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The Effects of Roads on Pronghorn Antelope (*Antilocapra americana*) Behaviour and
Habitat Use

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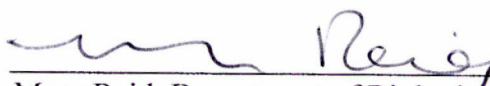
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The Effects of Roads on Pronghorn Antelope (*Antilocapra americana*) Behaviour and Habitat Use" submitted by Shannon Dawn Gavin in partial fulfilment of the requirements of the degree of Master of Science.



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Abstract

The risk-disturbance hypothesis proposes that organisms will perceive human disturbances as a predation risk. I investigated whether pronghorn antelope, *Antilocapra americana*, exhibited risk avoidance behaviour towards road traffic consistent with the risk-disturbance hypothesis. I compared observations of activity budgets and faecal pellet distributions across increasing traffic levels and proximity from roads. Pronghorn showed trends of higher vigilance and lower foraging times along high traffic roads. These behavioural expenses along high traffic roads may have influenced their preference for habitat near lower traffic roads. Roads create edges and if perceived as risky, may affect the distance pronghorn use habitat from the edge. Pellet densities were highest at intermediate distances from roads suggesting that individuals assess a degree of risk near the edge and reflected back into the habitat. Increases in densities of high traffic roads can disrupt behaviour, leading to changes in habitat use and potentially reducing population productivity.

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Table of Contents

Approval Page.....	ii
Abstract.....	2
Acknowledgements.....	3
Table of Contents.....	4
List of Figures and Illustrations	6
 CHAPTER 1: GENERAL INTRODUCTION: A CONCEPTUAL FRAMEWORK FOR THE EFFECTS OF HUMAN ACTIVITY ON WILDLIFE.....	
Study Objectives.....	8
Study Species.....	13
Study area	15
Study Design	19
Thesis Organization.....	21
 CHAPTER 2: PRONGHORN ANTELOPE ACTIVITY BUDGETS IN RESPONSE TO ROAD TRAFFIC	
INTRODUCTION	23
METHODS	23
Study Area	28
Study System	28
Study Design	30
Analyses	32
RESULTS	34
Behavioural Trade-Offs.....	34
Vigilance.....	36
Foraging.....	38
Resting Behaviour	40
Group Structure: Solitary Individuals versus Herds.....	42
Other Indicators of Risk Perception	44
Herd Size.....	44
Distribution of Males and Females.....	45
DISCUSSION	45
 CHAPTER 3 THE EFFECTS OF ROAD TRAFFIC ON PRONGHORN ANTELOPE HABITAT USE	
INTRODUCTION	57
METHODS	57
Study Area	63
Study System	63
Study Design	63
Faecal pellet surveys.....	65
Vegetation Surveys.....	68

Analyses	69
RESULTS	72
Pellet Group Surveys.....	72
Edge Response.....	73
Gradient of Risk	76
No Road Areas	79
Resource Mapping.....	79
DISCUSSION	82
Edge Response.....	82
Other Influences on Edge Response.....	85
Gradient of risk.....	89
Resource Mapping.....	91
CHAPTER 4: GENERAL CONCLUSIONS.....	94
Significance	99
Management Implications.....	100
LITERATURE CITED	104

List of Figures and Illustrations

Figure 1.1 Pronghorn antelope habitat range (grey area) in southeastern Alberta	17
Figure 1.2 Map of wildlife management units (WMU= numbers) with corresponding antelope management areas (AMA= letters) that were surveyed in this study.....	20
Figure 2.1 The percentage of each behaviour type across all the observations bouts (N=75).....	35
Figure 2.2 The proportion of time pronghorn spent being vigilant was correlated with the proportion of time spent foraging to examine whether pronghorn trade off between these two behaviours.	37
Figure 2.3 The proportion of time pronghorn individuals spent being vigilant across three traffic level categories (N=75).	39
Figure 2.4 Proportion of time pronghorn spent foraging within habitat along roads of three different traffic level categories during two different seasons.....	41
Figure 2.5 Pronghorn foraging proportion across two distance categories that were estimated by sight for herds (A) and solitary individuals (B) (N=75).....	43
Figure 2.6 The distribution of observed herds sizes when fawns were present versus absent from the group.	46
Figure 3.1 Three behavioural responses to an edge boundary; a) positive response (individuals attracted to the edge), b) neutral response (response consistent across distance), c) negative edge response (avoid edge).....	60
Figure 3.2 Pronghorn pellet densities (#/0.09 ha plot) at four distances from roads, regardless of traffic level of the roads (N=672).....	74
Figure 3.3 Pronghorn pellet densities (#/0.09 ha plot) found along transects placed at different orientations along roads (N=672).....	75
Figure 3.4 The average percentage of each vegetation coverage along the four transect orientations (N=672).	77
Figure 3.5 Pellet group densities (#/0.09 ha plot) counted at four distances from fenced roads of different traffic levels (N=672).	78
Figure 3.6 Average pellet densities (#/0.09 ha plot) for areas along four traffic level categories and no road areas (N=872).	80

Figure 3.7 Average pellet densities (#/0.09 ha plot) across five distances from roads regardless of traffic level (N=872). Plotted are means $\pm$ one standard error	81
Figure 3.7 Illustration of the bouncing effect hypothesis.	86

CHAPTER 1: GENERAL INTRODUCTION: A CONCEPTUAL FRAMEWORK FOR THE EFFECTS OF HUMAN ACTIVITY ON WILDLIFE

Human disturbances can have an extensive influence on wildlife behaviour and distribution (Boyle and Samson 1985; Jalkotzy et al. 1997; Forman et al. 2003). Animal responses from exposure to these disturbances have varied from negative to positive responses (Jalkotzy et al. 1997; Forman et al. 2003). The general focus has been the effects of human disturbances on trade-offs either between anti-predatory behaviour and other fitness behaviours (Walther 1969; Verhulst et al. 2001) or resource use and habitat avoidance (Forman and Alexander 1998; Forman and Deblinger 2000) but there is no comprehensive study linking the behavioural response with their distribution within the disturbed area. Few of these studies test the responses under a conceptual model which may contribute to some of the variation observed in the responses.

Using principles from the predation risk literature, the risk-disturbance hypothesis provides a model that can be tested in studies investigating human impacts on wildlife. It proposes that animals will assess risk or danger towards human disturbances based on particular characteristics that are analogous to a natural predator (Frid and Dill 2002). This study examines whether pronghorn antelope (*Antilocapra americana*) may perceive risk towards human disturbances by measuring activity budgets and animal distribution around the disturbance.

Predator-prey interactions have shown that organisms can track short term changes in predation risk and alter their behaviour accordingly to minimize the risk of mortality (Lima and Dill 1990; Lima 1998). Individuals under the constraints of a natural predation hazard appear to assess trade-offs between minimizing the predation risk with

changes to other fitness behaviours, as well as the selection of habitat (Lima and Dill 1990; Brown et al. 1999). The risk-disturbance hypothesis predicts that if human activity is perceived as a predation risk then wildlife behavioural activities would reflect these trade-off patterns produced under natural predation (Frid and Dill 2002). The strength of the response is expected to depend on the level of risk perceived, with stronger responses when the perceived risk is greater.

For trade-offs to occur, individuals must assess potential fitness benefits and costs of performing specific behaviours. The benefit of anti-predatory decisions is a lower probability of encountering predators and thus mortality (Lima 1985). The cost of increased anti-predator behaviour is lowered energy intake or reproductive output which can affect their long term survival (Lima 1998). For example, a remnant caribou population selected habitat with low predation pressure but also lower forage phytomass which has led to reduced antler and body size (Ferguson et al. 1988). The ability of animals to assess predation risk may be affected by direct cues (presence of a predator) or non-lethal indirect cues such as habitat characteristics and grouping behaviour. Predator-prey interactions often focus on the actual mortality event but the perceived risk of mortality, even when predators are absent, can also elicit similar increases in anti-predatory behaviours to minimize potential encounters (Lima 1998).

The effects of predation risk on animal distribution have been examined with organisms exhibiting ideal free distribution where individuals are of equal competitive ability and are free to move between habitat patches to obtain the greatest resource intake (Fretwell and Lucas 1970; Moody et al. 1996). The presence of predators may cause deviations from the ideal free distribution leading to resource-rich habitats being

underexploited when associated with increased predation risk (Sih 1980; Holbrook and Schmitt 1988; Utne and Aksnes 1994). Non-lethal indirect cues that influence the perceived “riskiness” of a habitat area such as cover or light intensity may also shape animal distributions because it may affect the probability of being detected (Underwood 1982; Clarke 1983). If intra-specific competition in the safer habitat reduces individuals’ foraging rates, individuals may accept greater risk to obtain sufficient resources (Moody et al. 1996; Holbrook and Schmitt 1988). The number of individuals within the riskier habitats may reflect how foraging benefits and predation costs are assessed and indicate their overall fitness. Individuals in poorer energetic condition may be found in riskier habitats to obtain necessary energy requirements (Lima 1998).

The risk-disturbance hypothesis predicts that exposure to long term intense human disturbances will affect animal distribution by causing individuals to shift into habitat away from the predation hazard (Frid and Dill 2002). Habitat shifts may depend on the costs and benefits of leaving that current area and whether alternative habitat is available. If the perception of risk is high and the cost of performing risk avoidance behaviours outweigh the benefit of using that habitat, then individuals may shift into different habitats. A potential consequence of shifting into a new area may include moving into lower quality areas with fewer food resources or refuge areas (Vistnes and Nellemann 2001). The strength of the response can be measured by comparing animal distribution as a function of distance from the disturbance. The “effect distance” which represents the distance at which animals show a significant response to the disturbance has been demonstrated for several species (Forman et al. 2003) but these studies lack a connection with the underlying ecological process. The perceived level of risk associated with the

disturbance may be influenced by the type of disturbance and how it changes the habitat. Some disturbances, such as roads, may create boundaries between habitats and the perceived risk towards the traffic may affect animal movement and distribution around the road boundary.

Studies have shown wildlife exhibiting negative (avoidance), positive (attracted) and neutral (habituation) responses towards human disturbances (Ries et al. 2004). It might be suggested that animals who show positive or neutral responses to human disturbances do not perceive any risk towards the disturbance which would contradict the risk-disturbance hypothesis. Yet species may be attracted to disturbances because they create new habitat allowing the expansion of geographic ranges or human alteration to the surrounding vegetation may create new foraging opportunities (Getz et al. 1978; Camp and Best 1994). Wildlife distribution can also show a neutral response where animals that are protected from human caused mortalities such as hunting, habituate towards human activity (Schultz and Bailey 1978; Steidl and Anthony 2000). Hunting pressure or other human caused mortalities may reinforce the predation risk aspect of the risk-disturbance hypothesis. In hunted populations, overestimating the risk towards human disturbances can lead to a reduction in fitness-related activities but underestimating the risk could lead to mortality. Individuals who overestimate the predation hazard rather than underestimate it will have higher fitness (Bouskila and Blumstein 1992).

Natural predation pressure incorporates both lethal and non-lethal aspects where the very act of predation often results in mortality (Lima 1998). Predation risk is the non-lethal aspect that results from individuals making behavioural decisions based on factors

that influence their probability of being attacked. An argument against the risk-disturbance hypothesis is whether animals will actually associate a human disturbance as a predator. Even though the actual stimulus may be new to their evolutionary history, prey have evolved responses to predation hazards based on general characteristics such as the speed or angle of the approaching predator rather than whether it is a lion or a vehicle (Frid and Dill 2002). For example, zebra danios exhibited similar flight initiation distances towards a largemouth bass and a black dot on a film (Dill 1974). The danios based their flight initiation on the speed of the approaching stimulus and when it reached a particular loom rate threshold, the danios fled. Animal responses to stimuli that cross a threshold value innate in their evolutionary history could result in analogous responses towards human disturbances that exhibit these characteristics.

Mortality caused by the human disturbance or hunting pressure may influence the intensity of the responses towards the disturbances. Individuals in areas under hunting pressure may elicit stronger predation risk behaviour towards human disturbances because it is associated with humans (Verhulst et al. 2001). Frid and Dill (2002) compared the responses to human stimuli that were new to an animal's evolutionary history with the introduction of new predators into an area. However, for the local community to learn that the new predators are dangerous and not habituate, they must experience negative encounters with these individuals. The risk-disturbance hypothesis focuses on wildlife responses to non-lethal disturbances based on innate characteristics of threatening stimuli yet the additional effects of mortality caused by humans can elicit stronger wildlife responses.

Study Objectives

The objective of this study was to investigate whether pronghorn antelope exhibit behaviour in response to a human disturbance consistent with the risk-disturbance hypothesis. Studies of the effects of human activity on pronghorn antelope from a behavioural approach are limited. Some pronghorn populations have shown avoidance of various degrees of human activity from recreational trails (Fairbanks and Tullous 2002) to fenced interstate highways (van Riper and Ockenfels 1998) but no apparent behavioural disruptions to military noise disturbances (Krausman et al. 2004). Most of these studies observed populations within protected national parks where responses may be weaker towards human disturbances because there is no cumulative effect of hunting pressure and natural predation. As well, there have been no studies of the impact of human activity on populations at their most northern range where they are already vulnerable to mortality from severe weather (Martinka 1967; Barrett 1982). In northern populations, suitable habitat is paramount for winter survival where individuals may trade off minimizing predation risk with utilizing the good quality habitat despite the higher risk. Even in the absence of avoiding riskier habitats, individuals utilizing risky areas may still exert more energy towards other risk averse behaviours such as vigilance. Long term consequences of high energy expenditure towards anti-predatory behaviour may be decreased body condition and individual fitness (Ferguson et al. 1988). My study tests the risk-disturbance hypothesis by measuring pronghorn behaviour and habitat use towards human disturbances which will provide new and more detailed perspectives of human impacts on wildlife.

The disturbance I chose to examine was road traffic because activity within pronghorn range has been increasing due to residential expansions and increasing oil and gas industry which all require road networks into the landscape. Road traffic is a useful representative of the human activity within an area because people generally gain access to these isolated areas with the use of vehicles. Various studies have shown the impacts of roads on different species, including mammals (Dau and Cameron 1986; Joyce and Mahoney 2001; Gibeau et al. 2002; Rondinini and Doncaster 2002); and birds (Reijnen et al. 1996; Forman et al. 2003). Several general reviews on road effects on wildlife have also been published (Jalkotzy et al. 1997, Forman and Alexander 1998; Forman and Deblinger 2000; Trombulak and Frissell 2000).

If organisms respond to generalized characteristics of threat stimuli, pronghorn may perceive road traffic as a risk because vehicles can exhibit fast and direct approach rates. Pronghorn may also experience mortality through vehicular collisions or increased access by hunters which can heighten their risk perception towards road traffic. Reported pronghorn vehicle caused mortality is moderate with 30 documented deaths from 1999 to 2003 (Quentin Isley, pers comm. 2003) which did not affect the average provincial populations at that time (16, 603). However, some animals may be injured and die later after they have moved further into the habitat. Moreover, some reported wildlife vehicle collisions did not specify species so this number could underestimate vehicle caused mortality rates for pronghorn. No information of pronghorn mortality related to hunters having increased access into pronghorn habitat exists. In Alberta, pronghorn are rated as one of top big game for hunters (Glasgow 1990).

I examined whether pronghorn may perceive risk towards road traffic and whether higher traffic or human activity may correspond to a higher risk perception. Specifically, I investigated whether pronghorn exhibited different behaviours towards various levels of road traffic which may reflect risk assessment. I focused on vigilance and foraging behaviours because they are good indicators of individuals assessing risk towards a stimulus (Lima and Dill 1990; Treves 2000). I predicted that pronghorn perceive road traffic as risky so that the time they spend being vigilant would increase with increases in traffic and proximity to roads while foraging would decrease. If these differences in behaviour are strong enough, they may also influence pronghorn habitat use in areas surrounding roads. Therefore, I predicted that if areas near higher traffic level roads and within close proximity to roads are perceived as riskier than areas experiencing less traffic and further away, there would be a relatively lower abundance of pronghorn in these areas.

Study Species

Pronghorn antelope belong to the Order Artiodactyla where they are the sole surviving species of the family Antilocapridae. Since many characteristics of the families Bovidae and Cervidae overlap in pronghorn, controversy still exists concerning the taxonomic placement of the Antilocapridae. Family Antilocapridae is usually placed within the suprafamily Bovoidae based on physical and chemical characteristics (O’Gara and Yoakum 2004).

Pronghorns are mid-sized animals reaching a shoulder height of 810-1040 mm and a weight of 36-70 kg (Nowak 1991). Males are usually 10% larger than females and

can be distinguished by facial markings. Both have tan coloured pelage with white patches on the face, neck underside and rump. Males have a black patch on the side of the cheek and rostrum coloration is darker than in females (Nowak 1991). Both have horns that consist of a permanent bony core that is covered with a keratinous sheath that are shed annually but female horns are seldom over 120 mm long while male's horns can reach up to 250 mm (Nowak 1991).

Pronghorn antelope distribution ranges from Mexico to Canada, and the western United States. Within Canada, pronghorn range includes the southeastern corner of Alberta (Figure 1.1) and the southwestern corner of Saskatchewan. The Canadian Forces Base Suffield lies within the Alberta pronghorn range which includes a National Wildlife Area (458 km²) where military activities and public access are restricted. This area may be included within some pronghorn home ranges but not all of the National Wildlife Area is suitable habitat for pronghorn such as areas with sandhills and wetlands; therefore, is limited in size. This area may provide pronghorn with minimal relief from hunting pressure and is the only refuge within their Alberta range. Pronghorn require low rolling prairies or grasslands that receive 250-380 mm precipitation and snow accumulations not exceeding 25-30 cm for prolonged periods (Glasgow 1990). Some populations can survive on the moisture obtained from the plant material they consume but generally require water sources distributed no more than 5-6 km apart (Glasgow 1990). Vegetative composition requirements include 40-60% grass, 10-30% forbs and 5-20% shrubs and a preferred vegetative height of 38 cm (Glasgow 1990).

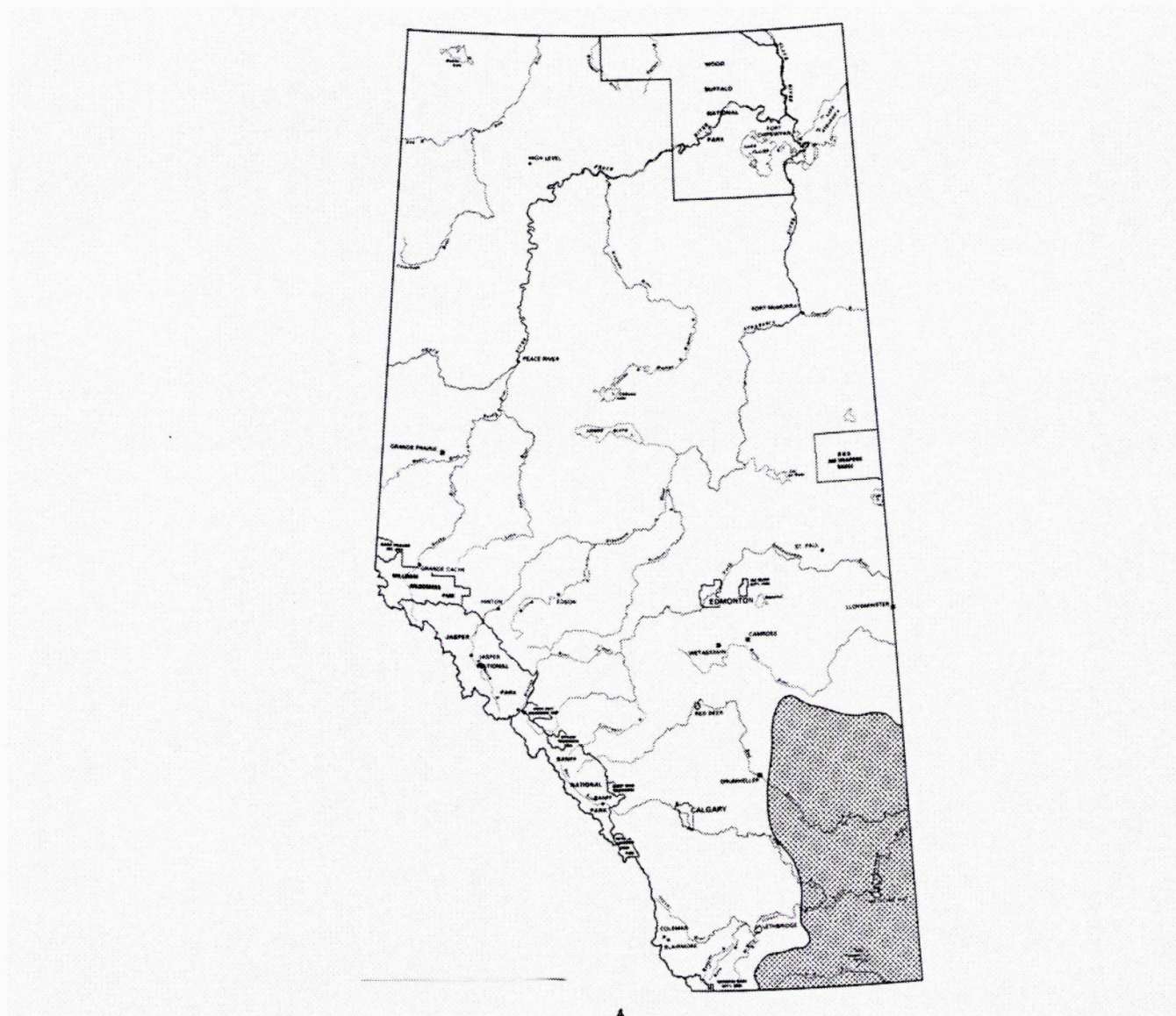


Figure 1.1 Pronghorn antelope habitat range (grey area) in southeastern Alberta (map credit from Glasgow 1990).

Winter range is paramount for pronghorn survival in their northern ranges and requires adequate supplies of sagebrush (*Artemisia cana*). Northern populations tend to show migratory behaviour where pronghorns move to wintering areas that represent only 8% of their summer range in Alberta (Barrett 1982). Migrations can be impeded by livestock fencing, roads and railways which may act as movement barriers or cause mortality (Hepworth 1966).

