EINP) is situated 40 kilometres east of Edmonton, Alberta, Canada. It is surrounded primarily by agricultural lands and acreages except for the southern boundary that borders the Cooking Lake-Blackfoot Grazing, Wildlife, and Provincial Recreation Area. EINP is divided by the four lane Highway 16 into a 136 km^2 Main Park north of the highway and the southern 59 km^2 Isolation area. Both areas of the park are completely fenced with a 2.2 m mesh wire fence while the main park is further bisected by a highway that is oriented north and south.

Elk Island is situated in the aspen-parkland ecozone that is transitional between prairie to the south and boreal forest to the north. The area around EINP is commonly known as the Beaver Hills, described as knob and kettle topography that resulted from differential melt of buried remnants of glacial ice (Blyth 1995). This topography also supports numerous small lakes and wetlands.

Vegetation in the park is dominated by trembling aspen (*Populus tremuloides)* and balsam popular (*Populus balsamifera*). Forest stands include white birch (*Betula papyrifera),* Alaska white birch *(Betula neoalaskana)*, white spruce (*Picea glauca)*, black spruce (*Picea mariana)* and tamarack (*Larix laricina)*. Common shrubs and herbs include hazel *(Corylus cornuta*), prickly rose (*Rosa acicularis),* willow (*Salix spp),* sedges (*Carex* *spp.*) and grasses (Gramineae family).

The climate for this region is typical of northern mid latitude continental with associated variations in daily and seasonal temperatures. Mean minimum temperatures of −19.5° C occur in January while mean maximum temperatures of +23°C occur in July while annual average precipitation is 48 cm. (Blyth 1995).

Elk Island National Park supports high densities of large ungulates including plains bison (*Bos bison bison*) and wood bison (*Bos bison athabascae*), wapiti (*Cervus elaphus canadensis*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). With the exception of the coyote, lynx (*Felis lynx*) and red fox (*Vulpes vulpes*), most of the historically resident larger carnivores such as grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), wolf (*Canis lupus*), cougar (*Felis concolor*), and wolverine (*Gulo gulo*) have been extirpated from Elk Island National Park. In EINP, lynx and red fox sightings are uncommon and reports of transient wolf, black bear or cougar are exceptionally rare. Although coyotes are the numerically dominant and largest resident carnivores in EINP, it has been speculated that this area was historically at the northern periphery of its range and that extirpation of wolves and human alteration of the environment has facilitated the expansion of coyote's range (Gipson 1974, Blyth and Hudson 1987).

Density

Data on the location of coyotes were gathered using radio-telemetry (Chapter 3). These data were integrated into a Geographic Information System (ArcView by ESRI ™) and overlaid on a UTM map of Elk Island National Park to identify coyote home ranges.

Complete home ranges (95% utilisation distribution) and core areas (50% utilisation distribution) were created for each coyote. The Animal Movement Analysis Arcview Extension (Hooge and Eichenlaub 1997) was applied to all of the locational point data to calculate a fixed kernel home range utilisation distribution (Worton 1989) for each selected probability (*i.e.* 95% UD and 50% UD). In addition, a polygon shapefile for each selected probability, an associated attribute table containing probability and area fields, and the area calculations for each probability were used to create composite and individual home range and core area maps (Chapter 3).

Density of coyotes in EINP was calculated by adding the number of packs, pairs and solitaires per square kilometre (modified after Kamler and Gipson 2000). I determined the number of packs by dividing the size of EINP (excluding the largest lakes) by the mean core area size for packs assuming contiguous non-overlapping core areas. For these calculations, I used a conservative estimate of three adult coyotes per pack core area. Although coyote packs in the study were observed with as many as six adults, the greatest number of animals that I had collared in a pack was two thus, I was not able to determine the actual core area of a complete pack. In light of this, the use of a relatively low number of coyotes per pack should compensate to some extent for underestimating composite core areas. This same method was used for solitaires assuming full overlap of pack home ranges. Because the extent of overlap or exclusion of other coyotes that is exhibited by pairs is not clear, they were treated both as having complete overlap or being completely excluded from pack ranges and this resulted in a range of potential densities. Lastly I compared the density of coyotes in EINP with that reported elsewhere in North America.

Fence permeability

EINP is divided by a four lane highway into a 136 km^2 "Main Park" area located north of Highway 16 and a smaller southern 59 km^2 "Isolation" area (Blyth and Hudson 1987). Both areas of the park are completely fenced with 2.2 m mesh wire. The perimeters of both park areas were walked during the winter of 1996 - 1997 and the summer of 1997 and each opening under the fence was measured with a tape measure and assigned a UTM location using a handheld global positioning unit. Additionally, the type of habitat adjacent to the hole was described in terms of the coarse vegetation type. These descriptions were used to define habitats within (*i.e.* inside) the park and those outside of the park fence.

Universal transverse mercator (UTM) locational data for each hole in the perimeter fence was integrated into a Geographic Information System (ArcView by ESRI™) and overlaid on a 1995 digital orthophoto map of Elk Island National Park. Maps of the hole locations were created for both summer and winter. The U.S. military Department of Defence Satellite Selective Availability of GPS locations ended on April 30, 2000 thus all locations collected prior to this date have a variable margin of error. As a result, holes on the GIS map were manually aligned with the Park fence using ground-truthed descriptions of habitats adjacent to each hole. Holes that were smaller than 15 x 15 cm (height by width) or larger than 150 cm in width were excluded from analyses. Small holes were considered too little for coyotes to pass through and very wide holes were often the result of fence sections that did not reach the ground and were not dug by coyotes. Finally, the orthorectified photo map was used to quantify: 1) the total length of the perimeter fence around EINP and, 2) the length of each habitat combination along the fence (Table 5-1) compared to the habitats where holes were located.

