Population Dynamics of Reintroduced Elk (*Cervus elaphus*) in Eastern North America

by

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Abstract

Studies that focus on identifying factors that influence reintroduction success have often taken an individual population approach; however, investigating multiple populations can provide additional insight. The overall objective of this research was to emphasize the value of using within- and among-population approaches to identifying factors that influence the population dynamics of a reintroduced species. Elk (*Cervus elaphus*), a species that was extirpated from eastern North America during the late 1800s, has been reintroduced to portions of its former range over the past century through several initiatives. Today, there are several established populations across eastern regions of the USA and Canada, for which extensive monitoring data are available, creating an opportunity to investigate reintroduction success. I aimed to use these data to identify factors associated with changes in the survival and population growth rates of 10 reintroduced elk populations across eastern North America. More specifically, I: (1) performed a literature review detailing the history of elk reintroduction in eastern North America over the past century, (2) identified factors associated with the variation in population growth rates (reintroduction success) for 10 reintroduced elk populations using an among-population approach, (3) identified and assessed how climate affected the population growth rates of 7 reintroduced elk populations, and (4) investigated direct causes of mortality (predation and train collisions) associated with a single elk population experiencing low population growth.

Although the number of successful elk restoration attempts has increased over the past century, there has been substantial variation in population growth rates among reintroductions. Major causes of elk mortality in restored populations differed between the pre- to post-acclimation phases of reintroduction. Population growth rates were negatively related to the percentage of coniferous forest within elk population range, suggesting that expansive areas of coniferous forests in eastern North America may represent sub-optimal elk habitat.

The Burwash elk population in Ontario had low growth rate compared to most other populations reintroduced into eastern North America. Predation and train collisions were the most important source of mortality for this population. The number of annual elk-train collisions, as well as their locations, were monitored and recorded over 14 years. Collision locations were highly site-specific and were positively correlated to the proximity of bends in the railway. By relating the number of annual elk-train collisions to various climate factors, I found that collision rates were positively related to snow depth. By analyzing field camera data, I found that elk used the railway mostly during the fall and spring, when elk commonly travel to and from wintering grounds. However, by examining VHF telemetry locations, I determined that elk were closer to the railway in winter than in any other season. Railways likely are perceived by elk as easy travel corridors, especially in the winter, and deep snow might prevent escape from oncoming trains.

Black bear (*Ursus americanus*) and wolves (*Canis lupus*) were the major predators of elk in the Burwash population. White-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*), were the ungulate prey species available to both predators. To determine if predators prefer one ungulate species over another, and to identify which predator species is likely to have a greater impact on elk survival, I investigated predator diets. To compare rates of ungulate use by predators in relation to prey availability, I calculated the relative abundance of each ungulate species. I found that wolves used juvenile and adult elk as their primary ungulate prey in greater proportions in comparison to their availability. Bears on the other hand, tended to use all ungulate species in proportion to their availability.

Climate is well known to affect ungulate population dynamics; however, several factors (e.g.: density, predator presence), can govern the response. Relating the annual growth rates of 7 elk populations to various climate factors I found that responses were population specific. Increased annual snow fall was associated with declines in population growth rates for 2 of the 7 populations assessed and only 1 population responded negatively to increased summer temperatures. Climate likely interacts with other environmental variables to influence fluctuations in annual population growth rates which warrants further investigation.

The results of this research will contribute to informed planning of future elk reintroductions and should support development through improved management. In addition, this research highlights the importance of using within- and among- populations approaches to investigating factors that influence elk reintroduction success.

Dedication

Nothing has inspired me to pursue my dreams more than my children, Shyla and Hunter Popp. Their very existence is a constant reminder to me that anything is possible. My children, and my husband, Michael Popp, have made me smile every single day, supported me relentlessly, and fueled my desire to make my dreams come true. I dedicate this dissertation to the most amazing people in my world, Shyla, Hunter, and Mike.

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Numerous people contributed to the development of this dissertation; however, my supervisors, Dr. Frank F. Mallory and Dr. Joseph Hamr were critical to its successful completion. Their guidance and unwavering support have been appreciated deeply throughout the years. Frank has graciously accepted my ongoing desire to work in his lab throughout several degrees and has unremittingly contributed to the development of my career. Joe has bestowed a wealth of elk knowledge upon me and in addition to contributing greatly to my new passion in life (elk!), has contributed significantly to the direction of my research. I will be forever grateful for their model supervision surrounding my project and everything they have done above and beyond what is expected. In addition, my committee members provided ongoing expertise through time spent in scheduled committee meetings, but also by making themselves available on a regular basis outside of meetings. Each of these members contributed significantly to the development of my thesis. I am very grateful for the time and expertise given to me by Dr. Mark S. Boyce, Dr. Jeff L. Larkin, and Dr. Michael Persinger.