Pronghorn herd composition varies considerably with season. During the fall and winter months, males and females aggregate to form large mixed sex herds. In early spring, the herd begins to break up with females moving to isolated areas to give birth in late May. A female generally gives birth to a single fawn during her first pregnancy, but later births usually results in twins (Nowak 1991). After the fawns have reached at least 3 weeks of age, they join other mothers and fawns in nursery herds (O’Gara and Yoakum 2004). Bachelor herds consisting of young males under 3 years old are also common during the spring dispersal until the onset of the rut. Male reproductive behaviour is plastic with populations switching from territorial to harem defence (Byers 1997). In Alberta, males defend territories and attempt to maintain groups of females on this space during rut which peaks in mid September.

Home range size and daily movements depends on habitat quality and quantity. Daily movement can range between 0.1-0.8 km in the spring and summer to 3.2-9.7 km in the winter months (Nowak 1991). Daily movements show longest distances during the autumn and shortest in the spring when forage is abundant (O’Gara and Yoakum 2004).

Main predators of pronghorn, more so for fawns, include coyotes, bobcats and golden eagles. Females with fawns are highly aggressive, often chasing coyotes away

compared to males and non-lactating females yet these females tend to be more apprehensive towards humans (O’Gara and Yoakum 2004). Hunting is also a large component of game management with pronghorn season lasting for 3 to 4 weeks in September for archery, one week in October for trophy pronghorn and 3 to 6 days for non-trophy animals (Glasgow 1990).

Study area

My study area encompassed habitat from the Montana border to north of C.F.B. Suffield, from the Saskatchewan border to Brooks. Pronghorn range is divided into antelope management areas (AMA) in which several Fish and Wildlife Divisions are responsible for specific units. This study was conducted throughout the antelope management units of C, D, E, F, and G (Figure 1.2). Each antelope management area is further divided into several wildlife management units (WMU).

Topography of southern Alberta consists of low to strongly rolling hills with elevations that range from 670 to 950 m (Mitchell 1980). This region is categorized as dry mixed grass which is the largest of the four grassland subregions (Alberta Environmental Protection 1997). The common vegetation in this area includes wheat grass (*Agropyron smithii*), spear grass (*Stipa* species) and blue grama (*Bouteloua gracilis*). This subregion is the warmest and driest in Alberta with high rates of evaporation, low precipitation, prolonged periods of drought and high variation in seasonal temperatures (Mitchell 1980). Summer temperatures can reach above 40°C while low winter temperatures of -30°C are often offset by south-westerly Chinook winds that reduce snow cover (Mitchell 1980).

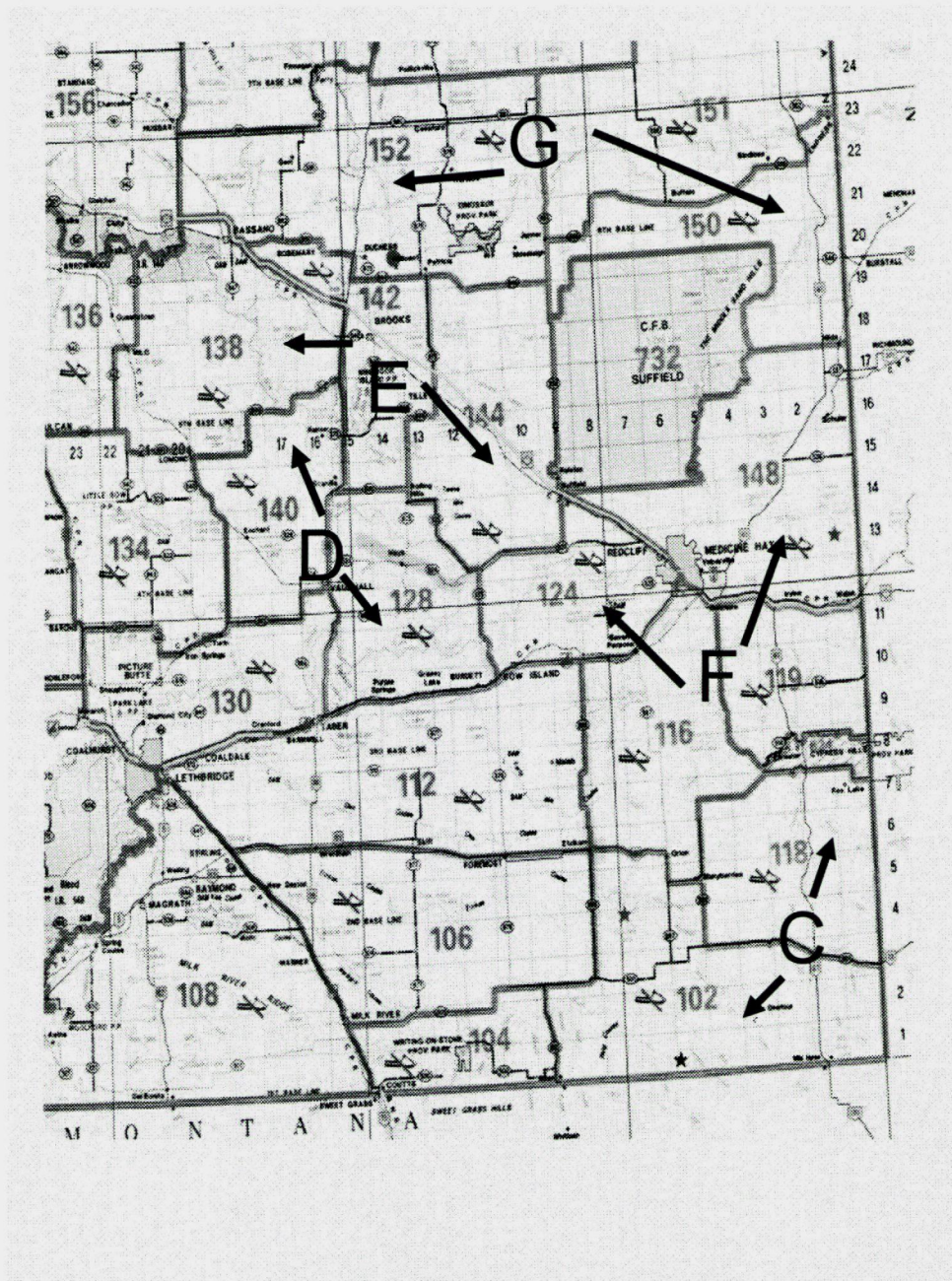


Figure 1.2 Map of wildlife management units (WMU= numbers) with corresponding antelope management areas (AMA= letters) that were surveyed in this study. (Map credit Fish and Wildlife 2003).

Activities such as agriculture, residential development, roads and the petroleum industry have caused a 61% decline of prairie habitat (Alberta Environmental Protection 1997). Habitat loss is a strong factor influencing pronghorn movement and leading to increases in human interactions as pronghorn attempt to find suitable habitat (Glasgow 1990). In their Alberta range, 12 areas designated as pronghorn winter range have been impacted by increasing cultivation of land where the proportion of cultivated lands on these winter ranges increased from 9.7% to 14.4% during 1950 to 1983 (Glasgow 1990). One area known as the Walsh Flats has recently been consumed by cultivated land and is no longer suitable pronghorn winter habitat (J. Taggart, pers. comm. 2003). In Alberta, road networks have increased drastically with over 95,000 km of roads, rails and wellsite roads in the grassland region (Alberta Environmental Protection 1997). The dry mixed grass region of Alberta has one of the highest road densities (1.07 km/km^2) compared to the other three natural regions (Alberta Environmental Protection 1997).

Study Design

Data were collected during the summer field seasons of 2003 and 2004. Stratified sampling of pronghorn range was used to select survey areas that consisted of similar land use practices (rangeland only), habitat, road fencing and pronghorn population densities (Patton 1992). Roads were categorized into traffic level ranges based on annual summer daily traffic counts for sections of that road supplied by the Alberta Transportation Department for 2002. Categories consisted of low (0-10 vehicles/day), medium (70-200 vehicles/day), high (>300 vehicles/day) and very high (>1000 vehicles/day). Traffic categories were chosen based on the roads available within

pronghorn range. Each traffic category consisted of two roads in 2002 field season and three different roads in the 2003 field season.

To assess whether pronghorn behaviour changed in response to traffic, I conducted observations across roads that increased in traffic level and as a function of increasing distance from roads. I used focal animal sampling which consists of observing a selected individual from the group for a specified amount of time and recording all instances of behavioural categories (Martin and Bateson 1993). Continuous recording of behaviour was used where each occurrence of a behaviour was reported with the time it began and ended to measure behaviour durations (Martin and Bateson 1993).

Pellet group surveys were conducted to examine changes in pronghorn habitat use in areas surrounding roads relative to increasing traffic level and proximity to roads. Pellet group surveys have been found to be effective measures of relative animal distribution within a landscape (Neff 1968; Telfer 1978; Rost and Bailey 1979; Loft and Kie 1988; Weckerly and Ricca 2000).

Thesis Organization

In this thesis, I explore whether pronghorn antelope change their activity budgets in response to road traffic (chapter 2) and whether this is reflected in their distribution around the roads (chapter 3). I analyze these observations to test whether the risk-disturbance hypothesis may provide a conceptual framework for this system. Finally, I discuss some management implications for pronghorn under increasing human activity in southern Alberta (chapter 4).

CHAPTER 2: PRONGHORN ANTELOPE ACTIVITY BUDGETS IN RESPONSE TO ROAD TRAFFIC

INTRODUCTION

Predation is a strong selective force influencing prey behaviour, distribution and population dynamics (Lima and Dill 1990, Brown et al. 1999). Some decisions animals make on a daily basis must involve assessing the risk of predation to effectively allocate behaviours – a trade-off between obtaining sufficient energetic resources within the constraints of predation. These choices can be reflected in changes to risk avoidance behaviour which may result in the reduction of other fitness related behaviours, increased stress or shifts into areas of lower predation risk. The benefits and costs of risk avoidance behaviour can depend on the level of predation risk with animals exhibiting higher risk avoidance behaviour under higher perceived risk (Lima and Dill 1990).

Studies have shown how predation can cause individuals to trade-off between avoiding predation and maximizing resource acquisition (Edwards 1983; Wolff and Van Horn 2003; Smith et al. 2004). Predation involves lethal aspects where the outcome is death and non-lethal aspects that cause organisms to change their behaviour in response to a higher risk of attack by a predator (Lima 1998). Prey response patterns observed under predation have been used to develop a conceptual model to investigate the effects of human activity on wildlife which was previously lacking in the current literature. The risk-disturbance hypothesis proposes that when animals are exposed to human disturbances, they will exhibit responses analogous to those under natural predation risk (Frid and Dill 2002). The hypothesis focuses on non-lethal aspects of predation that

influences risk such as differences in habitat structure, grouping behaviour or reproductive status. It assumes that organisms respond to threatening stimuli based on innate general characteristics which individuals use to respond to stimuli new to their evolutionary history (Frid and Dill 2002). Human disturbances that exhibit similar characteristics as threatening stimuli may elicit anti-predatory behaviour. The behavioural responses may be stronger if the organisms experience mortality from the disturbance or hunting pressure which reinforces the lethal aspect of natural predator.

Vigilance or foraging levels are generally used as measures of risk perception including other components that influence predation risk such as group size effects, sex of the focal animal and reproductive status (Elgar 1989; Treves 2000). The risk-disturbance hypothesis predicts that a disturbance stimulus that represents a human presence or object will elicit an animal's risk avoidance behaviour such as vigilance (Frid and Dill 2002). Many studies have shown negative to positive animal responses towards human disturbances but most have weak explanations of the underlying ecological processes mediating these responses, as well as explanations of the variation between responses (Camp and Best 1994; Schneider and Wasel 2000; Duchesne et al. 2000; Papouchis et al. 2001). Many of these studies present the observed patterns but do not link these to any ecological process or incorporate habitat quality as a confounding variable. In comparison, a few studies have incorporated a risk perception component which addresses principles of the risk-disturbance hypothesis. Verhulst et al. (2001) implied that oystercatchers might be perceiving humans on foot as a predation risk which disrupted their parental care abilities by reducing egg incubation rates and parental feeding rates of chicks. Gill et al. (1996) found pink-footed geese traded off between

using the available resources in the habitat with increased avoidance of the area containing high road activity. This suggests that the trade-off was analogous to trade-offs under predation risk because pink-footed geese were avoiding areas to minimize risk but with the cost of reduced resource consumption.

The level of perceived risk is influenced by extrinsic (group size, distance to refuge, obstructive cover) and intrinsic factors (sex, reproductive status, age) which determine vigilance durations (Elgar 1989; Lima and Dill 1990; Treves 2000; Frid and Dill 2002). Time spent being vigilant decreases with increasing group size, decreasing distance from refuge and minimal obstructive cover (Poysa 1994; Roberts 1996; Frid 1997; Frid and Dill 2002). The dilution and detection hypotheses have been proposed to explain why increasing group sizes should decrease vigilance duration. The dilution hypothesis proposes that more individuals in a group reduce the probability of any one individual getting attacked (Dehn 1990; Roberts 1996). For example, bighorn sheep that were located closer to other conspecifics diluted their predation risk relative to more solitary sheep (Mooring et al. 2004). The detection hypothesis suggests that with a cooperative effort in vigilance by all members of the group, approaching predators will be detected earlier (Dehn 1990; Lima 1995; Roberts 1996). Childress and Lung (2003) found that the overall group vigilance measured as the percentage of intervals with any elk scanning surroundings, was positively related to group size. Overall group vigilance is heightened by more individuals taking part in scanning for predators but each individual can also reduce their scan length to pursue other behaviours. In fact, the effects of group size may involve features of both the predator detection and dilution effect hypotheses (Dehn 1990). Intrinsic factors such as reproductive status can also

influence vigilance behaviour. Neonates are the most vulnerable to predation; therefore, females with young exhibit longer durations of vigilance corresponding with reduced foraging durations (Elgar 1989).

Foraging is another behaviour that may reflect an individual's perception of risk within a particular area (Sih 1980; Lima and Dill 1990; Brown et al. 1999; Kie 1999). In ungulates, the act of foraging puts individuals in a vulnerable position as they must place their heads among the vegetation obscuring the surroundings. Therefore, individuals should forage longer in areas that they determine as having low predation risk.

Kangaroos foraged longer when they were situated close to a refuge when in areas of high predator density (Banks 2001) and mule deer foraged less in riskier edge habitats (Altendorf et al. 2001). Individuals may find safety within larger groups allowing them to pursue activities other than vigilance such as foraging (Lima and Dill 1990; Treves 2000). The relationship between increasing foraging with increasing group size may be difficult to quantify. Longer foraging bouts may not necessarily translate to individuals in larger groups having more foraging opportunities but that intra-specific competition may cause individuals to forage longer to obtain sufficient energy (Elgar 1989). Overall group size effects on increasing foraging behaviour have been difficult to detect but differences may exist mainly between solitary individuals and those in herds regardless of group size (Lipetz and Bekoff 1982; Berger and Cunningham 1988; Mooring et al. 2004). Strong foraging differences have been detected between solitary individuals versus individuals in herds because without conspecifics for assistance in detection or dilution of predation risk, solitary individuals may have to compensate by increasing vigilance and foraging less (Lipetz and Bekoff 1982).

Research Objectives

I tested whether pronghorn exhibited behaviour consistent with the risk-disturbance hypothesis by measuring changes in their vigilance levels correlated with changes to their foraging level thus reflecting trade-offs between these behaviours that correspond with responses under a natural predation threat. To identify potential differences in risk assessment, I compared vigilance and foraging times across different traffic levels and distances from roads. Resting behaviour was also analyzed because this activity can put individuals into a vulnerable position for a predatory attack which may reflect their risk perception in that particular habitat. Pronghorn should increase their vigilance durations corresponding with a decrease in foraging durations when the perceived risk is high. Resting individuals should be found more often in less riskier areas. High risk would be associated with higher traffic levels which would correspond to higher predator density and close proximity to roads.

Other variables, such as herd size, sex and reproductive status have been shown to affect the degree of perceived risk under a natural predation threat which can influence vigilance and foraging levels. Pronghorn, like many other Artiodactyla species form groups for increased detection of predators and for dilution of the predation pressure (Lipetz and Bekoff 1982; O’Gara and Yoakum 2004). Vigilance durations should decrease with increasing herd size allowing individuals to have more opportunities to devote to other behaviours such as foraging. Solitary individuals may exhibit higher risk averse behaviour than individuals in herds and thus, group structure may affect foraging and vigilance behaviour. If pronghorn perceive human disturbances as a predation

hazard, these relationships with herd size should be observed in this study. I also examined whether using herd size as a function of distance from a road would indicate a level of perceived risk. Areas with larger herds might be associated with a higher level of perceived risk as individuals may try to dilute the predation pressure by joining herds.

Females with young should also exhibit more vigilance corresponding to lower foraging because pronghorn fawns are extremely vulnerable to predation. The presence of fawns may also affect their distribution as females should utilize habitat further away from the higher risk area around roads compared to males.

METHODS

Study Area

In Canada, pronghorn antelope are distributed across southeastern Alberta and southwestern Saskatchewan. Pronghorn range is divided into antelope management areas in which several Fish and Wildlife Divisions are responsible for specific units. This study was conducted throughout the antelope management units of C, D, E, F, and G. All data were collected during 2003 and 2004. Refer to Chapter 1 for a complete description of the study area and study system.

Study System

Pronghorn antelope have exhibited changes in their behaviour towards some human disturbances (Berger et al. 1983; van Riper and Ockenfels 1998; Fairbanks and Tullous 2002) but these responses were not associated with risk perception. One study found that the cumulative effects of hunting and resource extraction resulted in pronghorn

expressing higher vigilance levels in these areas, as well as forming larger herds which affected their foraging efficiency (Berger et al. 1983). My study complements Berger et al.'s (1993) study by incorporating a larger range of risk levels, combining behavioural patterns with habitat use (Chapter 3) and testing responses under a conceptual framework.

My study examines road traffic as the disturbance stimulus which may be a form of mortality for animals crossing the road. Moreover, road traffic may be associated with human presence which may influence pronghorn response in a hunted population. Pronghorn in southern Alberta generally do not occur in any protected national parks except the wildlife area on Canadian Forces Base Suffield and are otherwise exposed to natural predation pressure and annual hunting periods. Natural predators include coyotes, bobcats, eagles and in some parts of their range, cougars (O'Gara and Yoakum 2004). Coyote populations are relatively high in southern Alberta mainly due to the lack of hunting for their pelts but absolute numbers representing coyote densities are not routinely collected (J. Taggart, pers comm. 2003). Coyote presence was found in several of the habitats surveyed; therefore, some predation pressure on pronghorn exists. The hunting season is 3-4 weeks long in September for archery, one week in October for trophy pronghorn and 3-6 days for non-trophy pronghorn (Glasgow 1990). Hunters often utilize roads to locate pronghorns and the creation of road networks into once inaccessible areas may affect the predation pressure on pronghorn. Pronghorn may associate road traffic with human presence and therefore perceive it with a predation risk.

Study Design

Observation periods occurred within early morning and some late afternoons with each lasting 1 to 3 hours and consisting of several observation bouts on different focal individuals. Pronghorn were located for behavioural observations during these periods by driving along roads and scanning the surroundings, as well as, when individuals were located within the habitat during data collection for a concurrent study in chapter 3. Observations using binoculars or a spotting scope were made at a range of 100 m to 1000 m from the pronghorn when observers were within the habitat or within a vehicle (Bromley 1969; Goldsmith 1990; Maher 1991). Some observations of pronghorn within close proximity to the road were conducted using a method referred to herein as the Russian tank manoeuvre (RTM) that consisted of using the vehicle as a blind. The vehicle is positioned to block the pronghorns' view of the observer moving to hide in the vegetation along the road, followed by the vehicle driving further out of sight. The three approaches for observations, within a vehicle, within the habitat and RTM were used to take advantage of every opportunity for observations when individuals were located. The observer dictated the behaviours to a second person via radios who recorded and kept time using a digital stopwatch. Pronghorns normally flare the white hairs on their rump when alarmed or if they detect a human presence (O'Gara and Yoakum 2004). Unless they exhibited this behaviour, I assumed that researcher presence did not affect their behaviour.

Individuals were observed for 10 minutes using focal animal sampling where I recorded all instances of behavioural activities (Martin and Bateson 1993). When there were more than one animal, I only conducted one focal observation on an animal that was

arbitrarily selected from the group. Continuous recording of behaviour was used where each occurrence of a behaviour is reported with the time it began and ended to measure behaviour durations (Martin and Bateson 1993). Often when observing an individual, they may move behind an object (hill, bush). In this case, to maintain strict continuous recording protocol, the observation bout was stopped. Therefore, the duration of each behaviour category was converted to a proportion by dividing it by the observation bout length (Lipetz and Bekoff 1982; Maher 2000). For each focal observation, I recorded the size and herd composition (solitary versus herd), position in the group (peripheral, centre, solitary), sex and presence of fawns. I recorded all behaviours each individual exhibited, but for analyses, I focused on vigilance, foraging and resting behaviour while excluding social interactions, running and territory marking. Vigilance was defined as any time the individual had its head above shoulder height either standing still or walking. The head up position was used as an indicator of vigilance even though vigilance may occur during other periods of activities. The head up position is a useful indicator of vigilance because it is often the observed state of alertness when a predator is detected (Childress and Lung 2003). Foraging was defined as any time an individual was consuming vegetation or searching with their head below shoulder height (Lipetz and Bekoff 1982). Resting represented individuals lying within the vegetation.

Vigilance and foraging times were examined using a correlation analysis to test whether there were trade offs between the two behaviours. The times allocated to vigilance, foraging and resting were also analyzed based on the pronghorn's distance from the road and its traffic frequency. Distance from a road was estimated and categorized as 0-300 m and 301-1000m. Conducting pellet surveys at designated

distances along transects from roads for a concurrent study (chapter 3) helped establish the accuracy in estimating the distances pronghorn were from roads for behavioural observations. There were three traffic level categories, low (<10 vehicles/day), medium (70-200 vehicles/day), and high (>300 vehicles/day) which were based on 2002 average annual daily traffic (AADT) data provided by the Alberta Transportation Department. Over the two field seasons, each traffic category had a total of 5 roads that were used to locate pronghorn for behavioural observations. Season was divided into spring (May-June) and summer (July to August) because pronghorn exhibit seasonal behaviour. Spring consists of young males joining bachelor herds, mature males beginning to select territories, females isolating themselves from other pronghorn to give birth and when young fawns are most vulnerable to predation (Glasgow 1990). Summer consists of females with their young joining nursery herds and mature males defending territories (Glasgow 1990).