I determined whether habitat characteristics affected the distribution of coyote holes in the perimeter fence of EINP using a Chi-square goodness of fit test. This analysis was used to test the null hypothesis that the number of holes that coyotes dug under the perimeter fence did not differ from that expected based on the relative abundance of habitat types. These analyses were completed separately for winter and summer. To maximize the extent to which the Chi-square distribution approximates the true distribution, I combined habitat types when expected numbers of holes based on the habitat availability were less than 0.5 (Iman 1994). As a result Chi-square tests were completed using 15 habitat type categories for both summer and winter.

The Chi-square analysis was also used to test the null hypothesis that the number of holes established under the perimeter fence adjacent to roads outside of EINP does not differ from that expected based on the availability of roads. The Yates correction for continuity was used in this analysis to correct for one degree of freedom (Zar 1984).

RESULTS

Density

The mean home range size of pack members (3.4 km^2 ± 2.7 km^2) (mean ± 1SD) was less than that of pairs (10.2 km^2 ± 5.6 km^2) or solitaires (16.1 km^2 ± 2.7 km^2) respectively. Core areas (*i.e.* 50% UD) of adjacent packs did not overlap, whereas core areas for solitaires overlapped those of packs, pairs, and other solitaires. Because the extent of overlap or exclusion of other coyotes that is exhibited by pairs is not well

Table 5-1 Distances (metres) and relative abundance of habitat types adjacent to the perimeter fence around Elk Island National Park, Alberta, Canada.

Physical description In	Out	Length	Percent of total
Conifer	Conifer	114	0.13
Conifer	Deciduous	355	0.40
Conifer	Grassland	113	0.13
Conifer	Road	274	0.31
Deciduous	Conifer	98	0.11
Deciduous	Deciduous	17681	19.84
Deciduous	Grassland	3424	3.84
Deciduous	Wetland	2343	2.63
Deciduous	Road	30958	34.75
Grassland	Conifer	231	0.26
Grassland	Deciduous	2527	2.84
Grassland	Grassland	2329	2.61
Grassland	Wetland	1207	1.35
Grassland	Road	9127	10.24
Wetland	Deciduous	2196	2.46
Wetland	Grassland	378	0.42
Wetland	Wetland	3732	4.19
Wetland	Road	12009	13.49
Total		89096	100.00

understood in EINP, they were treated both as having complete overlap or being completely excluded from pack ranges. Using these data, I estimated a pre-whelping (winter) density of coyotes in EINP of 0.87 – 1.05 coyotes/km^2. When compared with other published accounts, coyote density in EINP is relatively high (Table 5-2).

Fence permeability

Excluding holes smaller than 15 by 15 cm or those that were formed by gates and fences that did not reach the ground (fence/gate holes for winter n=8; and summer n= 64), resulted in 155 holes in the winter and 344 holes in the summer. Chi-square analyses showed a significant difference (Chi square = 141.96, d.f. = 14, $P<0.001$) between the observed and the expected numbers of holes dug by coyotes in winter based on habitat availability (Fig. 5-1). During winter and with the exception of conifer-grass and grass-wetland combinations, coyotes established more holes in the perimeter fence when adjacent habitats were dominated by conifer and wetlands (range 161-2346% more than expected). In contrast, coyotes established disproportionately fewer holes than would be expected based on availability of habitat bordered by grassland. Lastly, coyotes dug holes in areas bordered by grass-deciduous and deciduous-deciduous habitats in approximate numbers that would be expected based on habitat availability. Where the Park fence bordered roads, coyotes dug markedly more holes when roads were bordered by wetlands and conifer but disproportionately fewer when roads were bordered by deciduous forest and grasslands (Fig. 5-1).

Table 5-2 Comparison of estimates of population density (number per km^2) of coyotes in North America. – data not available. Winter = pre-whelping.

Location	Year	Habitat	Month/Season	Density
Alberta[1]	1965-66	Forest & grassland	Winter	0.06 to 0.4
Alberta[1]	1966-67	Forest & grassland	Winter	0.09 to 0.6
Alberta[1]	1967-68	Forest & grassland	Winter	0.04 to 0.27
Alberta[2]	1974-77	Forest & grassland	Winter	0.35
			Post-whelping	0.46
Alberta[3]	1994-99	Forest & grassland	Pre-whelping	0.87 to 1.05
Arizona[4]	1992	Desert scrub & Residential	Jan.–Dec.	3.2 to 4.6
Colorado[5]	1983-86	Grasslands	Pre-whelping	0.29
Kansas[6]	1995-98	Forest & grassland	Pre-whelping	0.8 to 0.9
Montana[7]	1977-79	Riparian & grassland	Jan-Dec.	0.39
New Brunswick[8]	1995-97	Forest	Winter	<0.1
Nova Scotia[9]	-	Forest	Winter	0.04 to 0.14
Quebec[10]	1991	Forest	July	0.02-0.03
Tennessee[11]	1986	Forest & grassland	Jan-March	0.35
Texas[12]	1965-68	Semi-desert	Fall	1.5-2.3
Texas[13]	1985	Grasslands	Spring	2.0
Texas[14]	1978-79	Grasslands & wetlands	pre-whelping	0.8-0.9
			Fall	0.9-1.0
Utah[15]	1977-78	Shrub desert	Fall	0.19-0.59

[1]Nellis and Keith 1976, [2]Bowen 1978, [3]Alberta - this study, [4]McClure *et al.* 1996, [5]Gese *et al.* 1989, [6]Kamler and Gipson 2000, [7]Pyrah 1984, [8]Dumond 1997 cited in Dumond and Villard 2000, [9]Patterson and Messier 2001, [10]Samson and Crete 1997, [11]Babb and Kennedy 1989, [12]Knowlton 1972, [13]Windberg 1995, [14]Andelt 1982, [15]Davison 1980.