Over the years, two fellow grad students were of particular importance to the development of this dissertation. Tori Donovan and Dave McGeachy spent many days (and nights) listening to my statistics and study design rants, and were great friends that provided relentless support. For Tori and Dave, I am incredibly appreciative. In addition, fellow Ph.D. candidate, now Dr. Darryl Edwards, was integral to my understanding of statistics and I can’t thank him enough.

Much of this research would not be possible without the data I gathered from regional managers who participated in questionnaire surveys and provided population estimates, along with other information. These people included D. Crank, R. Rosatte, W. Wright, B. Mastenbrook, J. Yarkovich, J. Banfield, L. Stowell, L. McInenly, B. Ranta, L. Hansen, and J. Trottier.

Volunteers and undergraduate thesis students contributed to this project in many ways. J. Quittenton and M. Brown assisted with prey hair scale pattern slide preparations and Dr. D. Boreham, A. Zarnke, L. Doyle, J. Bates, C. Thome, M. Hall, and W. Kowbasniuk provided field assistance with fecal pellet surveys. C. Chan contributed through her undergraduate thesis to the understanding of the influence of railways on elk spatial distribution.

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Chapter 1

General Introduction

The planet is currently experiencing a biodiversity crisis where species are being lost at a rate about 1000 times faster than the background rate of extinction (Pimm et al. 2014). Conservation initiatives are key to ensuring the prevention of extinctions and extirpations. Unfortunately, management actions have not always succeeded in preventing extirpations and in those events, reintroduction has become a popular conservation tool. Reintroductions are the intended translocations of a given species to part of its historical range, where it has been extirpated (International Union for Conservation of Nature/Species Survival Commission 2013). Although an indispensable conservation tool for at least a century (Kleiman 1989; Popp et al. 2014), reintroduction biology has only recently become a field of research, developed partly in response to poor success rates (Armstrong and Seddon 2007; Seddon et al. 2007). Reintroductions can be costly (Lindburg 1992) and often are a last resort in the recovery of a species. Understanding the mechanisms influencing the outcome of reintroductions becomes pertinent in preventing the waste of conservation funds and effort. Because of this, there has been increased interest in identifying factors that influence reintroduction success by categorizing species into groups (e.g.: herbivores, game species) (Griffith et al. 1989; Wolf et al. 1996; Wolf et al. 1998). Although this approach has merit, it may result in a loss of information. For example, Griffith et al. (1989) determined that overall 86% of native game reintroductions resulted in success, but Popp et al. (2014) determined that elk (*Cervus elaphus*), a native game species, only had a 60% success rate. Studies that focus on species-specific success rates may more explicitly reveal factors associated with reintroduction success compared to those that use a multi-species approach.

Although many species have been reintroduced across the world, game species account for 90% of translocations (Griffith et al. 1989; Wolf et al. 1996). In North America, elk were extirpated from the eastern part of the continent and drastically reduced in the western regions after the arrival of Europeans (Bryant and Maser 1982). Prior to the arrival of the Europeans, it was estimated that 10 million elk were present in North America (Seton 1927). In eastern North America, elk were extirpated by the end of the 1800s; a decline that was attributed mainly to overharvest and habitat loss (O'Gara and Dundas 2002). By the late 1970s, approximately 500,000 elk remained, primarily in the western part of the continent – a 95% reduction in the overall population size (Bryant and Maser 1982).

Large mammalian herbivores like elk play pivotal ecological roles (Ross 2001). They alter landscapes and ecosystem dynamics in many ways, such as dispersing seeds (Lieberman et al. 1987), regulating landscape succession (Owen-Smith 1988), influencing plant species regeneration (Ripple and Larsen 2000; Beschta 2005), and creating trails that serve as movement corridors for other animals (Naiman and Rogers 1997). In addition to the provision of substantial ecosystem services, elk are also economically important because they provide hunting and wildlife viewing opportunities. By restoring species like elk to landscapes in which they once thrived, I not only improve economic and recreational opportunities for humans, but also contribute to restoring entire ecosystems to more holistic states (Gogan 1990).