Every pronghorn sighting was recorded even if a behavioural observation was not conducted. For each sighting, I recorded herd size, composition of the group, estimated distance from the road, road traffic level category, habitat features and general GPS coordinates from the road. Pronghorn sightings were recorded from the vehicle as well as when I was surveying within the habitat.

Analyses

Statistical analyses were conducted in JMP IN version 4.0 computer package (SAS Institute, 2001) and SAS/STAT software version 6.04 (SAS Institute, 2001). All tests used Type I error rate of $\alpha=0.05$ to determine significance.

I recorded a total of 10 hours of observations from focal animals who were solitary and from herds. To maintain independent observations, only a single focal observation from each herd was used in the analysis since individuals within a group may influence each other's behaviour (Martin and Bateson 1986). Individual animals were not marked; therefore, to avoid repeated observations of the same individual, focal observations from similar herd compositions and sizes along the same roads were excluded. Males tend to remain within selected territories and females are generally loyal to their groups in good quality habitat (O'Gara and Yoakum 2004).

Changes in pronghorn vigilance and foraging behaviour were converted into proportions to reflect the length of the particular observation bout (Lipetz and Bekoff 1982; Maher 2000). Data were transformed using arcsine of square root proportion to meet the assumptions of normality based on examination of the distributions using the Shapiro Wilks test. Where least square means (LSM) are reported, back transformations have been conducted which results in asymmetrical standard errors. Therefore, upper (USE) and lower standard errors (LSE) are reported. Stepwise backwards elimination was applied to ANCOVA models where non significant variables that contributed little to the overall model variation were removed because models with numerous variables and small sample sizes may have difficulty detecting relationships (Cohen 1969). To avoid multicollinearity or the correlation between independent variables, terms that had variance inflation factors (VIF) >10 were removed from the model. Apparent biologically relevant interaction terms were included in the initial model, but removed if VIF >10 and $p > 0.05$. Some variables that were not significant remained in the models as

they explained a substantial proportion of the variability in the model (R^2). In the final model, post hoc Tukey's pairwise comparisons were conducted on significant terms.

For each ANCOVA model, I measured which variables had the strongest influence on the dependent behaviour variable. To measure the strength of association between the effect and behaviour, I calculated the partial Eta squared (η^2) which represents the proportion of effect variation and error variation that contributes to the total variation (Tabachnick and Fidell 1996; Pierce et al. 2004). Partial Eta squared reports the amount of variance attributable to each factor as if it were the only variable in the model which means that the variability attributed to one factor is not masked by more powerful variables in the model (Tabachnick and Fidell 1996; Pierce et al. 2004).

Data combined from the recorded sightings of pronghorn and the behavioural observations that were conducted were used for analyses on the relationship between herd size and distance as an indicator of perceived predation risk from roads. I also examined the effects of distance on the proportion of males and females when fawns were present or absent. Non-parametric tests were used if data could not meet normality and homogenous variance assumptions.

RESULTS

Behavioural Trade-Offs

Vigilance occupied the largest percentage (45%) of pronghorn activity budgets compared to foraging and resting (Figure 2.1). The fourth category represents all other miscellaneous behaviour that was observed such as social interactions, running and marking territories. I assessed a potential trade-off between the amount of time

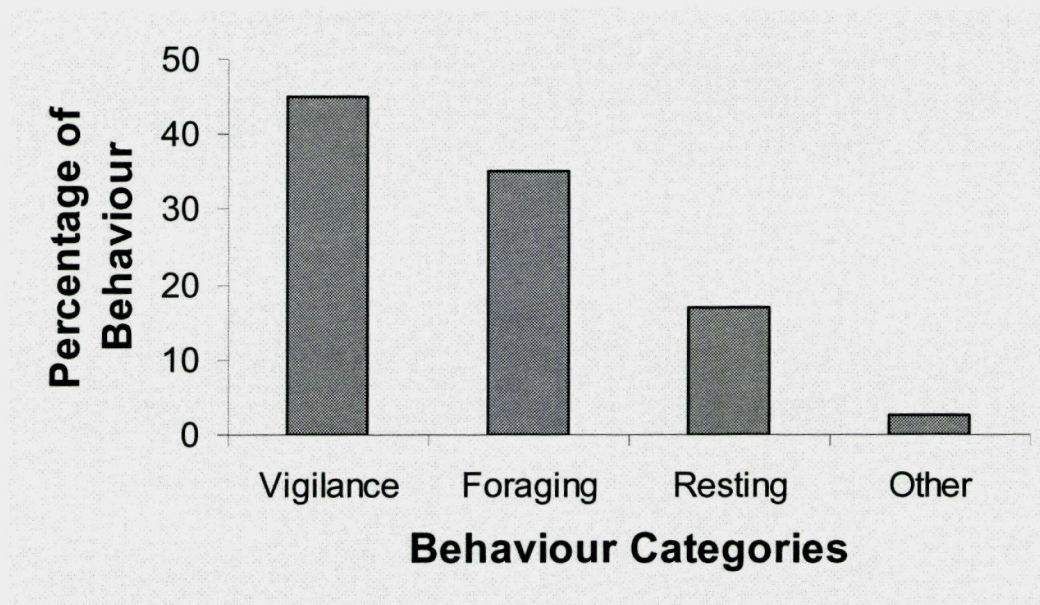


Figure 2.1 The percentage of each behaviour type across all the observations bouts (N=75). The other category includes social interactions, running and marking territories.

pronghorn spent being vigilant and when foraging using a Pearson's correlation test. Four observations were excluded from the analysis because the proportion of time pronghorn individuals were foraging and vigilant in these observation bouts equalled zero for both behaviours. These observations were not useful in testing for a correlation between vigilance and foraging because the focal animal was engaged in a different behaviour (i.e. resting) for that observation bout. For the remaining dataset which included all observations where both behaviours were observed, vigilance and foraging times were inversely correlated (Figure 2.2, Pearson's correlation $r=-0.5$, $p=0.0001$, $N=71$) suggesting a trade-off.

Vigilance

The amount of time pronghorn spent being vigilant was analyzed as a proportion of vigilance of the total observation period and transformed using arcsine of square root proportion to meet parametric assumptions. Stepwise elimination procedures were used to remove non significant variables in an ANCOVA comparing vigilance behaviour with several treatment groups (whole model before eliminations of non significant variables: $F_{21,53}=0.8$, $p=0.7$). Year was included in the initial model to account for any variation between the two field seasons but was removed because it was not significant ($F_{1,21}=1.2$, $p=0.3$). Position of the focal animal in the herd was also not significant and removed from the final model ($F_{3,21}=0.4$, $p=0.8$). Some non-significant variables were retained within the final model because they explained some of the variation and when removed, the model was an inadequate fit to the data.

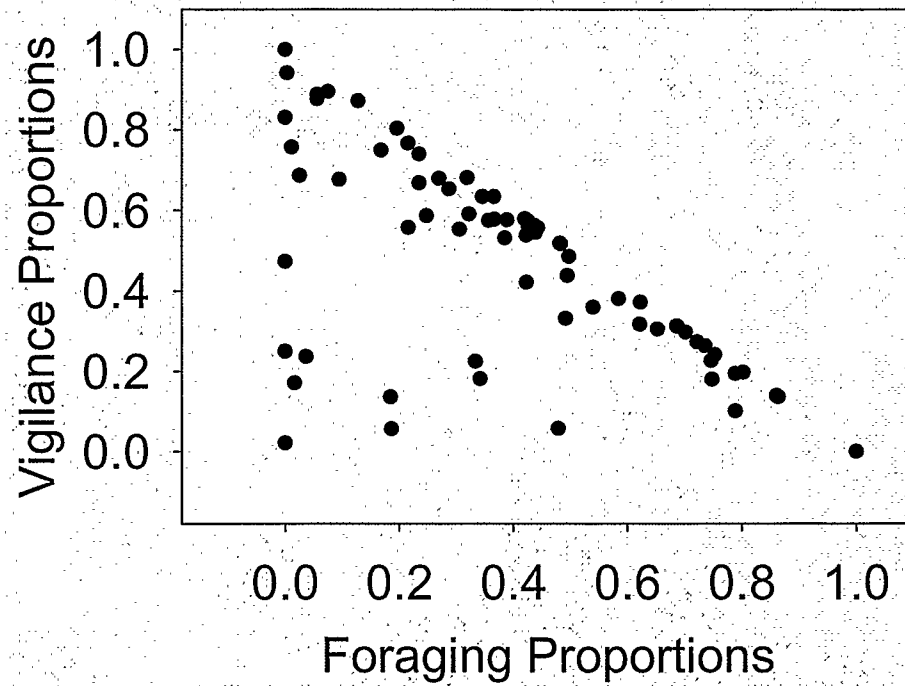


Figure 2.2 The proportion of time pronghorn spent being vigilant was correlated with the proportion of time spent foraging to examine whether pronghorn trade off between these two behaviours. The plotted vigilance and foraging proportions were back-transformed from an arcsine of square root transformation (N=71).

The final ANCOVA model after stepwise eliminations assessed whether the proportion of time pronghorn spent being vigilant varied across the treatments described below (whole model after stepwise eliminations of non significant variables: $F_{8,66}=1.6$, $p=0.1$, $R^2=0.16$). The proportion of time pronghorn spent being vigilant decreased as the number of individuals increased in a herd ($F_{1,8}=4.3$, $p=0.04$). Traffic level had a marginally significant effect on pronghorn vigilance (Figure 2.3; $F_{2,8}=3.0$, $p=0.054$). Vigilance proportions were two times lower along low traffic level roads (back-transformed least square mean (LSM)= 0.23, upper standard error (USE)=0.10, lower standard error (LSE)=0.08) compared to high traffic level roads (back-transformed LSM= 0.46 USE=0.09, LSE=0.08). The distance that pronghorns were located from roads did not affect vigilance levels ($F_{1,8}=1.0$, $p=0.3$). Vigilance was not affected by sex of the focal animal ($F_{2,8}=0.1$, $p=0.9$) or whether fawns were present ($F_{1,8}=2.4$, $p=0.1$). Finally, individual vigilance did not differ between early and late seasons ($F_{1,8}=2.2$, $p=0.1$).

The partial Eta squared analysis suggests that traffic ($hp2=8.4\%$) and herd size ($hp2=6.1\%$) are the variables that explain the largest proportions of the variation in the model.

Foraging

The amount of time pronghorn spent foraging was analyzed as a proportion of the total observation period and transformed using arcsine of square root to meet parametric assumptions. Stepwise elimination procedures were used to remove non significant variables in an ANCOVA comparing foraging behaviour with several treatment groups

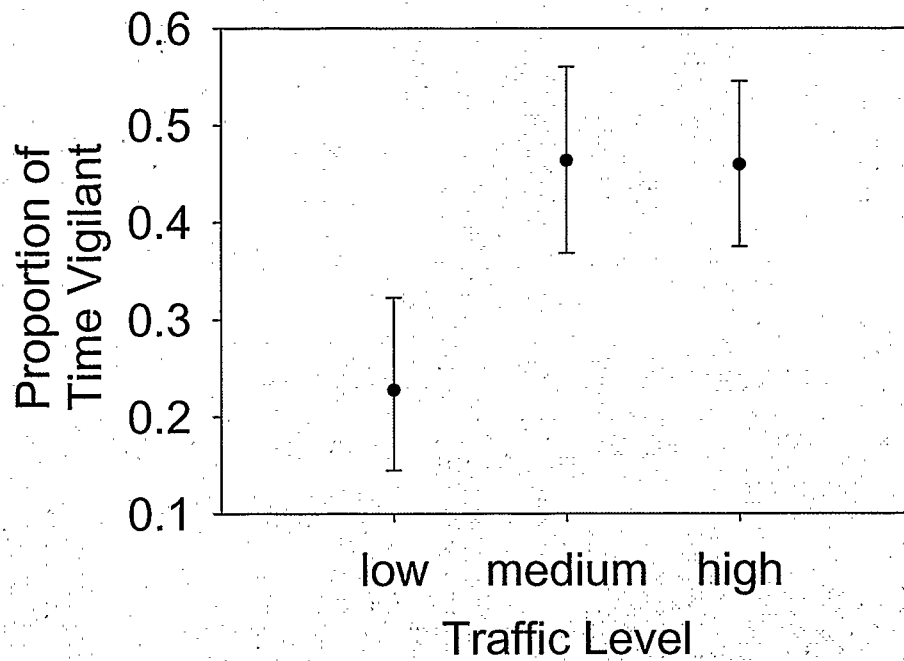


Figure 2.3 The proportion of time pronghorn individuals spent being vigilant across three traffic level categories (N=75). Reported are back-transformed least square means with standard errors.

(whole model before elimination of non significant variables: $F_{21,53}=1.1$, $p=0.3$). Group size ($F_{1,21}=0.35$, $p=0.6$), individual position within the herd ($F_{3,21}=1.1$, $p=0.3$) and sex of the focal individual ($F_{2,21}=0.5$, $p=0.6$) were not significant so they were removed from the final model.

The final ANCOVA model after stepwise eliminations assessed whether the proportion of time pronghorn spent foraging varied across treatments described below (whole model after elimination of non significant variables: $F_{8,66}=2.0$, $p=0.06$, $R^2=0.19$). Foraging was higher in 2004 than in 2003 ($F_{1,8}=6.2$, $p=0.02$) but was not directly affected by season ($F_{1,8}=1.3$, $p=0.3$). The effect of traffic on the proportion of time spent foraging showed a trend that depended on season (interaction $F_{2,8}=2.8$, $p=0.07$). In the spring season, foraging along medium level roads was higher (Figure 2.4a, back-transformed LSM=0.62, USE=0.13, LSE=0.14) compared to foraging times along high level roads (back-transformed LSM=0.15, USE=0.10, LSE=0.08). During the summer, foraging proportions were consistent across the three traffic levels (Figure 2.4b).

Whether pronghorns were within close proximity to roads or further away did not affect their foraging levels ($F_{1,8}=1.0$, $p=0.3$) nor did the presence or absence of fawns ($F_{1,8}=1.3$, $p=0.3$).

Year (hp2=8.6%) and the interaction between traffic and season (hp2=7.8%) contributed the largest proportion to the variation within the model.

Resting Behaviour

The frequency of resting was analyzed in a 2X2 table between low traffic level roads compared to a combination of all other traffic levels (medium and high). Resting

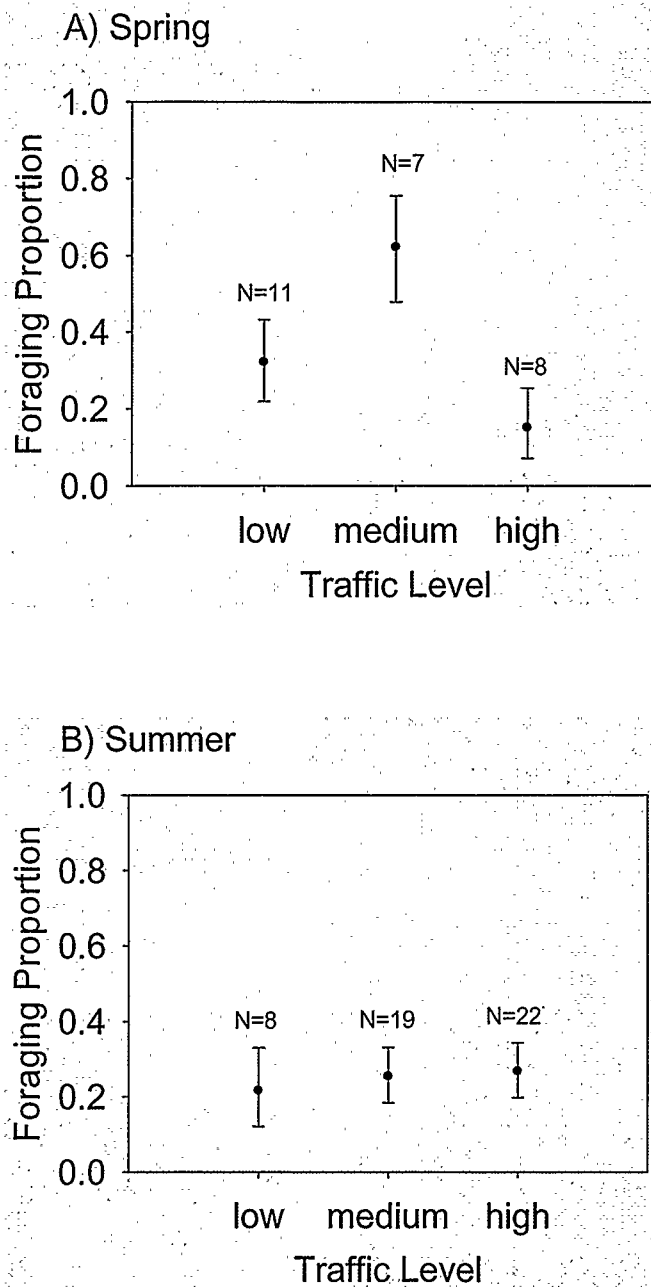


Figure 2.4 Proportion of time pronghorn spent foraging within habitat along roads of three different traffic level categories during two different seasons (2.4a spring, 2.4b summer). Reported are back-transformed least square means with standard errors (N=75).

behaviour was examined using a contingency table analysis rather than an ANCOVA because there were few observations of resting individuals (N=23). The number of pronghorn found resting in an area depended on traffic level of the road (Pearson Chi square $\chi^2=4.0$, $df=1$, $p=0.046$, $N=75$). The proportion of pronghorn resting along low traffic level roads was 47% while along higher traffic level roads; the proportion was 23%. Resting behaviour did not differ between the two distance categories from roads (Pearson Chi square $\chi^2=0.1$, $df=1$, $p=0.7$, $N=75$).

Group Structure: Solitary Individuals versus Herds

Individuals that are solitary versus those in herds may differ in their foraging and vigilance behaviours relative to the distance they are from roads and with varying traffic level. Potential differences could be obscured when solitary and herd individuals are combined together as they are in the group size variable above. Group structure (solitary versus herds) was not included in the previous models because there was a linear dependency with the data of the focal individual's position in the group. I therefore examined behaviour relative to group structure in more detail.

The effect of group structure on the proportion of time pronghorn spent foraging depended on the distance they were located from the roads (three-way ANOVA interaction: $F_{1,7}=7.4$, $p=0.01$). Individuals in herds had higher foraging proportions at distances more than 300m from roads (Figure 2.5, back-transformed LSM=0.41, USE=0.07, LSE=0.07) than near roads (back-transformed LSM=0.18, USE=0.06, LSE=0.05). However, solitary individuals did not differ significantly in their foraging proportions between the two estimated distances from roads (Figure 2.5). Traffic level

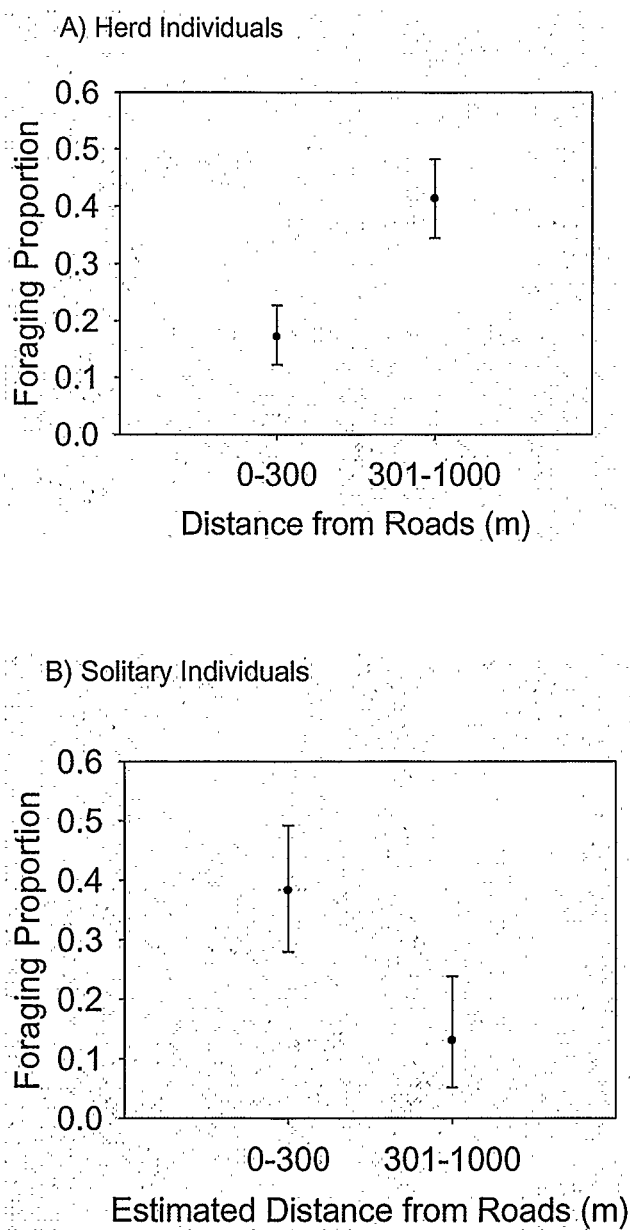


Figure 2.5 Pronghorn foraging proportion across two distance categories that were estimated by sight for herds (A) and solitary individuals (B) (N=75). Reported are back-transformed least square means and standard error bars.

had no effect on foraging for solitary or herd individuals (traffic level: $F_{2,7}=0.6$, $p=0.6$; interaction: $F_{2,7}=1.5$, $p=0.2$). Moreover, contrary to the above finding where all observations on vigilance were pooled, vigilance behaviour did not differ with respect to distance from roads or traffic level for either solitary or herd individuals (three-way ANOVA whole model $F_{7,67}=1.3$, $p=0.3$).

Other Indicators of Risk Perception

Data from the behavioural observations were then combined with pronghorn sighting data to enhance sample size. I investigated the effects of distance on herd size and the distribution of males and females as other indicators of individuals assessing risk towards road traffic. To minimize the inclusion of repeated observations, similar observations of group size and composition along the same roads were removed from the analysis.