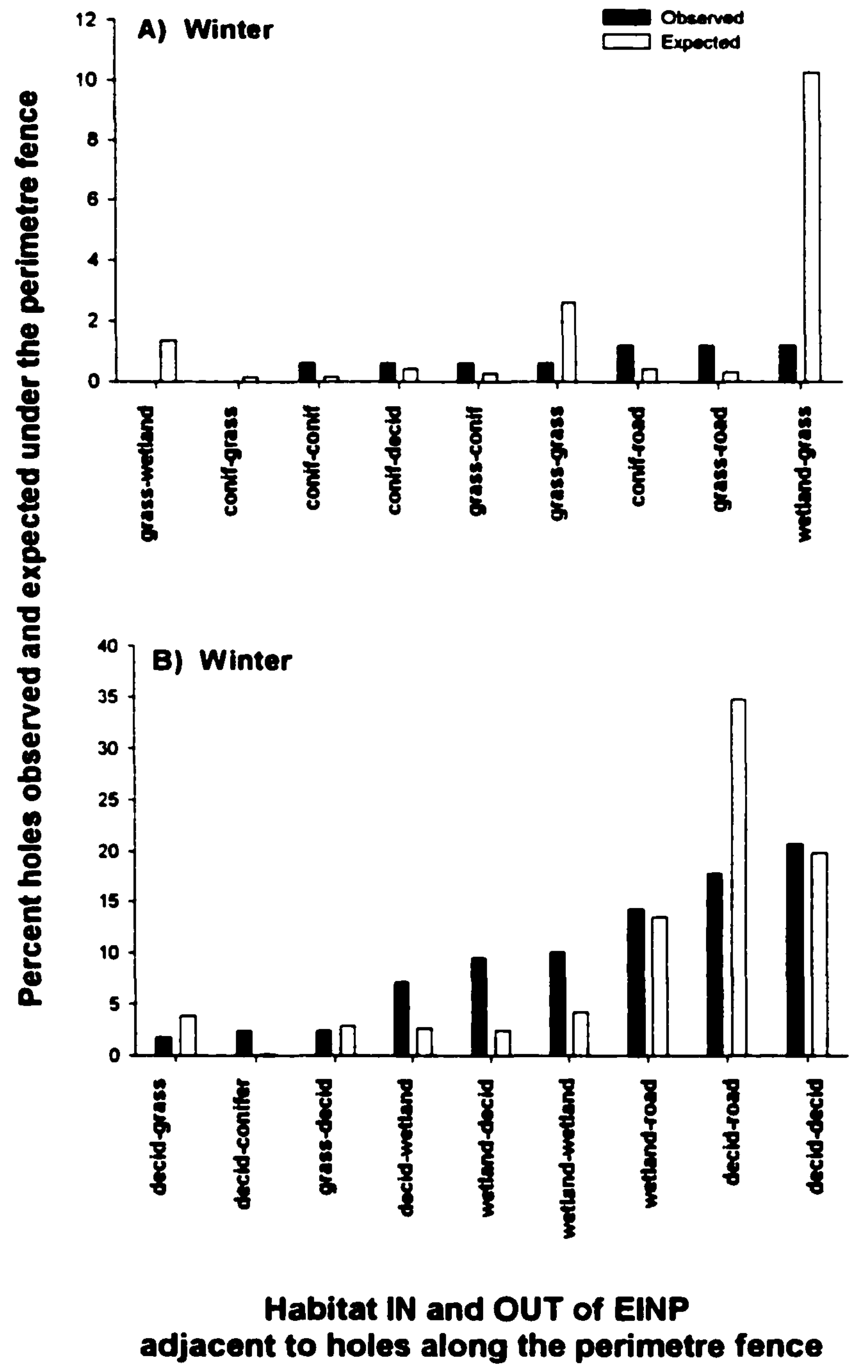

Fig 5-1 Comparison of observed and expected percent of holes dug by coyotes during winter under the perimeter fence for each habitat combination (IN-OUT) along the boundary in Elk Island National Park, Alberta, Canada. A) Observed percentages < 2%, B) observed percentages >2%.

Comparisons using Chi square analyses during the summer months also revealed similar differences between holes dug in different habitat types and that expected based on habitat availability (Fig. 5-2) (Chi square = 122.01, d.f. = 14, $P<0.001$). In the summer, the greatest differences between the numbers of holes observed and predicted tended to occur in habitats dominated by conifer or wetlands combined with all other vegetation types. Coyotes established disproportionately more holes in these areas than would be expected based on availability (percent difference: range 74 – 1057 %) (Fig. 5-2), the only exceptions were holes located adjacent to wetland-grassland and deciduous-wetland. In summer, coyotes established fewer holes adjacent to roads than expected except when roads were bordered by wetlands (Fig. 5-2).

In both summer and winter, coyotes dug significantly fewer holes under the perimeter fence when they were bordered by roads compared to when roads were absent (Winter: Chi square = 24.04, d.f. = 1, $P<0.001$; and summer: Chi square = 4.87, d.f. = 1, $P<0.05$) (Fig. 5-3). In winter, coyotes established 1.61 holes per km when the fence was bordered by roads but 1.95 holes per km when roads were absent. In the summer, perimeter holes occurred at a density of 3.37 holes/km along roads and 4.64 holes/km in areas that did not border roads.

Comparisons of hole heights and widths showed that holes dug by coyotes in the summer were significantly (t-test on log10 transformed data = 7.5, df = 466, $p<0.001$) higher (mean ± 1SD; summer =27.2 ± 10.4 cm) than those in the winter (20.8 ± 5.7 cm). Similarly, holes dug by coyotes in the summer (47.5 ± 30.5 cm) were also significantly wider than those in winter (39.2 ± 20.7 cm) (t-test on log10 transformed data = 3.0, df = 466, $p<0.001$).

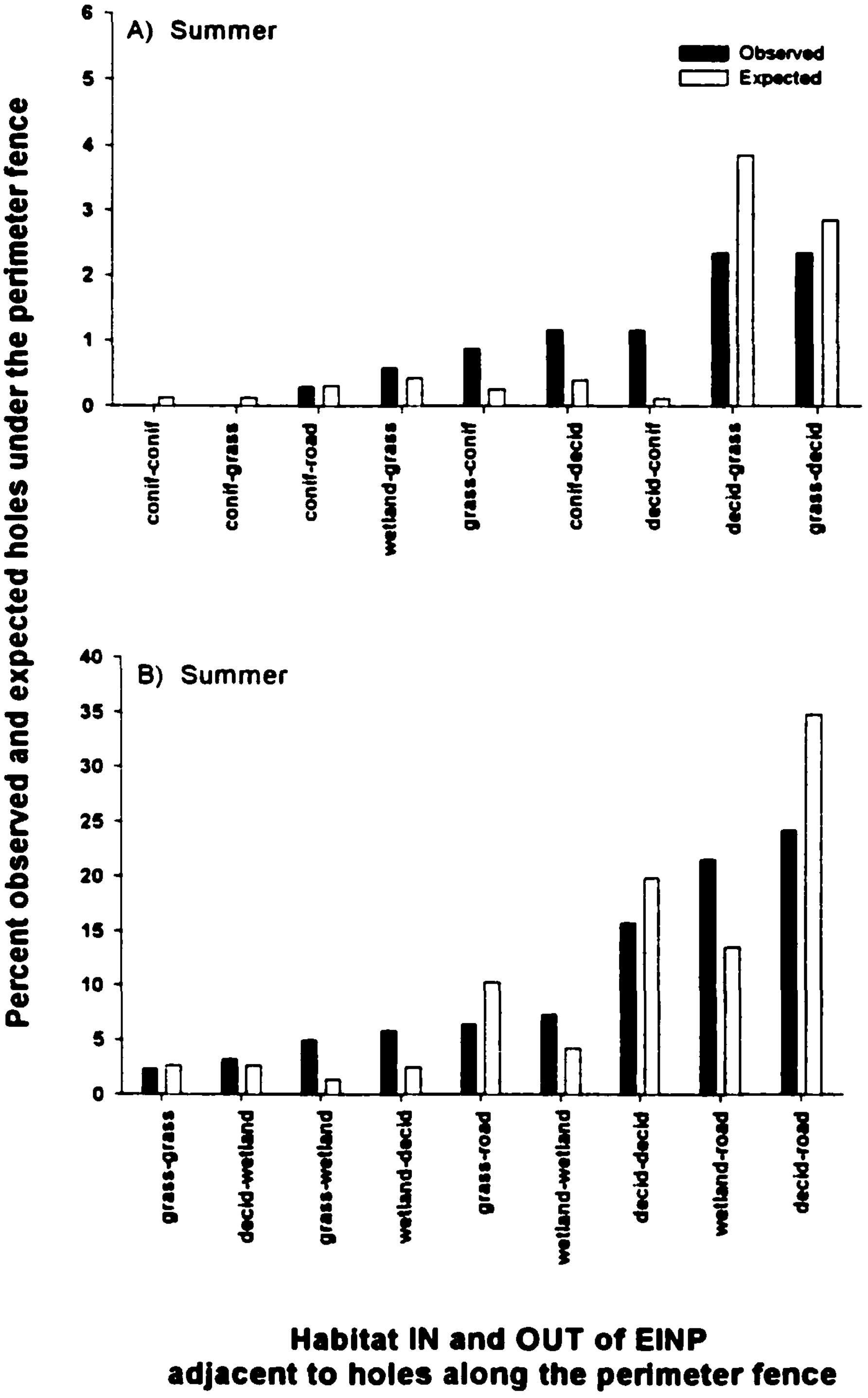

Fig 5-2 Comparison of observed and expected percent of holes dug by coyotes during summer under the erimeter fence for each habitat combination (IN-OUT) along the boundary in Elk Island National Park, Alberta, Canada. A) Observed percentages < 3%, B) observed percentages ≥3%.

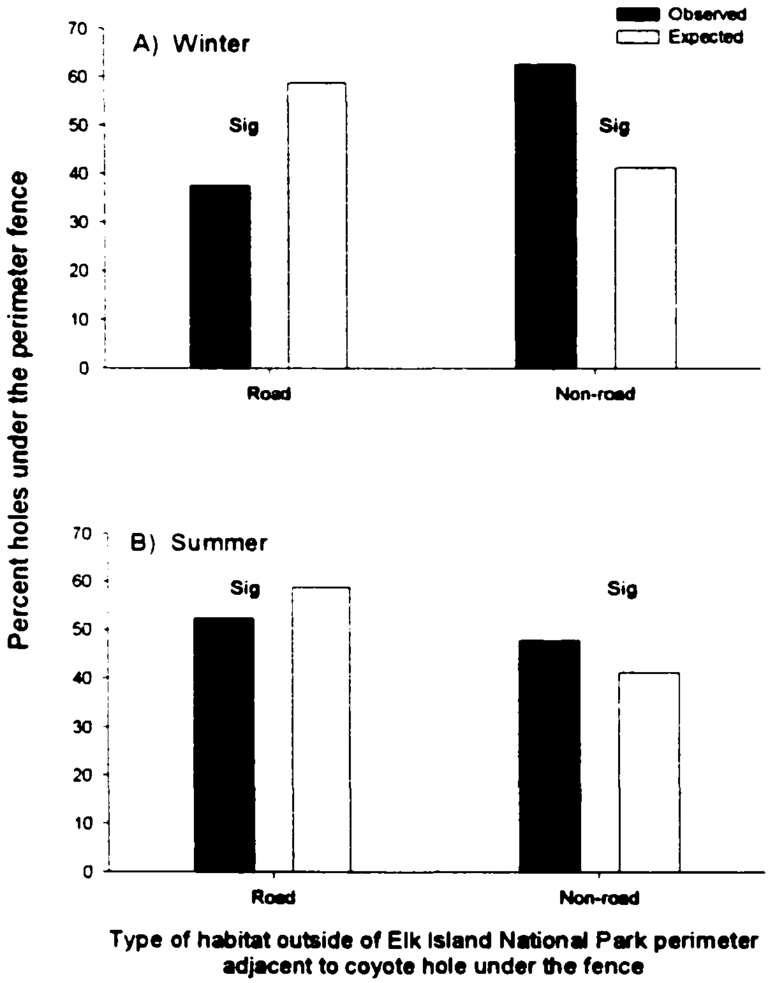

Fig 5-3 Comparison of observed and expected percent of holes dug by coyotes under the perimeter fence for habitat inside Elk Island National Park bordering outside road and non-road areas during A)Winter and B) Summer.