Herd Size

Larger herds (>5 individuals) were found more often further away from roads than at close distances (Kruskal-Wallis $\chi^2=8.5$, $df=1$, $p=0.004$, $N=274$). During the spring, larger herds were found significantly more often further away from roads (Kruskal-Wallis $\chi^2=3.7$, $df=1$, $p=0.002$, $N=136$) but there was also a similar trend in the summer (Kruskal-Wallis $\chi^2=3.7$, $df=1$, $p=0.0547$, $N=148$). Pronghorn herd size varied seasonally with significantly larger herds found more frequently in the summer than in the spring (Kruskal-Wallis $\chi^2=40.3$, $df=1$, $p<0.0001$, $N=284$).

Larger herds (>5 individuals) were more likely to have fawns present within the group than absent (Figure 2.6, Wilcoxon $\chi^2=112.3$, $df=1$, $p<0.0001$, $N=284$).

Distribution of Males and Females

The proportions of males to females were analyzed across the two distance treatments in 2X2 contingency tables, when fawns were present versus absent from the group. More females were observed at distances of 301-1000m ($N=87$) than 0-300m ($N=58$) and compared to males at further distances ($N=10$) when fawns were present in the group ($\chi^2=5.6$, $df=1$, $p=0.02$, $N=173$). There was no difference in the number of males and females observed at either distance when fawns were absent ($\chi^2=2.5$, $df=1$, $p=0.1$, $N=429$).

Contingency tables were also used to examine sex distributions relative to distance from roads for solitary individuals. Sex distribution of solitary individuals were not affected by the distance they were located from roads ($\chi^2=1.2$, $df=1$, $p=0.3$, $N=144$).

DISCUSSION

The objective of this study was to assess whether differences in vigilance, foraging and resting levels reflected patterns found under a natural predation threat. If pronghorns perceived road traffic as a predation risk, this would lend support to the risk-disturbance hypothesis. Areas with higher human activity in the form of higher traffic levels may be perceived as areas with more predators thus pose a larger predation risk. I observed pronghorn being more vigilant and foraging less in habitat containing high

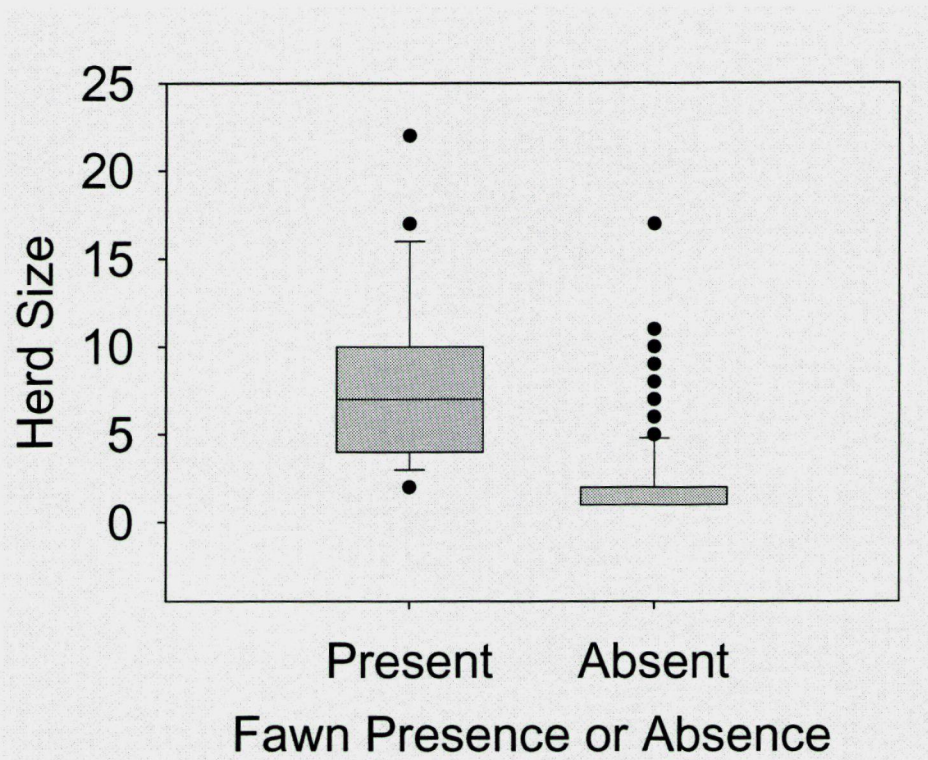


Figure 2.6 The distribution of observed herds sizes when fawns were present versus absent from the group. Larger herds were generally associated with the presence of fawns in the group (N=284).

traffic level roads. Road traffic should also affect social structure of pronghorn groups because of the presence of vulnerable fawns; therefore, females with young should be more risk averse than males. As predicted, social structure was affected by distance from the roads where females in groups with young were more likely to be further from roads compared to pronghorn groupings without young. Individuals in herds also foraged longer further away from roads than close to roads, unlike solitary individuals which did not show a difference in foraging. This could be influenced by the fact that larger herds tend to contain females with young who tend to be more risk averse to protect their young. This suggests that pronghorn may perceive lower traffic roads and distances >300 m from roads as habitat with lower predation risk. Therefore, the amount of human activity influences the degree of response by wildlife.

Other studies have found similar changes to risk avoidance behaviour in response to human activity (Papouchis et al. 2001). In Utah, pronghorns increased their vigilance rates when exposed to heavy traffic (>200 vehicles/week) associated with resource extraction and hunting compared to areas with low traffic (15 vehicles/week) (Berger et al. 1983). Ecotourism and recreational activity can also cause a similar response in wildlife. Caribou showed increased vigilance and reduced foraging when in the presence of tourists which was amplified as the number of people increased (Duchesne et al. 2000). These responses are comparable to responses towards natural predation. For example, elk under wolf predation had higher vigilance rates compared to predator-free environments (Wolff and Van Horn 2003).

Vigilance and foraging are often mutually exclusive behaviours that can be used to assess predation risk because an increase in one behaviour should correspond to a

decrease in another (Elgar 1989; Lima and Dill 1990). Qualitatively, pronghorn vigilance was highest compared to foraging, resting and other behaviours. In contrast, Byers (1997) found pronghorn activity budgets focused mainly on feeding and resting, during which rumination takes place. His study was conducted within the National Bison Range where hunting is prohibited so the pronghorn population may not exhibit strong predatory responses due to the relaxed predation pressure. Therefore, individuals with low predation pressure can allocate more time to foraging. Compared to Byers' (1997) study, pronghorn in my study exhibited higher vigilance levels, perhaps as a result of a stronger predation pressure combined by natural predation and hunters in my study population.

Trade-offs would occur if individuals exhibiting vigilance behaviour incurred a cost to another behaviour such as foraging. For example, teals in the presence of an osprey predator increased the proportion of time they spent scanning during a feeding bout which resulted in a reduction of forage intake (Poysa 1987b). These trade-offs are often assessed indirectly where researchers assume that increases in vigilance and decreases in foraging correspond to a trade-off without directly analyzing for a correlation (Wolff and Van Horn 2003; Childress and Lung 2003). Pronghorn foraging and vigilance were inversely correlated in this study, suggesting a trade-off relationship between these behaviours.

When vigilance levels were compared across areas of different traffic levels, pronghorn showed lower vigilance along low traffic level roads indicating a perception of risk towards the increased traffic activity. However, predation risk studies have shown confounding effects of group size, position in the group, presence of fawns and sex of the focal animal on vigilance rates (Lipetz and Bekoff 1982; Elgar 1989; Roberts 1996; Frid

1997; Mooring et al. 2004). Group size often has a negative correlation with vigilance rates suggesting that individuals can reduce their own level of vigilance without affecting the probability of detecting an approaching predator. The position of the individual within the group can also inflate the variance surrounding vigilance level. Individuals on the periphery generally have higher vigilance rates since they are at a greater risk of encountering an attacking predator compared to those within the centre of the group (Elgar 1989; Roberts 1996). My study suggests that group size and the presence of young are stronger determinants of risk avoidance behaviour than the position of the individual within the group because they explained a larger amount of the variation in the model. As more individuals gathered within the herd, pronghorn individuals exhibited lower individual vigilance rates. In another study, pronghorns were also found to benefit by grouping together because vigilance was lower for individuals in larger herds (Lipetz and Bekoff 1982).

Vigilance was significantly different when individuals in all group sizes were considered but not on a smaller scale between solitary and herd individuals possibly because by separating the observations into these groups, it lowers the sample size. I had predicted that solitary individuals should have higher vigilance levels than individuals in herds because solitary animals cannot dilute their predation risk with conspecifics. The unexpected lack of a significant difference in vigilance behaviour between solitary and those herd individuals may also be connected to how vigilance was measured. Vigilance behaviour may have been underestimated because scans for predators could occur during other activities such as pellet deposition or feeding on taller shrubs which was not included in these vigilance times. Vigilance was assumed when the individual had their

head lifted and scanned the surroundings. This could reduce the power of detecting possible vigilance differences between solitary individuals versus those in herds.

Group size can also indirectly reflect the presence of young because larger groups may contain pronghorn fawns to dilute their predation risk. Females with young tend to have higher vigilance rates compared to other females and males due to the vulnerability of the neonate to predation (Toigo 1999; Childress and Lung 2003; Wolff and Van Horn 2003). I focused on the effects of fawns being present in the group rather than comparing responses of mothers to other females because it was not always possible to identify mother and fawn pairs. Because focal animals consisted of mothers, other females and males, this could have contributed to finding no relationship between vigilance levels and the presence of fawns. Fawn presence did not directly affect vigilance levels but did affect female distribution around the road. Females in groups with young present were located more often at distances further away from roads compared to males.

The effect of increasing group size on decreasing vigilance also has implications for increasing foraging opportunities. Contrary to the prediction, group size did not affect pronghorn foraging proportions and was not included in the final ANCOVA model. Other studies have found no relationship with foraging and corresponding increases in herd size (Lipetz and Bekoff 1982; Berger and Cunningham 1988). Group structure (solitary versus herds) may be a stronger influence on foraging behaviour because solitary individuals have been found to have lower foraging and higher vigilance levels (Lipetz and Bekoff 1982). In my study, only individuals in herds were found to have higher foraging proportions when further away from roads compared to close to roads. Herds generally contain females with young; therefore, observations from these

individuals could contribute to the lower overall foraging in herds when close to the high risk road areas. If the effect of group size was the determining influence on foraging rates, herds should forage consistently at both distance categories. Yet even when individuals were within the safety of a group, they preferred areas away from roads suggesting that areas near roads had a higher risk associated with it. If solitary pronghorn are more vulnerable to predation, I might expect that these individuals would forage less and be more vigilant regardless of distance from roads. Solitary pronghorn foraging behaviour did not differ significantly across distance from roads even though the graphed means might appear to differ across the two estimated distances. The Tukey-Kramer test was used for pairwise comparisons between the group structure and distance interaction variable because sample sizes differed between the treatment groups. This analysis is more conservative in testing for significance when the differences in the sample sizes of the treatment groups is large such as the case with the solitary observations at 0-300m (N=15) and 301-1000m (N=7).

The risk of predation also influences decisions of where to feed because individuals may choose forage areas that minimize their predation risk (Lima and Dill 1990). Traffic level showed a trend of affecting pronghorn foraging behaviour, particularly within the spring season. The risk level associated with traffic may be enhanced during the spring season due to the births of vulnerable fawns. Pronghorn foraging rates are generally highest during the winter but females tend to forage longer in the spring than males due to gestation and lactation energy requirements (Byers 1997). However, sex of the focal individuals was a non significant term that was not included in the final model. Another study also did not find that the proportion of time pronghorn

spent foraging was affected by sex but instead found female foraging was influenced by the presence of fawns (Lipetz and Bekoff 1982). Previous studies have shown that the presence of active fawns can lower foraging rates of mothers as they increase their vigilance (Lipetz and Bekoff 1982; White and Berger 2001; Treves et al. 2003). Fawns are born in late May and are the most vulnerable to predation. In my study, the presence of fawns did not affect foraging rates when group size and sex were controlled but the relationship could be obscured because focal animals consisted of not only mothers but other females and males.

The spring season also represents the emergence of new vegetation growth. If the increases in foraging times corresponded to new vegetation growth or differences in energy requirements, the spring foraging times should be consistent across traffic levels. Yet foraging was least along high traffic level roads in the spring season suggesting pronghorn may assess higher risk levels along these roads. I had expected pronghorn to forage more in habitat along low traffic roads because it may be associated with lower risk but foraging was highest along medium traffic roads. Behavioural observations were conducted in similar areas as the vegetation surveys discussed in chapter 3 so I am using these surveys to examine any possible differences between low and medium traffic roads. Shrub coverage was affected by traffic level but there were no significant differences between shrub coverage along low and medium traffic roads. Cactus coverage also differed but pairwise comparisons could not detect any significant differences between the traffic categories. Cactus coverage which included ball cactus (*Mamillaria vivipara*) and prickly pear cactus (*Opuntia polyacanth*) was qualitatively lower along medium traffic roads compared to low. It is unlikely that vegetation differences caused the lower

foraging levels near low traffic roads compared to medium because cactus is only a minor component of pronghorn diet (Mitchell 1980) and no other major diet components were significantly different. The weaker foraging response along low traffic level roads could be due to the lower number of observations along this type of road (N=19) compared to medium (N=26) and high (N=30) traffic level roads. Differences in the observation numbers were due to the process of excluding observations that occurred in similar group sizes and composition along the same roads to avoid pseudo-replication.

Year was included in the model to help control for variation between the field seasons such as differences in vegetation availability between the two years which could influence foraging rates. The number of observations of individuals collected differed only slightly between the 2003 (N=35) and 2004 (N=40) field seasons. In 2003, behavioural observations were conducted in areas near the Montana/Saskatchewan borders which received lower precipitation than the areas surveyed in 2004. This could influence forage quality but pronghorn in areas with lower quality forage would be expected to forage longer to extract enough nutrients from the poorer vegetation. However, foraging proportions were higher in the 2004 field season perhaps due to differences in vegetation composition between the areas. Vegetation surveys discussed in chapter 3 showed vegetation differences between the two years. Wilcoxon analyses showed areas surveyed in 2003 had higher coverages of cactus and grass while areas in 2004 contained higher forbs and shrubs (chapter 3). Pronghorn diet in the spring (April-May) consists mainly of forbs and grasses while during the summer season (June-August), forbs and shrub predominate (Mitchell 1980). Therefore, the longer foraging bouts in areas in 2004 may be influenced by the higher coverage of shrubs and forbs

which contribute to the majority of their spring and summer diet. However, these areas were not replicated over several years so it is difficult to say whether vegetation differences or natural temporal variation is influencing differences in foraging times.

I also compared pronghorn resting periods across traffic level and distance as another behaviour which may indicate whether roads were perceived as a predation risk. An individual resting within the vegetation may increase their vulnerability to a predatory attack because escape effort would be hindered. Therefore, the location of resting individuals may represent areas where they perceive a lower risk level. The occurrence of pronghorn resting behaviour was different across traffic levels. The large difference between the ratio of not resting to resting individuals along higher traffic level roads suggest that pronghorn are less likely to rest near these roads. An interesting note during these observations was that some individuals were lying in the vegetation facing towards the road. This could indicate that individuals are sensing some risk towards roads; therefore, they prefer to keep the potential threat within sight. For example, African antelope prefer to keep potential predators within direct sight to allow them to assess whether a nearby predator is actively hunting or not based on postural cues (Underwood 1982).

Changes in herd size were examined as another possible indicator of whether pronghorns perceive a degree of risk associated with the human activity along roads. Individuals forming larger herds near a disturbance might suggest that they perceive a high degree of risk towards the disturbance. By grouping into larger herds, each individual can lower their probability of being attacked through the dilution effect and enhance the overall detection of predators (Dehn 1990). Fairbanks and Tullous (2002)

found pronghorn herd size was not correlated with distance from newly constructed recreational trails but groups with the smallest mean sizes were found significantly more often further away from these trails (Fairbanks and Tullous 2002). In contrast, another study found pronghorns remained in larger herds in an area disturbed by resource extraction even though their foraging efficiency was reduced (Berger et al. 1983). This suggests that the pronghorn were assessing a higher risk with the increased human activity but traded efficient energy intake for safety within numbers. Pronghorn herd sizes were tested against estimated distances from roads and larger groups were located further away from roads. This may seem to contradict what pronghorn should do under a predation risk but larger herds tended to contain fawns. Fawns are more vulnerable to predation so location further away from a predation risk would enhance survival. Even though individuals may be able to dilute their probability of attack within a large group, larger groups are also easier to detect by predators (Krebs and Davies 1993; Hebblewhite and Pletscher 2002). Coyotes may use some roads as corridors and hunters often locate pronghorn from roads. Predators that attack larger groups often have greater capture success because they tend to contain weak or old individuals (Hebblewhite and Pletscher 2002). From an individual standpoint minimizing the detection rate and thus potential predator attacks would increase their chances of survival contributing to individuals forming herds further away from the disturbance threat.

Pronghorn antelope behavioural activities were influenced by the traffic activity on roads that intersects their landscape. Pronghorn responses towards traffic are similar to behaviours exhibited under natural predation risk which supports the risk-disturbance hypothesis. Increases in traffic level reflected a gradient of risk levels which pronghorn

responded to by increasing their risk avoidance behaviour. Foraging behaviour was also reduced during the spring season at higher traffic levels. Moreover, groups that would be expected to be most risk averse, such as females with young, avoided areas within close proximity to roads. Understanding how pronghorn, already under predation and hunting pressure, respond to human perturbations will aid managers in minimizing the impact of new developments in pronghorn habitat. This will improve pronghorn management policies to assist in maintaining viable populations.

CHAPTER 3 THE EFFECTS OF ROAD TRAFFIC ON PRONGHORN ANTELOPE HABITAT USE

INTRODUCTION

The presence of predators can influence how an individual selects and uses a habitat patch for foraging, reproduction and other opportunities (Lima and Dill 1990; Lima 1998). The habitats that animals select often reflect a balance between avoiding predation and obtaining resources (food or mates). Individuals may shift between habitats depending upon the predation risk associated with the present habitat and whether adequate alternate habitat is available (Frid and Dill 2002). The boundaries or edges between habitat types may influence animal distribution depending on the predation risk associated with the feature because some generalist predators are associated with edge habitats (Fagen et al. 1999; Ries et al. 2004). The term “edge mediated effects” refers to how these habitat boundaries influence the behaviour of organisms which could involve assessing predation risk associated with the edge habitat (Fagen et al. 1999).

Human disturbances in the form of linear developments can also generate induced edge boundaries (Yahner 1988) which may have implications for wildlife distribution in the surrounding habitat. How animals respond to linear disturbances has received some attention but most studies do not link the proximate factors causing the patterns to an ecological process (Mace et al. 1996; van Riper and Ockenfels 1998; Dyer et al. 2001; Fecske et al. 2002; Gibeau et al. 2002; Berger 2004). Animals that perceive the linear disturbance as a predation risk may alter their distribution within that habitat to minimize

interaction with the disturbance which would lend support to the risk-disturbance hypothesis (Frid and Dill 2002). According to this hypothesis, exposure to these disturbances may cause animals to shift into habitats that could have reduced resources or cover from predators, or where locations of mates or migratory routes are obstructed which could lead to population declines.

Roads as Anthropogenic Edges

Road networks as a linear feature can fragment the landscape by separating contiguous pieces of habitat which may create an induced edge or boundary. Following the risk-disturbance hypothesis, whether or not individuals perceive a degree of risk towards the anthropogenic edge may be reflected in their distribution surrounding that edge area. Four fundamental mechanisms underlying the animal abundance patterns along edges have been identified: the ecological flow of material or organisms across the edge, using edges to gain access to spatially separated resources, species interactions along edges and resource mapping (organism's distribution reflecting resource distribution) (Ries et al 2004). My study incorporates components from three of these mechanisms: ecological flow, species interactions and resource mapping.

Ecological flow refers to the degree of movement or permeability across an edge which can influence animal distribution in habitat along that edge. Road permeability can be categorized as barriers (no movement across) or filters (permit some movement) (Jalkotzy et al. 1997; Forman and Alexander 1998). Depending on the specific population, roads as filters could pose a larger problem than barrier roads because it can

increase individuals encounters with direct (vehicular collisions) and indirect (predators, hunters) mortalities. Road characteristics that influence permeability may depend on road width and traffic level (Forman and Alexander 1998). Wider roads with high traffic loads may be perceived with higher risk resulting in low permeability and animals may aggregate along these edges. The distance animals are found from the edge can represent the degree of risk perceived towards it. Edge mediated effects can be represented as a function of distance from the edge which can be positive (attracted towards edges), neutral (response consistent across distance) or negative (avoid edges) (Ries et al. 2004; Figure 3.1). The accumulation of individuals within close proximity (positive) versus away from the edge (negative) may be influenced by the perception of danger associated with the edge. The higher the risk, the greater the distance individuals will be found from the edge.

Animal reactions towards roads have shown various responses from positive to negative distance effects. Positive edge responses towards roads have been found for several bird species that prefer to nest in road side verges rather than the frequently disturbed cropland (Oetting and Cassel 1971; Warner et al. 1987; Clark and Karr 1979; Laursen 1981; Camp and Best 1994). Rodents were attracted to newly developed interstates in Illinois because the denser vegetation maintained along the roads provided suitable habitat for individuals to disperse through heavily agricultural landscapes (Getz et al. 1978). Negative edge responses can result from increased exposure of either direct (vehicular collisions) or indirect (increased predation) mortalities that may alter animal behaviour, causing changes in home range, movement patterns, escape response and

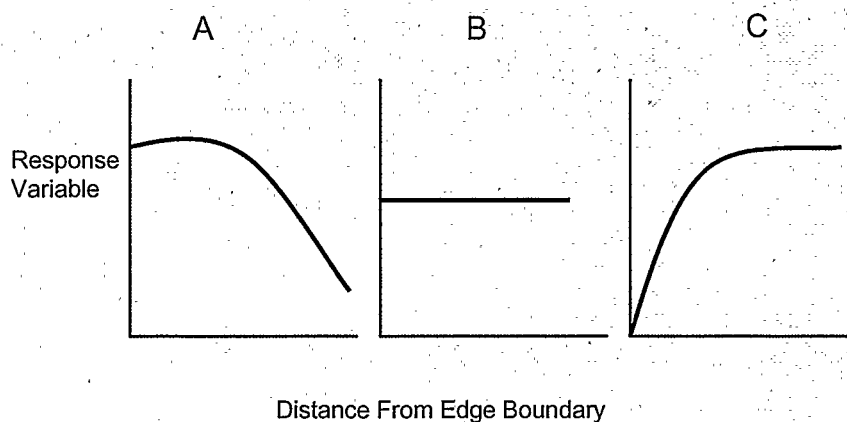


Figure 3.1 Three behavioural responses to an edge boundary; a) positive response (individuals attracted to the edge), b) neutral response (response consistent across distance), c) negative edge response (avoid edge). Figure re-created from Ries et al. 2004.

habitat use (Jalkotzy et al. 1997). Avoidance of habitat along roads is a concern for maintaining viable populations of various species. For example, bears, particularly females, avoid high traffic level roads even if quality habitat is nearby (Mace et al. 1996, Gibeau et al. 2002, Fecske et al. 2002).