DISCUSSION

Density estimates provide information about the abundance and spatial distribution of an animal population (Smallwood and Schonewald 1998). My review of the literature showed that coyote densities were highly variable. While this variance is likely affected by habitat quality, density estimates also vary with the time of year when they are calculated. My pre-whelping density of 0.87 to 1.05 is relatively high and is exceeded only by populations in Arizona (McClure *et al.* 1996) and Texas (Knowlton 1972, Windberg 1995). In Arizona, high densities are thought to arise in part from abundant urban food sources, as well as a prohibition on hunting and trapping in the neighbouring national park. The relatively high estimates of coyote density in Elk Island National Park (0.87 to 1.05 coyotes/km^2) may be a result of the high ungulate biomass in combination with other factors like increased protection.

An alternate view is that high population density estimates may result from biases in study site selection and these estimates may be higher than what the surrounding areas are capable of supporting. For example, Smallwood and Schonewald (1996) suggested that many study areas are chosen initially because of high densities and clustering of animal populations (Taylor and Taylor 1977). Consequently, spatial scale plays an important role in estimates and in a review of carnivore densities, Smallwood and Schonewald (1998) concluded that density consistently decreased as the study area increased. Thus, EINP may be a higher density patch or cluster of coyotes within a broader habitat matrix (Forman 1995). The most obvious boundary that delimits this ecological patch is the perimeter fence that contains corridors or "channelized routes" dug under the fence by the coyotes, which directs their access into and out of the park.

My comparisons of the density of holes among different habitats suggests that coyotes establish holes under the perimeter fence in a non-random fashion. In general, based on habitat availability, coyotes established disproportionately more holes than expected when lengths of the fence were next to conifer forest and wetlands but dug fewer than expected in areas bordering grasslands and roads. Although habitat use in home range studies may result from different pressures than that which govern the selection of habitats for runways under the perimeter fence, some similarities emerge. For example, Roy and Dorrance (1985) found that coyotes in Alberta preferred forested areas and avoided open areas near travelled roads during the day. In other studies, coyotes have been shown to occupy open grassland habitats less than expected (Gese *et al.* 1988), or that coyotes neither preferred nor avoided these habitats (Crete *et al.* 2001). Holzman *et al.* (1992) suggested that coyotes preferred to use brushy areas at night. My results showed that coyotes established disproportionately fewer holes in the perimeter fence when bordered by grasslands. The use of open or forested habitats may also be influenced by social grouping. For instance, Kamler and Gipson (2000) found resident coyotes used grassland habitat more than expected whereas transients used forested areas more than expected.

While the mechanisms determining why coyotes established disproportionately more holes in the perimeter fence when they were bordered by forests (in particular conifer) and wetlands is not known it may be related to reducing an animal's visibility. Because coyotes are primarily visual hunters (Wells and Lehner 1978, Bekoff and Wells 1980, Laundre and Keller 1984), solitary or transient coyotes may be more apt to trespass on established territories and home ranges under the cover of darkness (Chapter 3) and to access the Park adjacent to areas that offer visual protection. Additionally, my data indicate that all radio-collared coyotes spent some time outside of EINP where they become vulnerable to trapping, shooting, being chased and run over by snowmobiles, and being hit by vehicles. Coyotes may access areas outside of the Park by establishing holes adjacent to forests and wetlands because they reduce the probability of being detected by humans, or if encountered, provide habitats where coyotes can seek refuge. Both conifer and marshy wetland areas in EINP tend to provide dense, thick habitat structure, which would presumably offer cover. Alternately coyotes could establish holes in the perimeter fence alongside wetlands because these areas may contain saturated soils that could be easier to dig.

My results also indicate a reduced number of holes in the perimeter fence in the winter compared to the summer. Seasonal differences in the number of holes under the perimeter fence may be related to snow pack and the amount of time and energy required for coyotes to dig into frozen soils or to clear snow from existing runways under the fence. Grassland areas where coyotes would be particularly vulnerable during winter months were used less than expected or avoided altogether compared to the summer.

Roads often have negative effects on wildlife populations (Woods 1990, Clevenger *et al.* 2001) resulting from mortality during road construction, and vehicle collisions, or by reducing habitat quality through fragmentation of habitat, modification of animal behaviour, alteration of the chemical and physical environment, introduction of exotic species, and increased access and use of areas by human (Oehler and Litvaitis 1996, Trombulak and Frissell 2000, Clevenger *et al.* 2001). Not surprisingly, coyotes established significantly fewer holes than expected when the perimeter fence bordered a road. My results from EINP (Chapter 3) also indicate that humans were the source of 77% of the known coyote mortalities in this study and 27% of those were caused by collisions with vehicles. Alternately, coyotes could be attracted to and benefit from road-killed sources of food. Coyotes on roads may also be more vulnerable to hunters and snowmobilers. Visually, coyotes may be more obvious in winter as well as escape routes may be more limited if there is deep snow. Fur trappers around EINP also set traps closer to roads because of increased ease of access. Although significantly fewer holes were established adjacent to roads in both summer ($P<0.05$) and winter, the trend was more pronounced in winter ($P<0.001$). Additional research is required to determine whether the establishment of holes in the perimeter fence is related to reducing encounters with other coyotes and humans or due to soil properties.

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CHAPTER SIX

SYNTHESIS

BACKGROUND AND RATIONALE

Social and spatial organisation of carnivores is thought to be strongly affected by resource availability and dispersion (Bekoff and Wells 1980, Bowen 1981, Macdonald 1983, Bekoff and Wells 1986). There is often a positive association between the size of the animal and/or social group and the size of the prey consumed (Clutton-Brock and Harvey 1983, Macdonald 1983, Vezina 1985, Gittleman 1989). Increased group size is thought to enable animals to hunt co-operatively to capture larger prey (Nudds 1977, Gese *et al.* 1988). The adaptive value of belonging to a social group however also includes predator avoidance, increased vigilance and territorial boundary patrol, the delay or elimination of the costs of dispersal, increased inclusive fitness, and alloparental behaviour (Geist 1974, Bekoff *et al.* 1981, Messier and Barrette 1982, Gittleman 1989, Bekoff and Wells 1986, Creel 1996, Patterson and Messier 2001).

In the order Carnivora, as a general rule, home range size increases with metabolic needs (Gittleman and Harvey 1982, Mace *et al.* 1983). As a result, some of the variation in home range size can be explained by diet and resource distribution (Grant *et al.* 1992). Differences in canid social organization and the use of space are, in part, species-specific adaptations to differences in food resources (*i.e.*, size; temporal and spatial availability) (Bekoff *et al.* 1981, Geffen *et al.* 1996), particularly in species that display a highly flexible social structure (Bekoff and Wells 1986, Moehlman 1989, Gompper and Wayne 1996). Nonetheless, it is not well understood whether group formation develops as a direct response to prey availability or in reaction to other selective pressures. Although the mechanisms influencing social organisation in animals with flexible social structure are unclear, social organisation is also related to the use of space (Bowen 1981, Messier and Barrett 1982, Andelt 1985, Mills and Knowlton 1991, Patterson and Messier 2001). For example, the exclusion of con-specific competitors from core use areas in home ranges seems to be related to reproduction and the restriction of adult movement when pups are young (Andelt *et al.* 1979). The importance of a core area or territory for social animals with altricial young has been linked to neonatal and juvenile protection as well as a resource base from which to feed offspring (Messier and Barrette 1982, Allen *et al.* 1999). In fact, multi-generational site fidelity has been suggested for coyote packs where sharing and inheritance of home ranges may provide an advantage for offspring, particularly in cases when coyote density is high and dispersal territories are limited (Kitchen *et al.* 2000).

Coyotes in EINP exist at the northern limit of their historical range in a protected remnant of aspen parkland with an abundant intact ungulate guild. In the absence of the major competing carnivores such as bears, wolverines, cougars, and wolves, coyotes have become the largest and numerically dominant predator in the system. However, intense exploitation continues in areas surrounding EINP. Adaptation to these atypical circumstances and food resources within EINP should result in some differences in coyote survival, social and spatial organisation, diet, and density compared to coyote populations elsewhere in North America.

EVALUATION OF A MODIFIED NECK SNARE TO LIVE-CAPTURE COYOTES

I used diazepam tabs on a modified neck snare to decrease injuries and stress to captured coyotes (*Canis latrans*) during winter in Elk Island National Park (Chapter 2). I tested the following hypotheses: 1) diazepam tabs would sedate and calm the captured animals thereby reducing aggression and lacerations; and 2) the modified neck snare would have lower capture mortality and non-target captures while maintaining capture efficiency when compared to published results for padded and nonpadded leghold traps, foot snares, and regular neck snares.

Fifty-one coyotes were caught in this neck snare resulting in a cumulative capture efficiency of 5.4 coyotes/1000 trap nights with 96% of coyotes captured around the neck. Capture mortality was low (<2%) and the neck snare was highly selective; non-target animals comprised 5.5% of all captures. The addition of diazepam tabs significantly reduced the facial and oral lacerations when coyotes chewed and/or removed by the tranquilizer. Aggression of coyotes in the modified snare tended to be related to the presence of lacerations. Modified neck snares appear to be a humane technique for capturing coyotes during winter in forested areas without compromising capture efficiency or increasing capture of non-target species.

The placement of a sedative or anxiolytic on a live-capture snare to reduce stress and injury has not been reported in the literature. My results indicate that this technique has the potential to contribute to a more humane method of live-capture for coyotes and conceivably canids in general. One of the natural extensions of this research is to assess the effectiveness of a higher dosage of diazepam on the modified neck snare on coyote behaviour and injury rates. Behaviour and injury could then be compared to the presence of diazepam metabolites in the blood of captured coyotes. Additionally, the utility of this modified snaring technique could be assessed during the autumn prior to snowfall. Although the dosage used in this study was successful, higher dosages may have resulted in additional reductions in lacerations and stress. For example, ingestion of up to 400 mg of diazepam is still well within the safety range for a canid of coyote size and would produce more effective sedation without inducing compromising ataxia (D. H. Neil and T. F. Bayans, Veterinarians, University of Alberta, personal communication).

SURVIVAL AND EFFECTS OF SOCIAL AFFILIATION ON HOME RANGE CHARACTERISTICS OF COYOTES

The objectives of Chapter 3 were to quantify survival rates and home ranges of coyotes in EINP and to determine whether survival and home range were related to gender and social affiliation. Specifically, I tested the hypotheses that: 1) mean annual coyote survival in EINP is unaffected by gender, and using separate analyses, 2) coyote home range, core area, and perimeter size are unaffected by social organisation, gender and the interaction of these factors and; 3) coyote home range, core area, and perimeter are unaffected by social organisation, time of day (day or night), and season (summer or winter). I also a) determined causes of mortality of radio-collared coyotes and; b) tested for a relationships between: i) coyote survival and pelt price; ii) coyote survival of collared coyotes and total coyote trapping harvest in Alberta and; iii) annual sales of coyote pelts in Alberta with pelt price to understand potential factors affecting coyote survival. For comparative purposes, I contrasted survival rates of coyotes in EINP with previously published data from other studies.

Annual survival of coyotes in EINP was moderately variable and ranged from 0.6 to 0.9. EINP's small size and the ability of the coyotes to move freely beyond boundary fences into agricultural areas markedly increases their risk of human induced sources of mortality (*i.e.*, hunting, trapping or snaring, collisions with vehicles) which comprised 77% of confirmed mortalities. The length of time that coyotes survived following collaring was negatively related to the percent of telemetry locations that identified coyotes as being outside of EINP and/or Blackfoot recreation area. In contrast to the relatively minor differences in annual survival of females and males, differences in sex-specific survival were more pronounced when calculated over the entire study period. These calculations showed a seven-fold difference in survival of females (3%) compared to males (22%)for the 74 month period.