The alteration of ecological flows that result in the aggregation of organisms along edges may also enhance encounters with generalist predators (Yahner 1988; Fagan et al. 1999). Therefore, species interactions at edges are affected due to the mortality indirectly related to the edge effects. Edge boundaries may cause predators and prey to remain longer near the boundary where the shorter the length of the boundary, the more likely they are to encounter each other (Kaiser 1983). Nest predation and parasitism has been shown to increase along edges with increasing fragmentation (Andren 1992, Paton 1994, Burger et al. 1994; Wolf and Batzli 2001).

Habitat quality may be influenced by edge effects that cause changes to micro-climate gradients that can affect the plant distribution near that edge (Forman et al. 2003). Some variation in responses to linear disturbances may be associated with how that disturbance affects the habitat quality in that area. If animals map onto their resource distribution, then edge related changes to the resource distribution may result in the corresponding change in an animal's distribution (Kristan et al. 2003, Ries et al. 2004). How the animal assesses the habitat changes related to the disturbance may influence trade-offs between predation and resource acquisition because some individuals may utilize riskier habitats to obtain higher rewards (Lima 1998). Development of disturbances that increase vegetation diversity or density may attract some species to areas near the disturbance (Forman and Alexander 1998) while for other species pollutant

accumulation on plants (Harrison and Dyer 1984; Trombulak and Frissell 2000), introduction of invasive plant species (Tyser and Worley 1992), and increased noise disturbance (Reijnen et al. 1996; Forman et al. 2003) may contribute to habitat avoidance.

Research Objectives

The concepts of road effects understood to date suggest that positive or negative responses can be observed possibly due to varying levels of risk perceived along the edge created by roads. To test these concepts, I investigated whether pronghorn antelope, *Antilocapra americana*, exhibit patterns of habitat use consistent with perceiving a predation risk towards road traffic. If ecological flows are affected by roads, then the relative pronghorn distribution should differ between areas that had no roads to areas with roads of various traffic levels. I examined how the presence of a road may affect pronghorn distribution and measured the extent of the distance effect further into the habitat. If pronghorn perceive habitat near roads as a riskier area, based on the probability for increased interaction with predators or humans, pronghorn presence should correspond to a negative edge response. Because risk is often assessed at different levels along a gradient, pronghorn should perceive a greater risk in habitats containing higher traffic or human activity, resulting in a lower presence of pronghorn in these types of habitat.

Finally, to investigate whether pronghorn presence was influenced by an edge response or resource mapping, I measured specific habitat features to assess whether differences in vegetation existed across sites. If pronghorn do not consider habitat surrounding roads as risky areas, then pronghorn presence should be consistent with the

resource distribution of their preferred vegetation. If habitats near roads are risky, then pronghorn presence should reflect the behavioural decisions to avoid these areas.

METHODS

Study Area

In Canada, pronghorn antelope are distributed across southeastern Alberta and southwestern Saskatchewan. Pronghorn range is divided into antelope management areas in which several Fish and Wildlife Divisions are responsible for specific units. This study was conducted throughout the antelope management units of C, D, E, F, and G in southeastern Alberta. Each antelope management unit is further subdivided into wildlife management units. All data were collected during 2003 and 2004. Surveys were conducted in antelope management areas C and F in 2003 and D, E, F and G in 2004. Refer to Chapter 1 for a complete description of the study area and study system.

Study System

In their northern range, pronghorn antelope form large mixed sex herds during the winter and may migrate up to 160 km between their winter and summer ranges (Nowak 1991). In the greater Yellowstone range, they still exhibit long distance migration with a round trip of 550 km (Berger 2004). They migrate in accordance with snow depth and access to high energy forbs and shrubby browse (Dirschl 1963). Access to various landscape topographies on their summer range is also important for reproductive activities such as the birth of fawns and males establishing territories. Human development that impedes pronghorn movement in these areas can drastically alter their

behaviour, habitat use and population dynamics (Hepworth 1966, Oakley and Riddle 1974, van Riper and Ockenfels 1998).

Previous research has begun to examine how pronghorns respond to human activity; specifically, how human disturbances may affect habitat quality by creating movement barriers and increasing noise disturbance. One study found that fenced transportation corridors acted as a barrier to pronghorn crossing movement resulting in the isolation of two populations in Arizona (van Riper and Ockenfels 1998). The design of fences can influence pronghorn movement because pronghorns prefer to crawl under fences if there is adequate clearance (Hepworth 1966; Bruns 1977). Pronghorn habitat use was also affected by the creation of recreational trails in Antelope Island State Park resulting in pronghorn using areas further away from the trail areas compared to before the trails were opened (Fairbanks and Tullous 2002). The continued construction of a paved road within an important fawning area in the park caused females to shift into habitat at higher elevations to give birth to their fawns which may have contributed to the high fawn mortality rates recorded that year (Fairbanks and Tullous 2002). Pronghorn responses to roads have not been tested within their northern range where they are more susceptible to severe weather and barriers to migratory routes (Hepworth 1966; Oakley and Riddle 1974). In Alberta, pronghorn are not protected within any national parks, except for a small area on Suffield Military Base; therefore, the response of hunted populations to human activity may be heightened.

Pronghorn response to noise disturbances that can affect habitat quality was examined for a population on a military base (Krausman et al. 2004). Noise levels emitted by human disturbances do not appear to play a major role in altering pronghorn

behaviour. Although pronghorn, along with bighorn sheep and deer, have less acute hearing than humans (Krausman et al. 2004), they did use areas with lower sound pressure more often than areas of higher sound pressure. However, the areas of high sound pressure also had higher human activity associated with it (Landon et al. 2003). Pronghorns generally rely on their acute vision and smell to detect predators (O’Gara and Yoakum 2004) which could mean that risk perception towards roads may be related to the visual component such as the number of vehicles on the roads.

Study Design

Faecal pellet surveys

Stratified sampling of pronghorn range was used to select survey areas that consisted of similar land use practices (rangeland only), habitat, road fencing, and pronghorn population densities (Patton 1992). Differences in hunting effort between areas were minimized by selecting areas that had similar pronghorn population estimates. The number of hunting licenses issued for each wildlife management unit is dependent on the population estimates of that area. Each wildlife management unit had roads surveyed from low to high traffic level categories. Areas were sampled by systematic sampling where starting points were randomly selected along roads and plots searched at pre-determined distances along a transect perpendicular to each road (Neff 1968; Patton 1992). Roads were categorized into traffic level ranges based on annual summer daily traffic counts for sections of that road for which 2002 traffic data were supplied by the Alberta Transportation Department. Categories consisted of low (0-10 vehicles/day), medium (70-200 vehicles/day), high (>300 vehicles/day) and very high (>1000

vehicles/day). Traffic categories were chosen based on the roads available within pronghorn range. A total of 5 roads were sampled for each traffic level category over two field seasons. The very high category was the exception with one highway, the Trans-Canada, being surveyed in only 2004. The highway was surveyed in two different areas that were separated by 60 km of road. A secondary highway in the high traffic volume category was also used twice over the two field seasons but the survey areas were separated by almost 170 km. A fifth category consisted of an area that was over 1 km away from any roads and was referred to as the “no road” category. In this category, surveys were conducted perpendicular from fences that separated pastures to compare to the surveys along the fenced roads. Fences varied from 3-6 barb wire strings. There were a total of 10 areas used for this category which were selected in areas that included roads of various traffic densities. Most ungulates have a visual acuity of 1 km (Nowak 1991) therefore plots at distances beyond 1 km should be useful in comparing areas near roads and those away from roads. All plot and observation locations were recorded using GPS.

Each road had temporary 30 m² plots spaced at 0 m, 200 m, 400 m and 600 m along a transect perpendicular to a fenced road (Marques et al. 2001). Plots within the no road areas were designated distances of >1000 m from the road. The 0 m plots were placed at the fence line where road verges between the fence and road surface varied from 10-20 m in width. Each transect was placed at a minimum of 200 metres to >1km apart along the fence depending on topography such as the presence of a ravine. Each corner of the plot was flagged and the GPS coordinates recorded. Each road had a total of 40 plots where 20 plots were surveyed in the early spring (May-June) and the

remaining 20 plots surveyed later in the summer (July-August). Plots were searched in a grid-like fashion, with observers walking side by side scanning 1 metre in width around them. A pellet group was recorded if it contained >5 pellets of similar size, shape, colour and texture (Freddy and Bowden 1983; Rowland et al. 1984). I used the pellet counts/plot as an expression of pellet density. All pellets were recorded regardless of their deposition age. Aging of pellets was difficult because the openness of the grasslands increases exposure to weather and thus increasing rate of decay so seasonal effects could not be analyzed (Harestad and Bunnell 1987). Deer and pronghorn occur sympatrically in the area which could be a source of observer error by inaccurate identifications. However, the identification of pronghorn pellets was conservative to minimize any error. The identification of pronghorn pellets versus deer was based on descriptions of shape and size. Pronghorn pellets were normally ~19 mm in size and acorn shaped with a divot on the bottom. Deer pellets were normally >25 mm and cylindrical in shape. Pellets that did not fit these descriptions or were of intermediate size and shape were recorded as unknown samples (unknown samples found in 45% of the all plots).

Because road orientation can occur east to west and north to south resulting in each side of road being exposed to different micro-climatic gradients (Forman et al. 2003), I included transect placement across varying sides of a road within the analysis. Plots in the summer surveys were conducted on the opposite side of the road than in the spring. However, due to the selection criteria of roads for the traffic level categories and land access, plots surveyed are not balanced across the four transect directions (East= 126 plots, North=89 plots, South=223 plots and West=230 plots).

Road density for my study area was provided by Stefan Kienzle, a GIS specialist from the University of Lethbridge who calculated the road densities in the ArcView GIS program for each wildlife management unit surveyed.

Vegetation Surveys

Vegetation surveys were conducted in four circular plots of 5 m diameter randomly nested within the 30 m² plots used for the pellet surveys. The GPS coordinates of the centre of the circular plot was recorded. Vegetation data was averaged across the four plots for data analysis. I conducted all the vegetation surveys for the two field seasons to maintain consistency. I used the Daubenmire canopy coverage method to estimate the percentage of coverage by specific vegetation categories (Daubenmire 1959). I did not use the number of plants since a single large shrub could occupy more space than several small forbs. The categories for vegetation were sagebrush (*Artemisia cana*), pasture sagewort (*Artemisia frigida*), other shrubs, forbs, cactus, grass and ground. Pronghorn diet consists of forbs and grasses in the spring; forbs and shrubs in the summer; forbs, shrubs and grasses in the fall and winter (Mitchell and Smoliak 1971). Major food items include silver sagebrush (*A. cana*), pasture sagewort (*A. frigida*), grasses, ball cactus (*Mamillaria vivipara*) and western snowberry (*Symphoricarpos occidentalis*) (Mitchell and Smoliak 1971). For statistical analyses, sagebrush was combined with other shrubs and pasture sagewort was combined with other forbs.

Analyses

Statistical analyses were conducted in JMP IN version 4.0 computer package (SAS Institute, 2001) and SAS/STAT software version 6.04 (SAS Institute, 2001). All tests used a Type I error rate of $\alpha=0.05$ to determine significance. For pairwise comparisons of significant interactions, the Dunn Sidak correction term was used to adjust the α level based on the number of comparisons conducted $(1-(1-\alpha)^{1/k})$. This lowers the Type I error for each comparison so that the probability of making a Type I error over the entire series of comparisons does not exceed the experimentwise error rate ($\alpha=0.05$) (Sokal and Rolf 1981).

Pellet group surveys have been found to be an effective tool in measuring the relative abundance of animals in an area (Neff 1968; Telfer 1978; Loft and Kie 1988; Weckerly and Ricca 2000). To confirm this relationship, I compared relative pellet densities to relative pronghorn population estimates. Relative pellet densities were calculated by dividing the total pellet count by plot size (0.09 ha) (Loft and Kie 1988). A pronghorn population estimate per antelope management area (AMA) for 2002 was supplied by Alberta Fish and Wildlife. Assuming that each wildlife management unit (WMU) was surveyed equally to produce the overall population estimate for the AMA, the pronghorn population estimate was divided by the number of wildlife management units within that AMA to represent a relative estimate for each WMU. This allowed me to compare relative pronghorn density per WMU to the average pellet group density I observed in that WMU because not all wildlife management units in every AMA were surveyed in my study. Road density within each WMU could also influence pronghorn presence in those areas so I conducted a partial Spearman's correlation between relative

pellet density and pronghorn population densities with road density per WMU held constant.

Habitat use was examined by poisson regression which tests the number of occurrences of an event as a function of several independent variables in space or time. The no road data was not included in this analysis because these areas were assigned different distance categories (>1000m) which were not surveyed on the transects of the other traffic categories. Total pellet counts were used since a poisson regression requires integer values. Poisson regression is a form of a generalized linear model (GLM) which applies the regression analysis to a poisson distribution rather than a normal distribution (Gardner et al. 1995). The poisson regression uses a link function for a log transformation to model the mean of the events as a linear function of the independent variables. The least squared means (LSM) and standard errors of those variables were back-transformed which produces asymmetrical standard errors. Therefore, I reported the upper (USE) and lower standard error (LSE) bars separately. Since the poisson regression assumes that the mean and variance are equal, the fit of the model is assessed by comparing whether the deviance value/df is close to 1. Values greater than one indicate overdispersion, values under 1 indicate underdispersion of the data to the model (McCullagh and Nelder 1989). One recommended approach involves introducing a dispersion parameter into the relationship between the variance and the mean which holds the scaled deviance value at 1 (Cox 1983; McCullagh and Nelder 1989; Gardner et al. 1995). This gives a correction term for testing the parameter estimates under the poisson model but the parameter estimates are not affected by the value of the dispersion parameter (McCullagh and Nelder 1989). The fit of my data to the poisson regression

model showed a modest overdispersion (deviance/df=1.43) due to a higher proportion of observed counts of zero leading to variances > means (Gardner et al. 1995). Therefore, I used the overdispersed deviance/df value as the estimate of the dispersion parameter rather than setting it to 1. I used stepwise backwards elimination to remove non-significant variables that did not contribute largely to the variation in the model.

To determine which model best approximates the data, I calculated the Akaike Information Criterion (AIC) for each model after each variable was removed. The model with the lowest AIC value represents the most parsimonious model which means it is the best balance between the variance and bias of the resulting parameter estimates (Burnham and Anderson 2002). Bias increases and variance decreases as the number of parameters in the model increase (Burnham and Anderson 2002). Because I used a dispersion parameter to correct for the slight overdispersion in the poisson regression, I incorporated the same correction term in the AIC calculation (Burnham and Anderson 2002). I then calculated the delta AIC values (Δ_i) that describe the relative difference between the global model with all the variables included to the model with the minimum AIC value. If the relative values of Δ_i fall between 0-2, this suggests that the model strongly supports the data; 2-4 moderately fits and more than 7 represents a model that does not fit the data (Burnham and Anderson 2002).

A Kruskal-Wallis analysis was used to compare pellet densities across the four traffic levels and the no road areas. Plots within no road areas were assigned distances of >1000 m and compared with the other distance measures to examine the extent of the edge response. If the test was significant, I used a non-parametric pairwise comparison test that compares the difference of the mean ranks of each comparison to an adjusted

critical value of z based on the number of comparisons (Siegel and Castellan 1988). If the rank differences are greater than the adjusted critical value than the null hypothesis can be rejected.

To examine the possibility that animals may be mapping onto the resource gradients in the habitat surrounding the edge created by the road, I wanted to assess whether the vegetation coverages differed among the habitats along these various roads. Vegetation coverages were not normally distributed so the non-parametric test Kruskal-Wallis was used to compare vegetation coverage across distance from roads and traffic levels including no road areas.

RESULTS

Pellet Group Surveys

Relative pellet density represents the pellet group count divided by the plot size (0.09 ha) and averaged for each WMU. Pronghorn densities were based on population estimates from antelope management units divided by the number of wildlife management units in that AMA. Relative pellet density increased with pronghorn density (Partial Spearman's $r_s=0.96$, $p=0.003$, $N=7$) while controlling for road density suggesting that pellet group counts are an indicator of the distribution of pronghorn.

A poisson regression was used to examine the effect of road density, distance from a road, traffic, transect orientation, vegetation, year and biologically relevant interactions on the total pellet groups counted. Year was included as a random variable to account for any variation between the two field seasons. I will discuss variables separately as an edge response, gradient of risk and resource mapping but all were

included in a single poisson regression model with the lowest AIC value (AIC=185.6; $\Delta_i=0$).

Pellet densities were higher during the 2003 field season compared to 2004 ($G=6.14$, $p=0.01$, $df=1$, $N=672$). Wilcoxon analyses were conducted to compare vegetation coverages between the areas surveyed for the two field seasons. Both shrub ($\chi^2=5.8$, $p=0.02$, $N=672$) and forb ($\chi^2=29.4$, $p<0.0001$) coverages were higher in habitats surveyed in 2004. However, cactus ($\chi^2=14.6$, $p=0.0001$), grass ($\chi^2=6.3$, $p=0.01$) and ground ($\chi^2=8.8$, $p=0.003$) coverages were higher in habitats surveyed in 2003.

Edge Response

Pellet densities first increased with distance from a road, reaching a maximum at 200 m (back-transformed least squared mean (LSM)= 0.21, upper standard error (USE)=0.09, lower standard error (LSE)=0.06) and 400 m (back-transformed LSM=0.30, USE=0.11, LSE=0.08) but then declined with increasing distance (Figure 3.2; $G=33.37$ $p<0.0001$, $df=3$, $N=672$).

Road orientation varied across the surveys therefore placement of the plots along these roads were analyzed with pellet densities (Figure 3.3; $G=77.71$, $p<0.0001$, $df=3$, $N=672$). Plots placed on the north side of the roads had the highest pellet densities (back-transformed LSM=1.33, USE=0.57, LSE=0.40) compared to all three other directions. Kruskal-Wallis analyses were used to compare each vegetation category by transect orientation. Non-parametric pairwise comparisons between the treatments were conducted on significant tests using differences between the rank means (Siegel and Castellan 1988). All vegetation categories differed across transect orientation (Figure

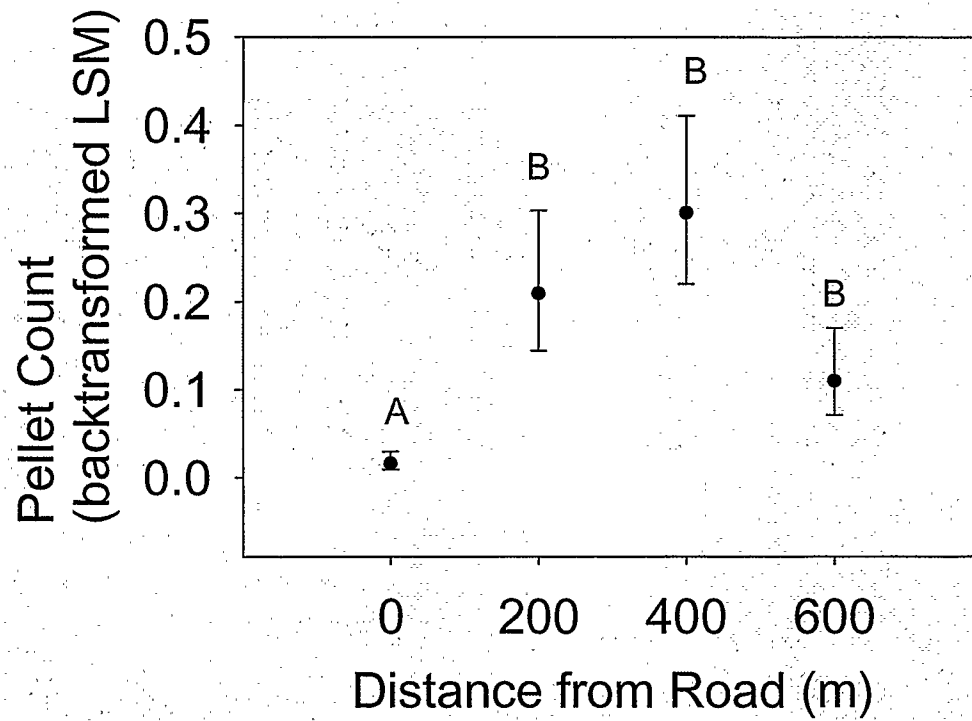


Figure 3.2 Pronghorn pellet densities (#/0.09 ha/plot) at four distances from roads, regardless of traffic level of the roads (N=672). Similar letters indicate no significant difference between least square means. Plotted are back-transformed LSM and standard error bars.