Annual survival of coyotes in EINP was negatively related to prices paid to trappers for coyote pelts. This negative relationship between survival of the EINP coyote population coincides with a moderately strong relationship between coyote trapping effort (*i.e.* annual number of pelts sold from Alberta) and pelt prices, however the weak relationship between EINP coyote survival and Alberta pelt sales may partially be explained by the high mortality rate of coyotes not trapped for fur.

Results of my study indicate significant effects of coyote social organisation on home range, core area, and perimeters of solitaires, members of a pair, and members of a pack. Individual home range, core area, and perimeters decreased significantly with increasing group size (*i.e.*, one (solitaires), two (pairs) and three or more (packs)). Solitary coyote home ranges consistently overlapped home ranges of all social group types and were almost nine fold larger than those of pack members. With the exception of the use of core areas by solitary coyotes, diurnal and nocturnal home ranges were not significantly different within social groups. In addition, coyotes in EINP did not exhibit seasonal (*i.e.* summer/winter) variation in home ranges within each social group. Although all coyotes travelled beyond boundary fences, linear regression showed that home range area typically increased as coyotes spent more time outside of EINP. Home range sizes for coyotes in EINP are comparable to those published elsewhere in North America and my results indicate that variation in home ranges results from differences in social organisation rather than gender.

Survival rates and home ranges of coyotes in this study may provide some insight into the effectiveness of a small, protected area like EINP. For single species estimates, average female home range size is thought to be a better predictor of critical reserve size than population density thus extrapolating from the literature, a female in a coyote pair with a home range of 73 km^2 would require a critical reserve size of approximately 800 km^2 (Woodroffe and Ginsberg, 1998). The concept of reserve size changes when considering assemblages of species. Gurd *et al.* (2001) estimated minimum reserve sizes in eastern North America would have to be 5037 km^2 (95% confidence intervals = 2700-13,296 km^2) to ensure that reserves would not lose terrestrial mammals because of insularization. Clearly, it would appear that EINP is too small for most carnivores to function as a conservation area.

My comparisons of coyote survival and home range sizes both supports previously published studies as well as providing new information. For example, annual survival rates of 0.6-0.9 and the negative relationship between individual home range size and increasing group size has been reported previously. However, long-term survival is rarely quantified. While survival of coyotes in Elk Island National Park is in the upper range of coyote survival estimates, these rates are seemingly low for a protected area. My results also identified a negative relationship between length of time that coyotes survived following collaring and the percent of telemetry locations that identified coyotes as being outside of EINP. Although other studies have documented diurnal and nocturnal movement rates (metres/hour or a linear measure between successive telemetry locations), proximity to roads, and diel habitat use (Woodruff and Keller 1982, Roy and Dorrance 1985, Holzman *et al.* 1992, Gibeau 1992) there is little information on diurnal and nocturnal patterns in home range or core area use. My results showed that core areas for solitaires were significantly larger at night compared to the day and that this difference may reflect temporal avoidance of conspecifics.

Further research into the social and spatial organisation of coyotes in EINP could involve investigations of the age at which juvenile coyotes disperse and to describe dispersal patterns in relation to age and sex. Juveniles/pups could be collared prior to the fall dispersal period. Genetic relationships of pack members could also be studied and the social organisation of coyotes outside of EINP in surrounding agricultural lands could be compared to those within EINP. The obvious difficulty with the latter point is having coyotes live for a sufficient period of time in an agricultural setting to allow data collection. Finally, insights into the overall demographics of coyotes in Alberta could be gleaned from the high numbers of coyotes that comprise annual trapping harvest.

SEASONALITY AND EFFECTS OF SOCIAL AFFILIATION ON THE DIET OF A NORTHERN POPULATION OF COYOTES (*CANIS LATRANS*)

The objectives of Chapter 4 were to examine the seasonality of coyote diets in Elk Island National Park and evaluate the differences in diet of solitaires, pairs, packs in summer and winter. Specifically, I tested the hypotheses that 1) diet is unaffected by seasons (*i.e.* months), and 2) proportion of ungulates as food items in the coyote diet would not differ between social groups during summer and winter.

My study showed that coyotes in EINP ate at least 36 different identifiable food items. On average, mammals accounted for 89 ± 11% (mean ± 1SD) of the major food items in the annual coyote diet in EINP, which on a seasonal basis resulted in 82% and 95% mammal content in the summer and winter, respectively. Small mammals, particularly rodents, were a primary food source for coyotes on a year round basis with the peak of usage in December (46%). After mice and voles, muskrats were the most important food source (19% of major food items) and highest use occurred in May (36%) and September-December (range 23%- 30%) coinciding with the main muskrat dispersal periods. Although beaver are not as common in the diet of EINP coyotes, they still occurred as a major food item throughout the year (1%-17%). Fruits contributed 24% of the major food items in coyote diets in July and August when the frequency of mammals as major food items was the lowest.

Ungulates were a major ($\geq$ 40% faecal content) food item in 25% of all scats (43% frequency of occurrence) collected from EINP on an annual basis but were highest in winter with a secondary peak in June which may be related to the consumption of young ungulates, particularly bison and white-tailed deer. Although the difference in ungulate percentage in scats between June and the highest months in winter (excluding March) is only 3%.

Differences in coyote diets in EINP based on their social affiliation were investigated by comparing the diets of solitaires, pairs and packs as well as diets of individuals that changed social affiliation during the study period. These comparisons indicated that the percentage of ungulates as a major diet item was significantly affected by social affiliation in winter (P=0.001) when packs had significantly higher proportions of ungulates in their diet compared with solitaires and pairs. Although the difference is not statistically significant (P=0.07), packs tended to consume higher numbers of ungulates compared with pairs and solitaires in the summer.

My results support previously published studies, which have shown differences in diet among animals belonging to different social affiliations. However no other study has documented changes in diet when an individual animal switches from one social affiliation to another. My results showed that changes in the social affiliation by four coyotes during the study period confirmed that in three of four coyotes, becoming a member of a pack was associated with a significant increase in the proportion of ungulates as food in their diet.

My results also suggest that changes in diet related to changes in social organisation are affected by season and that this complexity needs to be considered when evaluating benefits of group membership. Two hypotheses have been posed to explain variation in the social organization of coyotes. The food resource hypothesis states that group size is determined by the size and distribution of their prey (Camenzind 1978, Bekoff and Wells 1980, Bowen 1981). Under this hypothesis, group size increases, whereas individual territory and home range sizes decreases when food resources are abundant, clumped and defendable. Other benefits accrued from group living include: increased predator vigilance, defence of territories and carcasses, increased inclusive fitness, delay or deferral of dispersal, alloparental behaviour, and the possibility of inheriting the familial territory (Bekoff and Wells 1980, Messier and Barrette 1982, Macdonald, 1983, Carr and Macdonald 1986, Moehlman 1981, 1989, Patterson and Messier 2001). In contrast, the competing delayed dispersal / habitat saturation hypothesis (Andelt 1982, Messier and Barrette 1982, Gese 1988, Patterson and Messier 2001) contends that group living in coyotes is a result of delayed or unsuccessful dispersal that can result from late sexual maturity of offspring or high coyote density and habitat saturation resulting in a scarcity of unoccupied territories or home ranges.

Elk Island provides a unique opportunity to discriminate between these two hypotheses. EINP supports one of the highest ungulate densities in North America, whereas intensive coyote exploitation in areas surrounding EINP likely results in available vacant territories (Blyth and Hudson 1987). Because coyotes are able to move freely from EINP into adjacent habitats, pack formation likely results from or is facilitated by an abundance of large, clumped, defendable food resources, consistent with predictions of the food resource hypothesis. Given the high levels of human exploitation around EINP, delayed dispersal, because of habitat saturation, in the areas surrounding EINP is unlikely.

EINP actively manages bison and elk and is in the process of reducing the density of ungulates. Future research could investigate the extent to which these changes alter coyote population density and social organisation and whether such changes are associated with changes in diet. The reduction in ungulate density should have a significant effect on the availability of ungulate food resources particularly in the form of carrion and winter kill.

COYOTE DENSITY AND FENCE PERMEABILITY IN ELK ISLAND NATIONAL PARK

The objectives of Chapter 5 were to quantify the density of coyotes in Elk Island National Park and compare this density estimate with those found previously for coyotes occupying a range of habitats in North America and secondly, to quantify the number and location of holes in the perimeter fence surrounding Elk Island National Park. Specifically, I tested the null hypotheses that the density of holes is unaffected by: 1) habitat attributes adjacent to the fence (*i.e.*, agricultural grasslands, forest, wetlands, and roads); 2) season (winter, summer); and 3) adjacency to roads.

Density estimates provide information about the abundance and spatial distribution of an animal population (Smallwood and Schonewald 1998). My review of the literature showed that coyote densities were highly variable and that the EINP pre-whelping density of 0.87 to 1.05 is relatively high and may be a result of the high ungulate biomass in combination with other factors like increased protection. Alternately, wolves and coyotes are thought to have effective compensatory responses to high levels of human exploitation (*i.e.* outside of EINP) where the removal of dominant individuals within packs is thought to relax social factors that would otherwise restrict population growth (Camenzind 1978, Packard and Mech 1980, Harrington *et al.* 1982, Windberg 1995).

My comparisons of the density of holes among different habitats suggests that coyotes establish holes under the perimeter fence in a non-random fashion. Based on habitat availability, coyotes established disproportionately more holes than expected when lengths of the fence were next to conifer forest and wetlands but dug fewer than expected in areas bordering grasslands and roads.

While the mechanisms determining why coyotes established disproportionately more holes in the perimeter fence, when they were bordered by forests (in particular conifer) and wetlands is not known, it may be related to reducing an animal's visibility. Coyotes may access areas into or out of the Park by establishing holes adjacent to forests and wetlands because they reduce the probability of being detected by humans or conspecifics, or if encountered, provide habitats where coyotes can seek refuge. Both conifer and marshy wetland areas in EINP tend to provide dense, thick habitat structure, which would presumably offer cover. Alternately coyotes could establish holes in the perimeter fence alongside wetlands because these areas may contain saturated soils that could be easier to dig. My results also indicate reduced numbers of holes in the perimeter fence in the winter compared to the summer. Seasonal differences in the number of holes under the perimeter fence may be related to snow pack and the amount of time and energy required for coyotes to dig into frozen soils or to clear snow from existing runways under the fence. Grassland areas where coyotes would be particularly vulnerable during winter months were used less than expected or avoided altogether compared to the summer.

Coyotes established significantly fewer holes than expected when the perimeter fence bordered a road. Although significantly fewer holes were established adjacent to roads in both summer ($P<0.05$) and winter, the trend was more pronounced in winter ($P<0.001$).

Few studies have evaluated the extent to which fences are a barrier to wildlife movements and whether habitat characteristics adjacent to the fence affect its permeability. My study demonstrated that the extent to which a fence is a potential barrier is strongly affected by the physical environment in which the structure exists. Further, these results suggest that by digging routes under the fence, coyotes have created a semi-permeable barrier where holes are established disproportionately more often in some habitat types compared to others. The extent to which barriers restrict movement of wildlife species is poorly understood. An animal's ability to transverse barriers may be affected by the degree to which wildlife can navigate or modify barriers and whether other behavioural considerations (*e.g.* reducing encounters with other species or conspecifics) constrain movement choices.

Future research is required to determine whether the establishment of holes in the perimeter fence is related to reducing encounters with other coyotes and humans or due to soil properties. Alternately, if the location of holes is related to reducing visibility, the hypothesis that slope profiles and vegetation biomass should differ between areas where coyotes establish holes compared to where they do not could be tested by collecting site-specific measurements from locales where coyotes established holes compared to where they do not exist.

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