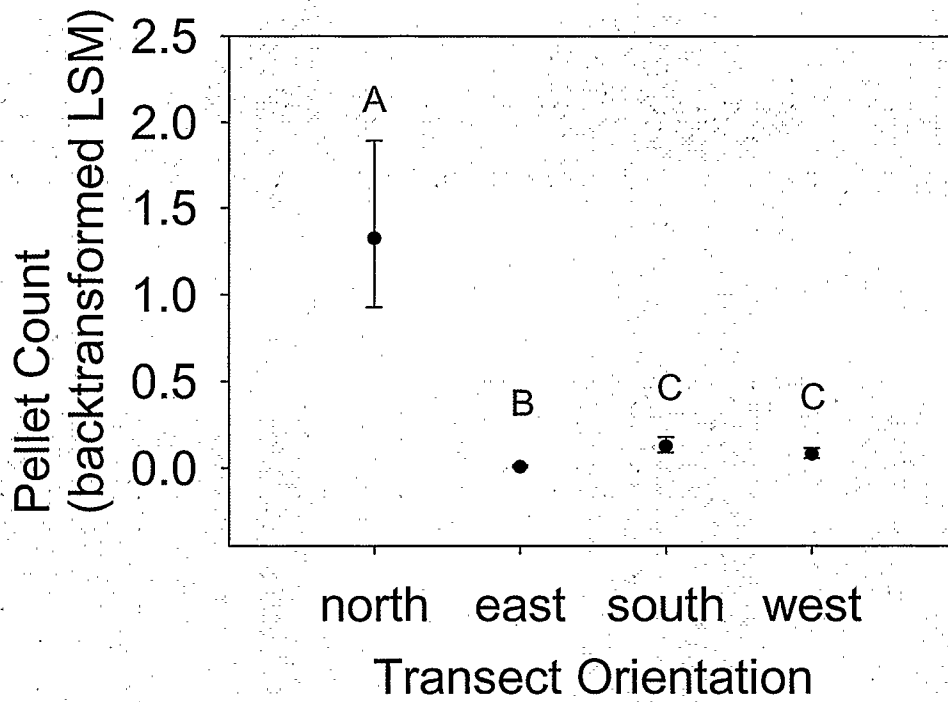


Figure 3.3 Pronghorn pellet densities (#/0.09 ha/plot) found along transects placed at different orientations along roads (N=672). Similar letters indicate no significant difference between least square means. Plotted are back-transformed LSM and standard error bars.

3.4, all $p < 0.05$). North transects had lower forb coverage than east and south transects (Kruskal-Wallis $\chi^2 = 49.2$, $p < 0.0001$, $df = 3$, $N = 672$). Shrub coverage was also lower along north transects compared to other three transect orientations ($\chi^2 = 77.2$, $p < 0.0001$, $df = 3$, $N = 672$). East transects had the lowest coverage of cactus compared to south transects with the highest coverage ($\chi^2 = 14.6$, $p = 0.002$, $df = 3$, $N = 672$). Grass coverage was highest along north transects compared to the other three transect orientations ($\chi^2 = 27.2$, $p < 0.0001$, $df = 3$, $N = 672$). Pellet density was also affected by road density within the wildlife management unit surveyed. Pellet densities decreased with increasing road densities ($G = 4.85$, $p < 0.028$, $df = 1$, $N = 672$).

Gradient of Risk

Pellet densities differed across distance depending on the traffic level of that road ($G = 26.2$, $p = 0.002$, $df = 9$, $N = 672$). Pairwise comparisons of this interaction were conducted using an adjusted alpha level based on the Dunn Sidak equation that adjusts the alpha level relative to the number of comparisons ($\alpha = 0.009$). Along medium level roads, pellet densities at 0 m (back-transformed LSM=0.05, USE=0.04, LSE=0.02) were significantly lower than at 200 m (back-transformed LSM=0.56, USE=0.32, LSE=0.20) from the road (Figure 3.5b; $G = 11.62$, $p = 0.0007$, $N = 672$). Along high level roads, pellet densities at 0 m (back-transformed LSM=0.02, USE=0.02, LSE=0.008) were 16 times lower than at 600 m (back-transformed LSM=0.31, USE=0.21, LSE=0.12) from a road (Figure 3.5c; $G = 11.11$, $p = 0.0009$, $N = 672$).

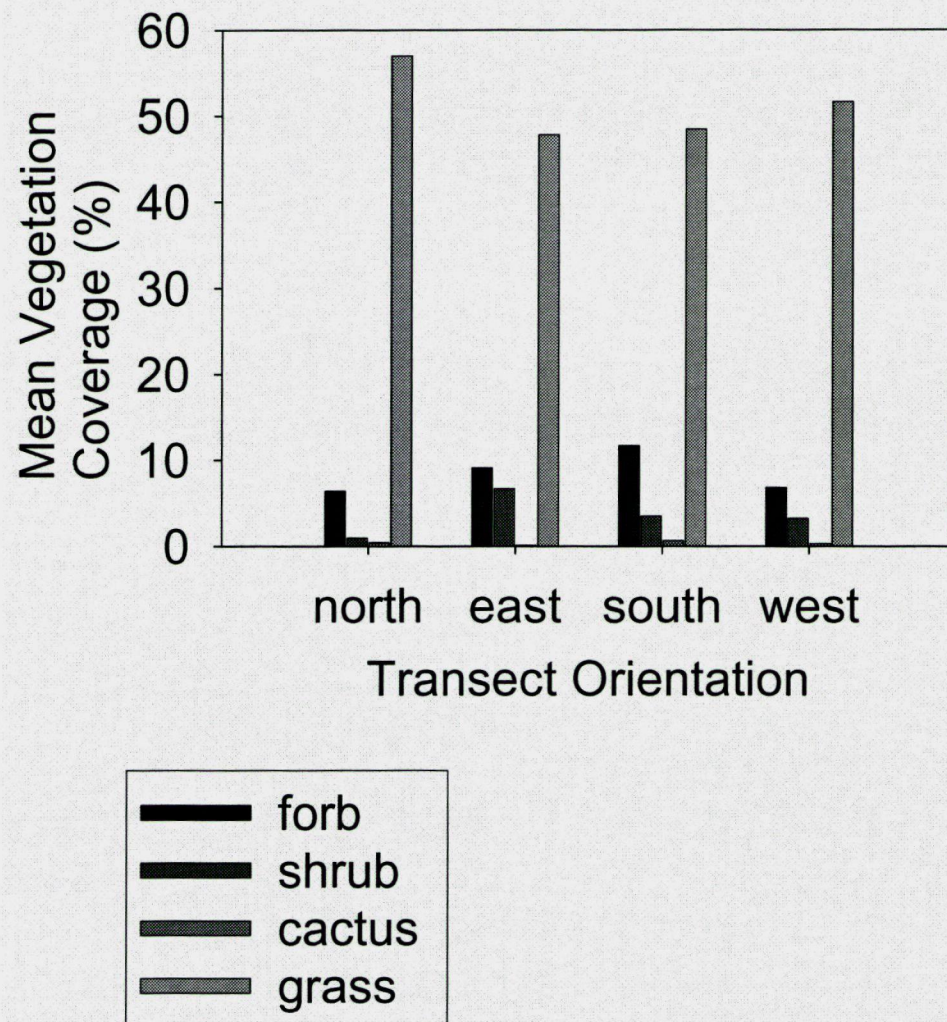


Figure 3.4 The average percentage of each vegetation coverage along the four transect orientations (N=672).

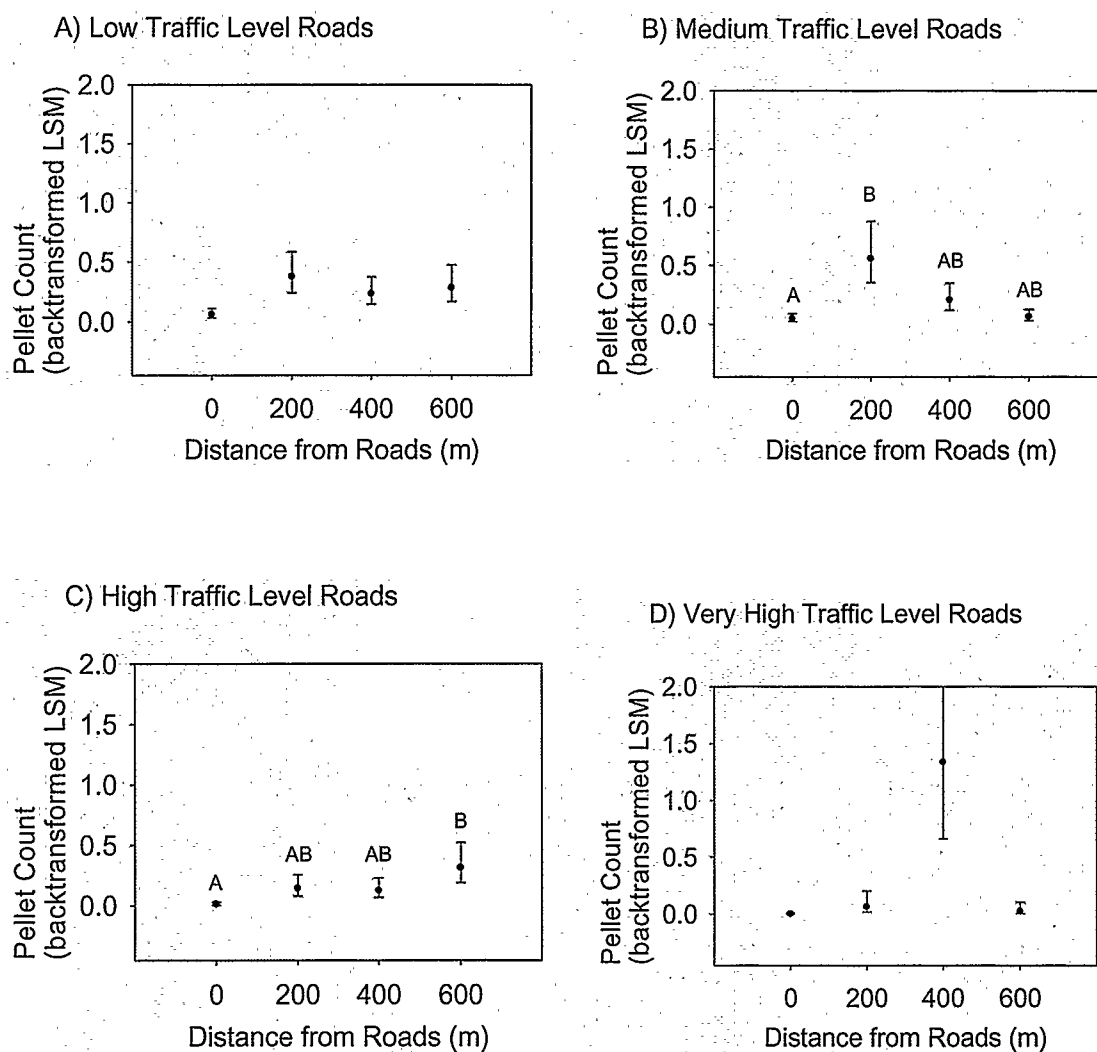


Figure 3.5 Pellet group densities (#/0.09 ha/plot) counted at four distances from fenced roads of different traffic levels (N=672). Similar letters indicate no significant difference between least square means. Plotted are back-transformed LSM and standard error bars.

No Road Areas

Pellet densities differed across traffic and no road categories ($\chi^2=9.8$, $p=0.04$, $df=4$, $N=872$) with no road areas having the lowest pellet densities across all of the traffic categories (Figure 3.6). The non-parametric pairwise comparison test could not detect any significant differences (all $p>0.05$) but the comparison with the largest difference was the no road areas compared to medium traffic level roads.

All plots in the no road areas were designated a distance measure of 1000m. At this distance, I found the lowest pellet densities compared to the other four distance categories (Figure 3.7). Pellet densities differed between the distance categories ($\chi^2=10.5$, $p=0.03$, $df=4$, $N=872$) but no significant pairwise comparisons could be detected (all $p>0.05$). The comparison between distances of 400m and 1000m had the largest difference between the mean ranks in the pairwise comparison test.

Resource Mapping

Kruskal-Wallis analysis was used to examine whether vegetation patterns in the habitat varied based on traffic level and distance from the road. Shrub coverage (Kruskal-Wallis $\chi^2=18.7$, $p=0.0009$, $df=4$, $N=872$) and cactus coverage ($\chi^2=14.3$, $p=0.007$, $df=4$, $N=872$) differed across the traffic levels but forb, grass and ground did not ($p>0.05$). Non-parametric pairwise comparisons between the treatments were conducted on significant tests (Siegel and Castellan 1988). Shrub coverages were lower within no road areas compared to areas along medium and high traffic roads ($p<0.05$). Pairwise comparisons between cactus coverage and traffic level could not detect

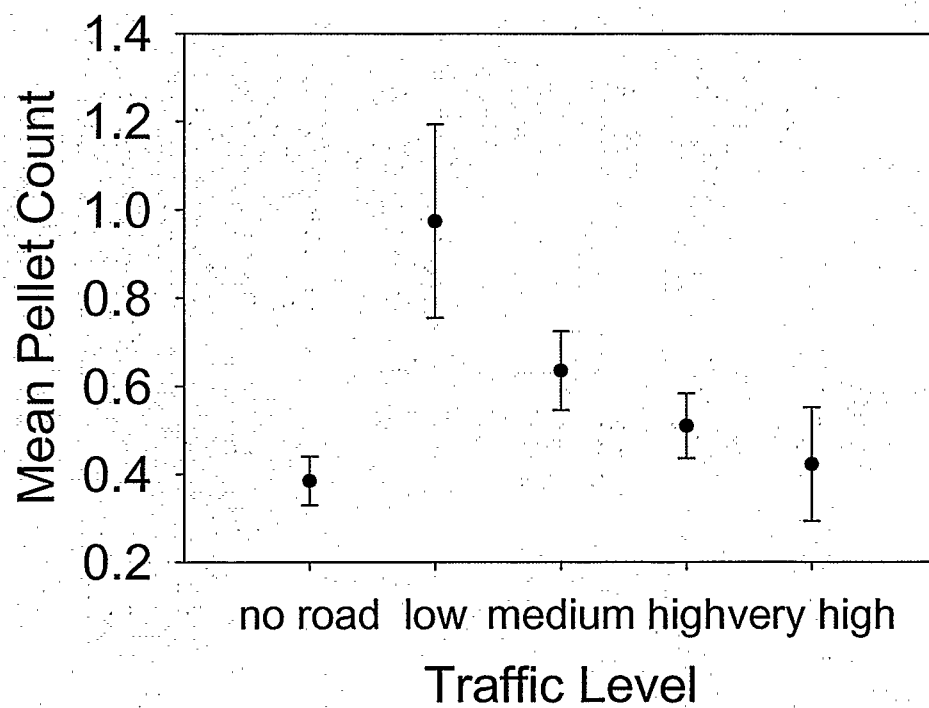


Figure 3.6 Average pellet densities (#/0.09 ha/plot) for areas along four traffic level categories and no road areas (N=872). No road areas represent areas more than 1 km away from roads. Plotted are means $\pm$ one standard error.

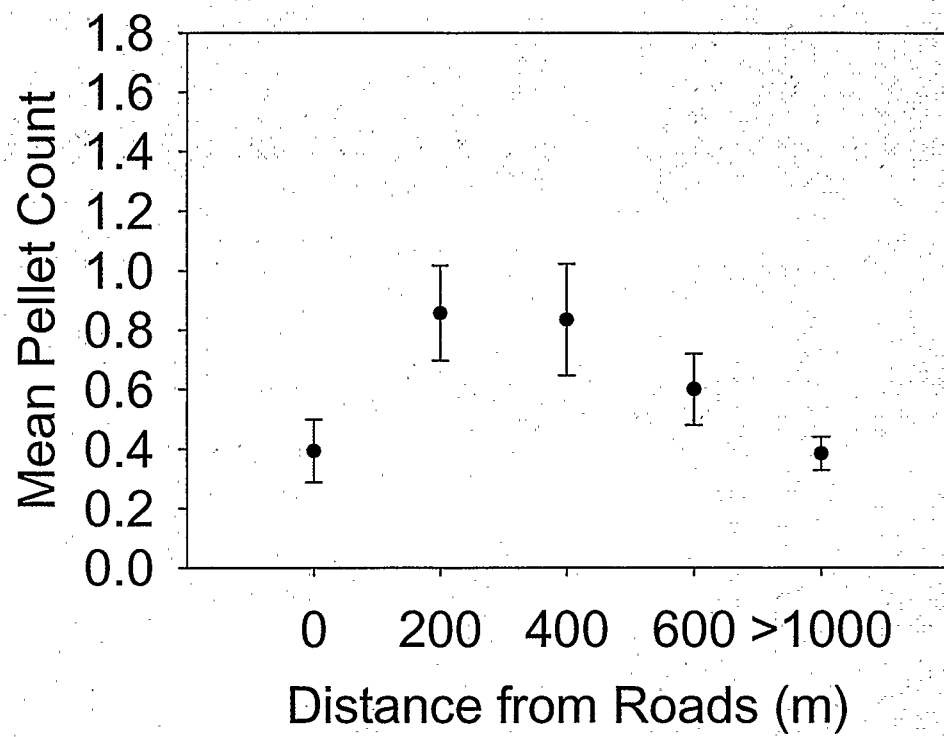


Figure 3.7 Average pellet densities (#/0.09 ha/plot) across five distances from roads regardless of traffic level (N=872). Plotted are means $\pm$ one standard error.

significant differences ($p > 0.05$). All vegetation categories did not vary with distance from a road (all $p > 0.05$).

The relationship between pellet densities and vegetation coverages were compared in the poisson regression. Pellet densities varied with shrub and forb coverage depending on the traffic level of the roads (Shrub*Traffic: $G=13.89$, $df=3$, $p=0.003$; Forb*Traffic: $G=11.74$, $df=3$, $p=0.008$). Multiple pairwise comparisons found pellet densities were affected by shrub coverage along high level roads compared to low level roads ($G=10.68$, $p=0.0011$). Along low traffic roads, pellet densities were highest and shrub coverages were lowest while pellet densities along high traffic roads were lower but had higher shrub coverage. Pellet densities were also affected by forb coverage along high level roads compared to medium level roads ($G=7.13$, $p=0.0076$). Medium traffic roads had higher pellet densities and lower forb coverage compared to high traffic level roads.

DISCUSSION

Corresponding with other studies using pellet group surveys, estimates of pronghorn density were reflected within the pellet distribution (Neff 1968; Fernanda et al. 2001). Pellet groups were a useful tool in measuring pronghorn distribution within specific habitats.

Edge Response

Pronghorn that assess human disturbances analogous to assessing a predation hazard, should avoid areas within close proximity to that disturbance. In this study, the human disturbance was road networks that create edges throughout the contiguous

grasslands. When roads are impermeable to dispersal, animals may accumulate at these edges (Ries et al. 2004). It has been shown that highways in Arizona have become barriers to pronghorn movement and effectively separated populations whose habitat was located within National Parks (van Riper and Ockenfels 1998). I observed some pronghorn individuals crossing low and high traffic level roads which suggest that these roads are not impermeable barriers to movement, but rather only filters that may hamper pronghorn movement. Pronghorn pellet distribution in response to the road edge resembled a negative edge response where pellet densities were lowest near roads but highest at intermediate distances away from the road. This suggests that pronghorn assess some level of risk close to roads; therefore, prefer to use less riskier areas at intermediate distances away from roads. The idea of roads being perceived as a risk is supported by behavioural observations presented in chapter 2, where I show that risk averse behaviours are observed more often closer to roads with higher traffic levels.

Other studies have found similar patterns with deer and elk avoiding areas within 200m of roads (Rost and Bailey 1979) and woodland caribou avoiding areas within 250m of roads and seismic lines (Dyer et al. 2001). Animals may be avoiding areas along the edge to minimize interactions with humans or predators using roads as travel corridors. It has been suggested that woodland caribou avoid linear features like seismic lines and roads due to the increase in traffic and predators (Whitten and Cameron 1983; Curatolo and Murphy 1986, Dau and Cameron 1986; Dyer et al. 2001) which may impede the caribou's ability to avoid harsh weather and deep snow (Eide et al. 1986). In forested areas, these same linear features are used as conduits by wolves which provide them

increased access into caribou range and thus caribou who occupy habitat near a road suffer higher predation (James and Stuart-Smith 2000).

The risk of neonatal mortality by coyote and eagle predations may dictate which habitat patches a female occupies. Pronghorn fawns adopt a hiding strategy in which the female maintains a distance from the fawns to minimize relaying any information to potential predators but also remaining close enough to drive away these predators (O’Gara and Yoakum 2004). Coyotes prefer to use corridors as habitat and are frequently seen crossing well travelled roads to move throughout an urban landscape (Tigas et al. 2002). To a small extent, coyotes do use roads to travel along in a grassland landscape (personal observations). Coyote tracks have been recorded along truck trails within the landscape more often compared to deer and elk (Forman et al. 2003). Because coyotes are also scavengers, they may be attracted to roads where vehicle collisions with wildlife often occur (Forman et al. 2003). Other sources of predation occur in the form of hunters who often locate pronghorn from roads. The potential higher exposure to predation hazards within close proximity to roads could contribute to pronghorn avoiding areas right along roads.

A negative response to an edge should asymptote with further distances from the edge (Ries et al. 2004) but pronghorn pellet densities were lower in areas more than 1000 m away compared to the intermediate distances from roads. This pattern does not fully support the asymptote shape of the distance function. Rather, my results suggest that the shape of the curve is a “hump” showing the lowest densities within 200 m of the road, highest between 200-400 m and then declining again. Depending on the degree of risk perceived towards the road which may be based on traffic level, individuals may bounce

off the boundary producing a pellet distribution that aggregates at intermediate distances from roads. Figure 3.7 illustrates how some individuals may interact with the edge boundary causing the bouncing effect. The landscape is divided into distance strata where each segment of the movement line within a distance stratum represents the proportion of time an individual remained at that distance. If the length of each line within each distance stratum is measured, the longest segments occur within the intermediate distance strata. This model simulates the findings in this study with higher pellet densities found at intermediate distances from the roads. The strength of the bouncing effect may be influenced by the degree of risk individuals perceive towards the various traffic levels. Pronghorn along low traffic roads may exhibit behaviour like individual A who perceives low risk towards the road edge and continues to cross the boundary. Individuals B and C approach the road edge but perceive a risk of danger towards the edge and reflect off the boundary returning into the habitat. Along high traffic level roads, individuals may not have to approach as close to the edge before detecting the visual stimulus. Individual C perceives a higher risk towards the road edge and may remain at that intermediate distance or move further back into the habitat.

Other Influences on Edge Response

Road orientation may also influence edge response. Road orientation is a variable that has not been considered often in literature exploring the effects of roads on wildlife

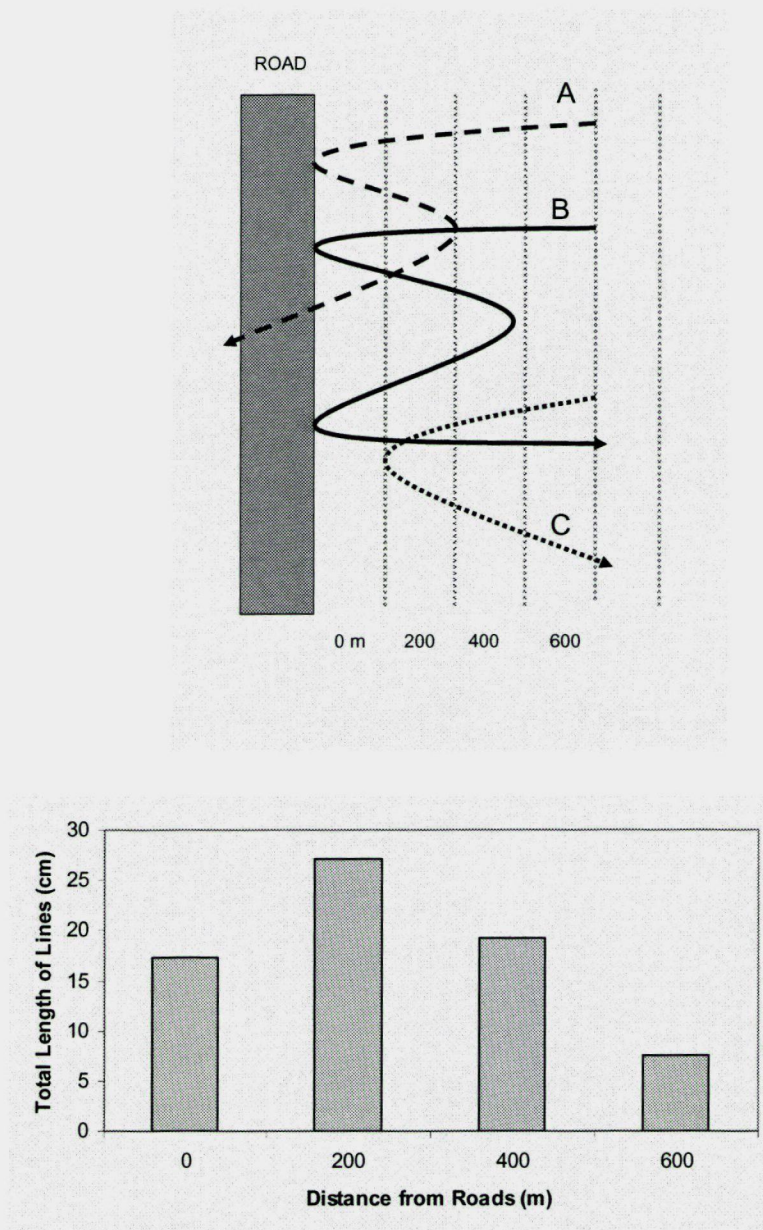


Figure 3.7 Illustration of the bouncing effect hypothesis. Individuals approach edge boundaries to investigate and reflect off the boundary returning back into the habitat. Individual A assesses lower risk level towards the edge boundary and continues to cross the road. Individual B has a stronger risk avoidance response bouncing off the road boundary while individual C perceived even greater risk towards the boundary. Dotted vertical lines represent increasing distance strata from a road. A digital map wheel was used to measure length of lines representing movement of individuals in each stratum. Bar graph represents the total length of lines in each stratum to represent the proportion of time individuals were located in those strata.

distribution (Forman et al. 2003). In temperate forests, south edges had stronger edge effects because of the increased sun exposure compared to the north (Ries et al. 2004). Along a north-south highway through open pastureland, soil temperature was highest on the west facing side but there was no significant difference in temperature and relative humidity beyond 8 m from the road (Ellenberg et al. 1981). For pronghorn, road orientation may influence wind exposure, noise disturbance, or plant exposure to vehicle emissions. In this study, pronghorn pellet densities were highest on the north side of roads. Conceivably, this could be a result of better forage on the north side. However, the north side of the roads that were surveyed had the least shrub and forb coverage compared to the other directions. Therefore, it seems that habitat along the north side of roads lacked some preferred pronghorn vegetation characteristics yet pronghorn were still attracted to these areas. Individuals using habitat on the north side of the roads would also be exposed to the frequent southwest winds which would expose individuals to traffic noise. Yet pronghorns were not affected by noise disturbances generated by military activity which may have been due to their low hearing acuity (Krausman et al. 2004). Generally pronghorn rely on their keen eyesight to detect predators but scent that is carried by the wind is also an effective early detection measure (O’Gara and Yoakum 2004). The selection of areas exposed to wind may be more valuable for predator detection.

Road density within the area sampled is an important factor that might influence animal abundance because with the increase in road networks, the habitat patch becomes smaller and more dominated by edges (Ries et al. 2004). For example, bobolink presence was lower near double edge plots compared to the single edge plots, where it was still

lower than in the grassland interior (Fletcher 2005). Multiple edges also increased the distance of edge influence for these grassland birds. Studies of the effect of road densities on carnivore distributions suggests that the main threat of high road densities is the increase in human accessibility leading to wildlife accidental or intentional deaths (Thiel 1985; Van Dyke et al. 1986; Mech et al. 1988; Clevenger et al. 1997). For pronghorn, higher road densities may lead to higher accessibility into areas by hunters. Pronghorn are also a migratory species in their northern habitat and require habitat with few natural or anthropogenic barriers. Higher impermeable road densities may trap herds in particular areas (van Riper and Ockenfels 1998) which can impact pronghorn survival during already harsh winter months (Martinka 1967; Oakley and Riddle 1974). Higher road densities are also often associated with higher human activity which pronghorn may avoid, as indicated by the finding that pellet densities were highest in areas with lower road densities. Pronghorn pellet densities were highest in wildlife management unit 102 with a road density of 0.19 km/km² and lowest in unit 148 with a road density of 0.62 km/km².

Habitats surveyed in the 2003 field season had higher pronghorn pellet densities recorded than in 2004. There were vegetation differences between the areas in the two years with higher forb and shrub coverages within habitats in 2004. Habitats surveyed in 2003 had higher cactus, grass and ground coverages which are unlikely strong influences on pronghorn distribution since cactus and grass are not large components of pronghorn annual diet. Qualitatively, road densities differed between the areas surveyed with lower road densities (0.19 km /km²) in some of the habitats surveyed in 2003, compared to lowest road density area surveyed in 2004 (0.43 km /km²). Pronghorn may prefer habitat

near areas surveyed in 2003 because of the lower overall human activity and development.

Gradient of risk

Whether an animal disperses across the edge of a patch may depend on the type of edge contrast. It is assumed that edge responses will be weaker along low contrast (soft) edges compared to high contrast (hard) edges (Ries et al. 2004). Human development that fragments the landscape can create sharp boundaries or edges between natural habitat and often unsuitable habitat (Kristan et al. 2003). The response to the edge contrast of roads can be species specific. While edge boundaries may be barriers to smaller mammals such as hedgehogs (Rondinini and Doncaster 2002), road edges are frequently crossed by larger mammals depending on traffic level (Van Dyke et al. 1986; Thurber et al. 1994). The permeability of these edges to dispersal depends on the level of risk associated with crossing the feature, which in the case of edges created by roads, depends on the traffic level. Pronghorn habitat use was more common in areas of low traffic level roads indicating that these areas have a lower risk associated with traffic activity. Pronghorns may perceive humans as a type of predator where lower traffic level roads translate into lower human activity thus lower risk. Risk can be in the form of potential hunters or potential collisions with motor vehicles. Moose vehicle collisions were found to be dependent upon traffic level where higher traffic levels were associated with greater collisions (Joyce and Mahoney 2001).

Pronghorn did not completely avoid areas near higher traffic level roads. If competition between conspecifics in safer habitats reduce overall forage intake, some

individuals may choose to forage in riskier habitats to obtain higher resource rewards (Lima and Dill 1990; Lima 1998). Habitat near high traffic level roads had indeed higher coverage of shrubs. Pronghorn using these “riskier” areas could be subordinates that have been displaced to the lower quality habitats. Dominant lesser snow geese displaced subordinate geese to gain benefits in higher nutrient absorption rates of cotton-grass (Hupp et al. 1996). This dominance situation may be common among pronghorn males especially during rut for territories or harems. Female herds also have dominance ranks but lower ranking females try to avoid agonistic interactions by occupying the periphery of the herd (Byers 1997). Even though individuals were utilizing this riskier habitat, pronghorns were located at greater distances (600 m) from higher traffic roads than along lower level roads where highest pellet density was at 200-400 m from the road. This supports the idea of a higher risk associated with more traffic or human activity.

I had predicted that if pronghorns perceive danger from roads, pellet distributions should be highest within areas that only had a fence present but no major roads. However, no road areas actually had the lowest pellet densities found compared to the other areas with roads. The bouncing effect hypothesis may explain these lower pellet densities because if there is no perceived risk with the boundary causing individuals to reflect off from, individuals may be more spread out within these areas and thus fewer pellet counts.

One might argue that pronghorn are attracted to roaded areas either because of a higher quality of vegetation or differences in predator density. Shrub coverage was lower at no road areas compared to medium and high traffic roads and areas dominated by shrubs may be used more often as winter habitat. It is unlikely that the shrub coverage

along roads is attracting pronghorn to these areas because even though medium and high traffic roads had higher shrub coverage, pellet densities were still highest along low traffic roads. As well, fenced roads often act as snow breaks resulting in deeper snows in that area (personal observation) which can interfere with their movement and foraging (Martinka 1967; Oakley and Riddle 1974). These pellet counts represent pronghorn distribution over many seasons which include periods where shrubs are not important dietary requirements and yet the pattern persists.

The effects of predator density on pronghorn distribution could not be analysed because coyote density estimates were not available for my study area. Other studies have shown that predators are also influenced by human activity and may avoid areas with higher human activity (Tigas et al. 2002; Atwood et al. 2004). If pronghorn were responding to natural predator density, we might see higher pronghorn presence in areas near high traffic roads. However these areas, in fact, had lower pellet densities. If predator densities were higher further away from roads, this might cause pronghorn to use habitat near roads. However, pronghorn behaviour and habitat use reflect a perception of risk towards the traffic activity. Pronghorn exhibited higher vigilance levels along higher traffic roads and pellet densities were higher further away from roads as traffic level increased. The bouncing effect may be the stronger influence in the distribution differences between roaded and no road areas.

Resource Mapping

Animal movement and aggregation are also influenced by resource distribution near the edges often referred to as resource mapping (Ries et al. 2004). It is not

surprising that pellet densities in my study were associated with shrub and forb coverage since those vegetation types contribute a large component to the pronghorn diet (Mitchell and Smoliak 1971). If pronghorn distribution is influenced mainly by resource distribution, then pellet distribution should follow the resources for maximum energy intake. However, other influences such as risk aversion from roads may have partially overridden effects of resource distribution.

Vegetation coverage did not differ by distance unlike pellet distribution which was highest at intermediate distances from roads. The patterns of shrub and forb coverages across traffic levels were also not reflected within pellet distribution. Pellet densities were affected by shrub and forb coverage depending on the traffic level. Along high traffic level roads, shrub coverage was highest compared to low traffic roads and forb coverage was highest compared to medium traffic roads. This is the opposite pattern compared to the pellet distributions where densities were highest along low traffic level roads which did not have abundant coverage of shrub and forbs.

Fragmentation of the landscape by road networks can impact species that utilize different habitat types for various breeding and seasonal requirements. Pronghorn migrate to wintering grounds that are abundant with sagebrush and cover from wind exposure. Fawns require specific microhabitat features during the first 2-3 weeks of their life such as gently rolling hills and areas near sagebrush bushes for cover (Barrett 1984). Therefore, as human development and road networks increase in the grasslands, there is reduced available habitat with varying microclimates to meet the needs of the pronghorn. Overall, pronghorns appear to perceive a level of risk hazard towards road traffic which is consistent with the risk-disturbance prediction that long term exposure may cause

habitat avoidance near the human disturbance. Pronghorn are affected by the increasing road networks and traffic which should be factored into pronghorn management plans.

CHAPTER 4: GENERAL CONCLUSIONS

Studies on the effects of anthropogenic activity on wildlife have shown changes in their behaviour and habitat use (Boyle and Samson 1985; Forman and Alexander 1998; Jalkotzy et al. 1997; Trombulak and Frissell 2000; Forman and Deblinger 2000) but few address the potential ultimate factors of these proximate responses. The risk-disturbance hypothesis proposes that if organisms perceive human activity as a predation risk, they may exhibit analogous risk avoidance behaviour (Frid and Dill 2002). This is based on the assumption that organisms can track short term changes in natural predation hazards and allocate their risk avoidance behaviour accordingly to avoid predation (Lima and Dill 1990; Lima 1998). This study examined whether pronghorn antelope, *Antilocapra americana*, exhibited behaviour and habitat use consistent with the risk-disturbance hypothesis towards road traffic. Pronghorn may perceive a degree of risk towards road traffic because it may be a source of mortality, either through vehicular collisions or increased hunter access. Pronghorn behaviour and habitat use were compared across varying levels of potential risk which included roads of increasing traffic activity and increasing distances away from roads.

The risk-disturbance hypothesis predicts that organisms will increase their risk avoidance behaviour based on the degree of risk they perceive from the human disturbance. This can include increasing vigilance levels, higher flight probabilities, using habitat near a refuge, or reduced foraging in an area (Lima and Dill 1990). Pronghorn vigilance and foraging behaviour was compared across various traffic levels and distances from roads to examine how these behaviours may change with increasing risk. Group size, sex and reproductive status were also incorporated into analyses of

pronghorn vigilance and foraging behaviour because these variables have been found to influence the behaviour of social species (Elgar 1989; Lima and Dill 1990; Treves 2000). Animals may form groups for reproductive opportunities but conspecifics can reduce the probability of any one individual getting attacked and more eyes scanning the habitat will increase the probability of detecting predators (Dehn 1990; Roberts 1996). Generally, as more individuals join a group, each individual can reduce their vigilance without affecting the overall vigilance of the group. Pronghorn individuals reduced their vigilance levels as herd size increased which corresponds to predation risk theory. Foraging behaviour may have a weaker relationship with group size and may be dependent on forage quality in the area (Elgar 1989). Sex may also potentially affect foraging rates because males and females have different seasonal energy requirements but many studies show that the presence of fawns contribute more to these differences (Elgar 1989). My study suggests that traffic level and the presence of fawns are strong influences on the degree of risk avoidance behaviour exhibited by pronghorn antelope towards roads.

Pronghorn may perceive the infrequent vehicles along low traffic roads with lower predation risk because their vigilance levels were lower along these roads compared to higher traffic roads. Pronghorn also showed a pattern of lower foraging proportions along roads of higher traffic levels particularly during the spring season (May to June). Pronghorn fawns are born during late May and mothers may exhibit stronger risk avoidance responses to reduce the risk of mortality of their young (Elgar 1989). Females were located more often at further distances from roads than males when the herds included fawns. Distance from the roads also affected foraging behaviour of

individuals in herds where individuals had higher foraging proportions when located more than 300 m from roads. Larger herds may be easily detected in the landscape and generally include fawns; therefore, to reduce potential predation risk to fawns, herds may avoid areas near a potential threat such as road traffic. Solitary individuals cannot dilute their predation risk using conspecifics and may maintain similar foraging and vigilance rates regardless of distance.

Pronghorn behaviour was affected by increasing traffic level and distance from these roads suggesting that some individuals may perceive road traffic as a predation risk. The energetic expenditures of these behaviours can cause organisms to shift into habitats away from the disturbance. If the behavioural disruption is strong enough, organisms may avoid areas near the disturbance. The higher risk associated with higher traffic roads caused pronghorn to increase their vigilance and forage less which corresponds to their lower presence along these roads. Assessing predation risk is often balanced with the ability of acquiring resources, such as food, territories or mates. Pronghorn pellet distribution was influenced by vegetation categories important to their diet. However, the potential risks associated with road traffic were stronger influences in pronghorn pellet distribution.

Risk perception towards human disturbances may be influenced by how that disturbance affects the features of the landscape. Human linear disturbances may create edge boundaries between habitats and animals can exhibit positive (attracted), neutral (no response) or negative (avoidance) responses towards the edge depending on the level of risk perceived towards it (Ries et al. 2004). The negative edge response where animal distribution increases further away from the edge supports the habitat shifting prediction

of the risk-disturbance hypothesis. Pronghorn pellet distributions revealed a close resemblance to a negative edge response with low pellet densities along roads but higher at intermediate distances rather than further away regardless of their traffic level. The bouncing effect hypothesis may explain how animal movement patterns in response to the edge can produce higher pellet densities at these intermediate distances. A human analogy to illustrate this hypothesis relates to how people move through a museum to view artwork. People will approach artwork to view it more intensely but then move back to the middle of the room to move to the next artwork. Similarly, pronghorn may be approaching fenced roads to assess the risk associated with it but then move away from the boundary to move through the landscape. This would create higher pellet densities at these intermediate distances from the road.

Other road features that also influence risk perception are road densities and orientation. Pronghorn preferred areas with lower road densities which can also reflect the overall human activity within that area. Transect placement had an unexpected relationship with pronghorn pellet distribution where the highest densities were along the north side of the roads surveyed. Wind exposure may influence this relationship where pronghorn may be able to detect predators earlier when the pronghorn are downwind. In my study areas, the prevailing wind direction comes from the southwest. Road orientation has been overlooked in the majority of studies examining the effects of roads (Forman et al. 2003). This relationship should be investigated further and incorporated into future road effect studies.

Overall, pronghorn antelope were responding to road traffic consistent with the risk-disturbance hypothesis which was supported by observing differences in behaviour

and habitat use along roads of increasing traffic levels and distances from roads. The responses towards this human activity may persist because of the hunting pressure on the population and the occasional mortality from vehicular collisions.

Understanding how pronghorn perceive and respond to human activity is an important tool in the management of sustainable populations. Relating their responses to situations under natural predation pressure would create useful tools in measuring the impact of human activity on pronghorn. Literature has shown how organisms tracking short term changes in predation hazard will alter the balance between avoiding predation and acquiring resources corresponding to the degree of risk perceived (Lima and Dill 1990; Lima 1998). The greater the risk of mortality, the higher intensity of risk avoidance behaviours exhibited at the expense of reduced opportunities for acquiring resources. A continual human disturbance that causes individuals to increase their vigilance or flight responses can be a substantial energy drain which can lead to individuals avoiding that area entirely (Frid and Dill 2002). Potential consequences may include individuals forced into lower quality habitat or if there is no available alternative habitat, individuals must endure energetic drains from continued risk avoidance behaviour. This can lead to reductions in body condition which can have severe consequences for survival during already energy draining time periods such as rut, gestation and winter. The cumulative effect of natural predation and human disturbances can alter pronghorn risk avoidance behaviour which can affect their habitat availability and distribution. Therefore, pronghorn behaviour towards human disturbances should be considered in management plans.

Significance

This study complements current knowledge because it examines whether an animals' behavioural response to a human disturbance will be reflected in their habitat use around the disturbance. Most studies focus on one particular aspect such as changes in population densities or specific behaviours relative to the disturbance but rarely connect these processes. It is important to understand the extent of the response which may reflect the degree of risk perceived because defining an organism's gradient of risk towards particular human disturbances will allow managers to assess the impact of new developments within the habitat. Exploring how changes in pronghorn behaviour are reflected by their habitat use or distribution across the landscape will allow for the mapping of current and potential areas of conflict.

Research on the impact of human activity on pronghorn behaviour has focused on populations within protected national parks which may not represent the full extent of the effect (van Riper and Ockenfels 1998; van Riper et al. 2001; Fairbanks and Tullous 2002). This study contributes to pronghorn management by examining populations that are not within protected areas because their behavioural responses to human disturbances will be influenced by the cumulative effect from natural predation, as well as, hunting pressure. In Alberta, the majority of pronghorn range does not occur in protected areas. The National Wildlife Area on the Canadian Forces Base Suffield may be considered habitat that offers some protection from hunting but provides minimal suitable habitat. In the National Bison Range, Montana where pronghorn predation pressure is greatly reduced and hunting is prohibited, this population is not exhibiting strong risk avoidance behaviour compared to other populations (Byers 1997). With the increasing loss of

natural habitat in pronghorn range, understanding how populations respond when not protected is paramount for maintaining the current pronghorn range in North America.

Another area that has been lacking in conservation research is the ability to explain to some extent why organisms are exhibiting particular behaviours towards human disturbances. These explanations may be rooted in ecological concepts based in the relatively well documented predator and prey literature but few studies compare wildlife responses under a conceptual framework. My study compares pronghorn responses to the risk-disturbance hypothesis that proposes organisms will perceive a predation risk towards human disturbances. The first step to understanding the mechanisms of how organisms respond to human perturbations in their landscape is being aware of why they might exhibit these specific behaviours.

Management Implications

Pronghorn populations in their northern range are already susceptible to mortality by severe weather such as droughts and harsh winters. The combined effect of human development within their habitat may enhance their vulnerability. Pronghorn antelope in Alberta migrate from their summer range to smaller winter ranges that represent only 8% of the entire summer range (Barrett 1982). Pronghorn winter survival depends on their ability to access suitable winter ranges represented by areas with high densities of their staple winter diet of sagebrush (*Artemisia cana*) and pasture sagewort (*Artemisia frigida*), and are located in areas that are exposed to the warmer Chinook winds that help reduce snow depths. Obstacles such as fencing have been found to be detrimental to their winter survival during cold winters with deep snow because it prevents pronghorns from crawling under the fences and moving to more suitable habitat (Hepworth 1966; Oakley

and Riddle 1974). Many recommendations have been made concerning fence modifications for pronghorns but in Alberta, it is not enforced. Recommendations include constructing fences with 3 barb wires with the bottom wire smooth and at least 41 cm from the ground; adjustable fences that allow some movement in the barb wire strands; keeping gates open when livestock are not using the pasture; flagging new fencing for pronghorns to become familiar with; and avoiding net wire fences that are movement barriers for pronghorn (Bruns 1977; Kie et al. 1996). Other features such as roads and railways also pose problems because during deep snows, pronghorn use these networks as corridors often resulting in their mortality by collisions.

This study has also shown how road traffic can interrupt pronghorn daily behaviours and possibly lead to displacement of individuals from quality habitat. Winter survival depends on conserving valuable energy reserves and allocating sufficient time to foraging. Individuals that are increasing their vigilance towards human disturbances risk depleting their energy reserves more quickly with the potential consequence of not having enough to survive the remaining winter. Bradshaw et al. (1998) modelled energetic losses in woodland caribou in response to multiple encounters with a disturbance from petroleum exploration. Caribou normally lose 10-15% of their autumn mass during the winter and 20-34 disturbance events would be required to exceed the normal winter loss. Caribou were exposed to five disturbance events in five years that could potentially lead to losses exceeding the normal winter loss. The birth and rut season are also very energy demanding time periods that can be confounded by the effects of human disturbances. Females may experience higher energy depletions because they tend to exhibit higher risk averse behaviour when young are present. If females with young are avoiding high

quality habitat or increasing vigilance towards human disturbances, this can have negative ramifications on their body condition. As well, stress induced by human activities can also affect body condition. Hoatzin juvenile chicks disturbed by ecotourists had stronger hormonal stress levels compared to individuals at undisturbed sites (Mullner et al. 2004). Corticosterone, which is produced under stress, metabolizes fat and protein which if in high levels can potentially reduce body weight (Mullner et al. 2004). The continuous decline of female body condition may negatively impact their reproductive ability. If this continues over a long term basis, this may affect the population productivity resulting in population declines.

Pronghorn require specific habitat characteristics for various seasonal periods such as winter ranges, travel corridors or fawn births (O’Gara and Yoakum 2004). Human disturbances that cause pronghorn to shift away from these areas may restrict individuals into habitat that does not represent suitable reproductive or winter ranges. Preferred bedding sites of fawns include terrain with gently rolling hills and areas near sagebrush bushes for cover (Barrett 1984). In Alberta, pronghorn have 12 identified winter ranges listed in their management plan but the winter range in the Walsh Flats area is no longer suitable winter habitat because of increased agricultural development (Glasgow 1990). This continued reduction in suitable habitat needs to be addressed in management plans, as well as related to road density and traffic level. Pronghorn that are bouncing off road edges are also exerting energy by moving back and forth throughout the landscape. When edge density increases as a result of higher road densities, individuals may exert even higher energy levels bouncing off more edges in the landscape.

Government support towards enhancing habitat or the creation of reserves that protect habitat for pronghorn is essential. Education programs geared towards private landowners explaining the role of pronghorn in the health of the ecosystem and providing them incentives to enhance pronghorn habitat on their land are needed. Development and expansion in the southeastern region of Alberta is a continual process but the disruption caused by new developments may be minimized. The creation of a critical pronghorn habitat map overlaid with road networks and the corresponding traffic levels will help managers in identifying sensitive areas. Limiting development during energy sensitive periods for pronghorn may minimize the impact of increases in risk avoidance behaviour or habitat shifts away from breeding or winter habitats. As well, the design of roads can be an integral factor in minimizing the impact of road activity on pronghorn antelope. Because pronghorn utilized areas near low traffic roads more often than higher traffic level roads, restricting the use of current low traffic roads in sensitive pronghorn areas will reduce avoidance behaviour. High road density areas where roads may continue to increase in traffic may eventually become movement barriers (van Riper and Ockenfels 1998) but the creation of overpasses along roads in pronghorn migratory corridors may facilitate the flow of animals across these roads.

I hope this study has illustrated the relationship between behavioural ecology and wildlife management. Understanding how wildlife perceive and respond to human perturbations in the landscape can assist in minimizing the impacts of both current and new developments.

LITERATURE CITED

Alberta Environmental Protection 1997. The Grassland Natural Region of Alberta: One of a series of reports prepared for the Special Places 2000 Provincial Coordinating Committee. Edmonton.

Altendorf, K., J. Laundre, C. Lopez Gonzalez, and J. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* **82**:430-439.

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794-804.

Atwood, T.C., H.P. Weeks and T.M. Gehring. 2004. Spatial ecology of coyotes along suburban-to-rural gradient. *Journal of Wildlife Management* **68**: 1000-1009.

Banks, P. 2001. Predation sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour* **61**:1013-1021.

Barrett, M. W. 1982. Distribution, behavior and mortality of pronghorns during a severe winter in Alberta. *Journal of Wildlife Management* **46**:991-1002.

Barrett, M. W. 1984. Movements, habitat use and predation on pronghorn fawns in Alberta. *Journal of Wildlife Management* **48**:542-550.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals.

Conservation Biology **18**:320-331.

Berger, J., and C. Cunningham. 1988. Size related effects on search times in north american grassland female ungulates. Ecology **69**:177-183.

Berger, J., D. Daneke, J. Johnson, and S. H. Berwick. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biological Conservation **25**:193-208.

Bouskila, A., and D. T. Blumstein. 1992. Rules of thumb for predation hazard assessment: Predictions from a dynamic model. The American Naturalist **139**:161-176.

Boyle, S. A., and F. B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildlife Society Bulletin **13**:110-116.

Bradshaw, C., S. Boutin, and D. M. Hebert. 1998. Energetic implications of disturbance caused by petroleum exploration to woodland caribou. Canadian Journal of Zoology **76**:1319-1324.

Bromley, P. T. 1969. Territoriality in pronghorn bucks on the national bison range, Boise, Montana. Journal of Mammalogy **50**:81-89.

Brown, J., J.W. Laundre, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. *Journal of Mammalogy* **80**:385-399.

Bruns, E. H. 1977. Winter behavior of pronghorns in relation to habitat. *Journal of Wildlife Management* **41**:560-571.

Burger, L. D., J. L.W. Burger, and J. Faaborg. 1994. Effects of prairie fragmentation on predation on artificial nests. *Journal of Wildlife Management* **58**:249-254.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, Second edition. Springer-Verlag, New York, NY, USA.

Byers, J. A. 1997. American Pronghorn: Social adaptations and the ghosts of predators past. The University of Chicago Press, Chicago, Illinois, USA.

Camp, M., and L. Best. 1994. Nest density and nesting success of birds in roadsides adjacent to rowcrop fields. *American Midland Naturalist* **131**:347-358.

Childress, M. J., and M. A. Lung. 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour* **66**:389-398.

- Clark, W. D., and J. Karr. 1979. Effects of highways on Red-winged blackbird and Horned Lark populations. *Wilson Bulletin* **91**:143-145.
- Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short eared owls and deermice. *Behavioural Ecology and Sociobiology* **13**:205-209.
- Clevenger, A. P., F. Purroy, and M. Campos. 1997. Habitat assessment of a relict brown bear, *Ursus arctos*, population in northern Spain. *Biological Conservation* **80**:17-22.
- Cohen, J. 1969. Statistical power analysis for the behavioral sciences. Academic Press Inc, New York, NY USA.
- Cox, D. R. 1983. Some remarks on overdispersion. *Biometrika* **70**:269-274.
- Curatolo, J. A., and S. M. Murphy. 1986. The effects of pipelines, roads and traffic on the movements of caribou, *Rangifer tarandus*. *Canadian Naturalist* **100**:218-224.
- Dau, J. R., and R. D. Cameron. 1986. Effects of a road system on caribou distribution during calving. *Rangifer Special Issue* **1**:95-101.
- Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. *Northwest Science* **33**:43-66.

Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. *Behavioural Ecology and Sociobiology* **26**:337-342.

Dill, L. 1974. The escape response of the zebra danio (*Brachydanio rerio*) I. The stimulus for escape. *Animal Behaviour* **22**:711-722.

Dirschl, H. J. 1963. Food habits of the pronghorn in Saskatchewan. *Journal of Wildlife Management* **27**:81-93.

Duchesne, M., S. D. Cote, and C. Barrette. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation* **96**:311-317.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* **65**:531-542.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. *Oecologia* **60**:185-189.

Eide, S. H., S. D. Miller, and M. A. Chihuly. 1986. Oil pipeline crossing sites utilized in winter by moose and caribou in Southcentral Alaska. *Canadian Field Naturalist* **100**:197-207.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Review* **64**:13-33.

Ellenberg, H., K. Muller, and T. Stottele. 1981. Strassen-Okologie: Auswirkungen von Autobahnen und Strasse auf Okosysteme deutscher Landschaften. Pages 19-122 *in* Okologie und Strasse. Broschurenreihe der Deutschen Strassenliga, Bonn, Germany.

Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *The American Naturalist* **153**:165-182.

Fairbanks, W. S., and R. Tullous. 2002. Distribution of pronghorn (*Antilocapra americana* ord) on Antelope Island State Park, Utah, USA, before and after establishment of recreational trails. *Natural Areas Journal* **22**:277-282.

Fecske, D. M., R. E. Barry, F. L. Precht, H. B. Quigley, S. L. Bittner, and T. Webster. 2002. Habitat use by female black bears in western Maryland. *Southeastern Naturalist* **1**:77-92.

Ferguson, S. H., A.T. Bergerud, and R. Ferguson. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia* **76**:236-245.

Fernanda, M., S.T. Buckland, D. Goffin, C.E. Dixon, D.L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from the line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* **38**:349-363.

Fletcher, R. G. 2005. Multiple edge effects and their implications in fragmented landscapes. *Journal of Animal Ecology* **74**:342-352.

Forman, R. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**:207-231.

Forman, R. T., and R. D. Deblinger. 2000. The ecological road effect zone of a Massachusetts (U.S.A) suburban highway. *Conservation Biology* **14**:36-46.

Forman, R. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. *Road Ecology: Science and Solutions*. Island Press, Washington, D.C., USA.

Freddy, D. J., and D. C. Bowden. 1983. Sampling mule deer pellet group densities in juniper pinyon woodland. *Journal of wildlife managements* **47**:476-485.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16-36.

- Frid, A. 1997. Vigilance of female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* **53**:799-808.
- Frid, A., and L. Dill. 2002. Human caused disturbance stimuli as a form of predation risk. *Conservation ecology* **6**:11.
- Gardner, W., E. P. Mulvey, and E. C. Shaw. 1995. Regression analyses of counts and rates: poisson, overdispersed poisson and negative binomial models. *Psychological Bulletin* **118**:392-404.
- Getz, L. L., F.R. Cole, and D. L. Gates. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy* **59**:208-212.
- Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation* **103**:227-236.
- Gill, J. A., W. J. Sutherland, and A. R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology* **33**:786-792.
- Glasgow, W. M. 1990. Management plan for pronghorn antelope in Alberta. Fish and Wildlife Division, Edmonton.

Goldsmith, A. E. 1990. Vigilance behavior of pronghorns in different habitats. *Journal of Mammalogy* **71**:460-462.

Harestad, A. S., and F. L. Bunnell. 1987. Persistence of black-tailed deer fecal pellets in coastal habitats. *Journal of Wildlife Management* **51**:33.

Harrison, P. D., and M. I. Dyer. 1984. Lead in mule deer forage in rocky mountain National Park, Colorado. *Journal of Wildlife Management* **48**:510-517.

Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* **80**:800-809.

Hepworth, W. G. 1966. A review of "the effects of livestock fences on pronghorn antelope movements" as reported by James Spillett and David Sill. Pages 9-21 *in* Proceedings of 2nd Annual Antelope States Workshop, Denver, Colorado, USA.

Holbrook, S. J., and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* **69**:125-134.

Hupp, J., R. White, J. Sedinger, and D. Robertson. 1996. Forage digestibility and intake by lesser snow geese: effects of dominance and resource heterogeneity. *Oecologia* **108**:232-240.

Isley, Q. 2003. Fish and Wildlife Division, Alberta Sustainable Resource Development.

Jalkotzy, M. G., P.I. Ross, and M. D. Nasserden. 1997. The effects of linear developments on wildlife: a review of selected scientific literature. Arc Wildlife Services Ltd., Calgary, Alberta, Canada.

James, A. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* **64**:154-159.

JMP IN version 4.0, 2001, SAS Institute Inc., Cary, NC, USA.

Joyce, T., and S. Mahoney. 2001. Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. *Wildlife Society Bulletin* **29**:281-291.

Kaiser, H. 1983. Small spatial scale heterogeneity influences predation success in an unexpected way: model experiments on the functional response of predatory mites (Acarina). *Oecologia* **56**:249-256.

Kie, J. G. 1999. Optimal foraging and the risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* **80**:1114-1129.

Kie, J. G., V.C. Bleich, A.L. Medina, J. D. Yoakum, and J. W. Thomas. 1996. Managing rangelands for wildlife. Pages 663-688 *in* T. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Kansas, USA.

Krausman, P. R., L. K. Harris, K. K. G. Koenen, and J. Francine. 2004. Effects of military operations on sonoran pronghorn. *Wildlife Monographs* **157**:1-41.

Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioural ecology, Third edition. Blackwell Scientific Publications, Oxford, UK.

Kristan, W. B., A. J. Lynam, M. V. Price, and J. T. Rotenberry. 2003. Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. *Ecography* **26**:29-44.

Landon, D. M., P. R. Krausman, K. K. G. Koenen, and L. K. Harris. 2003. Pronghorn use of areas with varying sound pressure levels. *Southwestern Naturalist* **48**:725-728.

Laursen, K. 1981. Birds on roadside verges and the effect of mowing on frequency and distribution. *Biological Conservation* **20**:59-68.

Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black capped chickadee. *Oecologia* **66**:60-67.

Lima, S. L. 1995. Back to basics of anti-predatory vigilance: the group size effect.

Animal Behaviour **49**:11-20.

Lima, S. L. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions.

Bioscience **48**:25-34.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation:

a review and prospectus. *Canadian Journal of Zoology* **68**:619-640.

Lipetz, V. E., and M. Bekoff. 1982. Group size and vigilance in pronghorn. *Tierpsychol.*

58:203-216.

Loft, E. R., and J. G. Kie. 1988. Comparison of pellet group and radio triangulation

methods for assessing deer habitat use. *Journal of Wildlife Management* **52**:524-527.

Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships

among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of*

Applied Ecology **33**:1379-1394.

Maher, C. R. 1991. Activity budgets and mating system of male pronghorn antelope at

Sheldon National Refuge, Nevada. *Journal of Mammalogy* **72**:739-744.

Maher, C. R. 2000. Quantitative variation in ecological and hormonal variables correlates with spatial organization of pronghorn males. *Behavioural Ecology Sociobiology* **47**:327-338.

Marques, F., S. Buckland, D. Goffin, C. Dixon, D. Borchers, B. Mayle, and A. Peace. 2001. Estimating deer abundances from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* **38**:349-363.

Martin, P., and P. Bateson. 1993. *Measuring Behaviour: An introductory guide*, Second edition. Cambridge University Press, Cambridge, UK.

Martinka, C. J. 1967. Mortality of northern Montana pronghorns in severe winter. *Journal of Wildlife Management* **31**:161-164.

McCullagh, P., and J. A. Nelder. 1989. *Generalized Linear Models*. Chapman and Hall Ltd., London, UK.

Mech, L., S. Fritts, G. Radde, and W. Paul. 1988. Wolf distribution and road density in Minnesota. *Wildlife Society Bulletin* **16**:85-87.

Mitchell, G. J. 1980. *The Pronghorn Antelope in Alberta*. University of Regina. Regina, Saskatchewan. 165 pp.

Mitchell, G. J., and S. Smoliak. 1971. Pronghorn antelope range characteristics and food habits in Alberta. *Journal of Wildlife Management* **35**:152-164.

Moody, A. L., A.I. Houston, and J. M. McNamara. 1996. Ideal free distributions under predation risk. *Behavioural Ecology and Sociobiology* **38**:131-143.

Mooring, M. S., T. A. Fitzpatrick, T. T. Nishhira, and D. D. Reisig. 2004. Vigilance, predation risk, and the allee effect in desert bighorn sheep. *Journal of Wildlife Management* **68**:519-532.

Mullner, A., K.E. Linsenmair, and M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation* **118**:549-558.

Neff, D. J. 1968. Pellet group count technique for big game trend, census and distribution: a review. *Journal of Wildlife Management* **32**:597-615.

Nowak, R. M. 1991. Walker's mammals of the world, Fifth edition. The Johns Hopkins University Press, Baltimore, Maryland.

Oakley, C., and P. Riddle. 1974. The impact of a severe winter and fences on antelope mortality in southcentral Wyoming. Pages 155-173 *in* Proceedings of the 6th Antelope States Workshop, Salt Lake City, Utah, USA.

Oetting, R., and J. Cassel. 1971. Waterfowl nesting on interstate highway right-of-way in North Dakota. *Journal of Wildlife Management* **35**:774-781.

O'Gara, B. W., and J. D. Yoakum. 2004. Pronghorn ecology and management. University Press of Colorado, Boulder, Colorado.

Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* **65**:573-582.

Paton, P. 1994. The effect of edge on avian nets success: how strong is the evidence? *Conservation Biology* **8**:17-26.

Patton, D. R. 1992. Inventory, evaluation and monitoring of forest habitats and wildlife. Pages 103-129 *in* Wildlife habitat relationships in forested ecosystems. Timber Press Inc, Portland, Oregon, USA.

Pierce, C. A., R. A. Block, and H. Aguinis. 2004. Cautionary note on reporting eta-squared values from multifactor ANOVA designs. *Educational and Psychological Measurement* **64**:916-924.

Poysa, H. 1987b. Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. *Behaviour* **103**:108-122.

Poysa, H. 1994. Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. *Animal Behaviour* **48**:921-928.

Reijnen, R., R. Foppen, and H. Meeuwsen. 1996. Effects of traffic on the density of breeding birds in dutch agricultural grasslands. *Biological Conservation* **75**:255-260.

Ries, L., R.J Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models and variability explained. *Annual Review of Ecological and Evolutionary Systematics* **35**:491-522.

Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* **51**:1077-1086.

Rondinini, C., and C. P. Doncaster. 2002. Roads as barriers to movement for hedgehogs. *Functional Ecology* **16**:504-509.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* **43**:634-641.

Rowland, M. M., G. C. White, and E. M. Karlen. 1984. Use of pellet group plots to measure trends in deer and elk populations. *Wildlife Society Bulletin* **12**:147-155.

SAS/STAT version 6.04, 2001, SAS Institute Inc., Cary, NC, USA.

Schneider, R. R., and S. Wasel. 2000. The effect of human settlement on the density of moose in northern Alberta. *Journal of Wildlife Management* **64**:513-520.

Schultz, R. D., and J. A. Bailey. 1978. Responses of national park elk to human activity. *Journal of Wildlife Management* **42**:91-100.

Siegel, S., and N. J. Castellan. 1988. *Nonparametric statistics for the behavioral sciences.*, Second edition. McGraw-Hill Inc, USA.

Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands? *Science* **210**:1041-1042.

Smith, A., S. Kelez, and H. Buchanan-Smith. 2004. Factors affecting vigilance within wild mixed species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*). *Behavioural Ecology and Sociobiology* **56**:18-25.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometry: the principles and practice of statistics in biological research.* W.H. Freeman and Company, New York, NY, USA.

Steidl, R., and R. Anthony. 2000. Experimental effects of human activity on breeding Bald Eagles. *Ecological Applications* **10**:258-268.

Tabachnick, B. G., and L. S. Fidell. 1996. Using Multivariate Statistics. Harper Collins College Publishers, NY, USA.

Taggart, J. R. 2003. Fish and Wildlife Division, Alberta Sustainable Resource Development.

Telfer, E. S. 1978. Cervid distribution, browse and snow cover in Alberta. *Journal of Wildlife Management* **42**:352-361.

Thiel, R. P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. *The American Midland Naturalist* **113**:404-407.

Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* **22**:61-68.

Tigas, L. A., D. H. V. Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation* **108**:299-306.

Toigo, C. 1999. Vigilance behavior in lactating female Alpine ibex. *Canadian Journal of Zoology* **77**:1060-1063.

- Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour* **60**:711-722.
- Treves, A., A. Drescher, and C. T. Snowdon. 2003. Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology* **109**:135-146.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**:18-30.
- Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). *Conservation Biology* **6**:253-262.
- Underwood, R. 1982. Vigilance behaviour in grazing african antelopes. *Behaviour* **79**:81-107.
- Utne, A. C., and D. L. Aksnes. 1994. An experimental study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult two-spotted goby *Gobiusculus flavescens*. *Journal of Experimental Marine Biology Ecology* **179**:69-79.
- Van Dyke, F., R. Brocke, H. Shaw, B. Ackerman, T. Hemker, and F. Lindzey. 1986. Reactions of mountain lions to logging and human activity. *Journal of Wildlife Management* **50**:95-102.

Van Riper, C., J. Hart, and J. Bright. 2001. Effects of fenced transportation corridors on pronghorn antelope movement in Petrified Forest National Park, Arizona. *in* D. Harmon, editor. Crossing Boundaries in Park Management: Proceedings of the 11th conference on research and resource management in parks and on public lands. The George Wright Society.

Van Riper, C., and R. Ockenfels. 1998. The influence of transportation corridors on the movement of pronghorn antelope over a fragmented landscape in Northern Arizona. Pages 241-248 *in* G. L. Evink, P. Garrett, D. Ziegler, and J. Berry, editors. Proceedings of the international conference on wildlife ecology and transportation, Ft. Myers, Florida.

Verlhuylt, S., K. Oosterbeek, and B. J. Ens. 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. *Biological Conservation* **101**:375-380.

Vistnes, I. and C. Nellemann. 2001. Avoidance of cabins, roads and power lines by reindeer during calving. *Journal of Wildlife Management* **65**:915-925.

Walther, F. R. 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella Thomsoni* Guenther 1884). *Behaviour* **34**:184-221.

Warner, R., G. Joselyn, and S. Etter. 1987. Factors affecting roadside nesting by pheasants in Illinois. *Wildlife Society Bulletin* **15**:221-228.

Weckerly, F. W., and M. A. Ricca. 2000. Using presence of sign to measure habitats used by Roosevelt elk. *Wildlife Society Bulletin* **28**:146-153.

White, K. S., and J. Berger. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* **79**:2055-2062.

Whitten, K. R., and R. D. Cameron. 1983. Movements of collared caribou, *Rangifer tarandus*, in relation to petroleum development on the arctic slope of Alaska. *The Canadian Field Naturalist* **97**:143-146.

Wolf, M., and G. O. Batzli. 2001. Increased prevalence of bot flies (*Cuterebra fontinella*) on white-footed mice (*Peromyscus leucopus*) near forest edges. *Canadian Journal of Zoology* **79**:106-109.

Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* **81**:266-271.

Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* **2**:333-339.