Almost immediately after the extirpation of elk from the east, numerous reintroductions began and have been ongoing since, with varying degrees of success (O'Gara and Dundas 2002; Popp et al. 2014). The landscapes, predator compositions, and elk population dynamics differ substantially between eastern and western North America (Keller et al. 2015). For example, there are less public lands and generally greater road densities in the east (Riitters and Wickham 2003; Radeloff et al. 2005). Elk movement patterns differ amongst eastern and western regions, where large-scale migrations are exhibited (Ruhl 1984; Wichrowski et al. 2005). Although Keller et al. (2015) found that survival rates of established adult and sub-adult elk were similar in the two regions, annual juvenile survival was higher, but adult female fecundity was lower and more variable in eastern populations. Predation (including harvest) was a major cause of mortality for juvenile elk in both eastern and western regions of the continent; however, the rate of predation was doubled in western populations. Vehicle collisions, nuisance culling, and meningeal worm (*Parelaphostrongylus tenuis*), a potentially lethal parasite to elk, were major sources of mortality in the east but rare in the west. Keller et al. (2015) suggested that documented vital rates, mortality factors, and population growth rates of western elk may not be applicable to restored eastern elk. For these reasons, elk research and management in the two regions of North America have been conducted, for the most part, separately.

Many of the earlier elk restoration attempts in eastern North America could have failed due to vehicle collision mortalities, inadequate habitat, poor release conditions, hunting or poaching, disease and parasites, and poor management (Witmer 1990; O'Gara and Dundas 2002). However, there was very little population monitoring of early restorations, and research in general was sparse (Larkin et al. 2001), which may have hindered managers from designing strategies to ensure restoration success. Recently translocated and established elk in several eastern states and Ontario, Canada, are monitored extensively. Variation in success rates (population growth rates) exist among populations and some of the more recently reintroduced populations are in decline (Popp et al. 2014). This variation in success makes elk an excellent study subject for examining how various factors influence reintroduction success using both within- and among-population research approaches.

The objective of my dissertation was to use within- and among-population approaches to analyze reintroduction success by assessing factors associated with changes in the survival and population growth rates of 10 reintroduced elk populations across eastern North America. More specifically, I aimed to: (1) perform a literature review detailing elk reintroduction in eastern North America over the past century, (2) identify factors associated with the variation in population growth rates (reintroduction success) of 10 reintroduced elk populations using an among-population approach, (3) identify and assess how climate affects the population growth rates of 7 reintroduced elk populations, and (4) investigate direct causes of mortality (predation and train collisions) in a population experiencing low annual growth rates. The results of this study will assist in the development of informed management strategies to help ensure success of future reintroductions.

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Chapter 2

A century of elk restoration in eastern North America*

Abstract

Over a century has passed since elk were extirpated in eastern North America. During that time, numerous attempts to reintroduce elk into eastern North America have resulted in varying degrees of success and failure. An overview of restoration efforts during the last 100 years is presented here with emphasis on the differences in rates of population change among regions and differences in major causes of elk mortality during both the pre- and post-acclimation periods. Approximately 40 % of recorded elk reintroduction attempts in eastern North America resulted in failure, with the majority of these having occurred in the first half of the 20th century. Although rates of population change in elk were highly variable, they were not related to founding population size. Major causes of mortality varied among regions and should be considered in future reintroduction attempts.

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Introduction

Prior to the arrival of the Europeans, it was estimated that 10 million elk were present in North America (Seton 1927). Historically the combined ranges had six subspecies (Roosevelt *Cervus elaphus roosevelti*); Tule *C. e. nannodes*; Rocky Mountain *C. e. nelsoni*; Merriam's *C. e. merriami*; Manitoban *C. e. manitobensis*; and Eastern *C. e. canadensis*) that occupied the majority of North America (O'Gara and Dundas 2002) (Fig. 1). The eastern elk was extinct by 1867 and Merriam's elk became extinct by the early 1900s (O'Gara 2002). The reduction in elk populations and range has been primarily attributed to overexploitation and habitat loss (O'Gara and Dundas 2002). By the late 1970s, approximately 500,000 elk were primarily found in the western part of the continent (Bryant and Maser 1982). Today, it is estimated that there are slightly more than 1 million elk across North America in several scattered populations (Fig. 1).

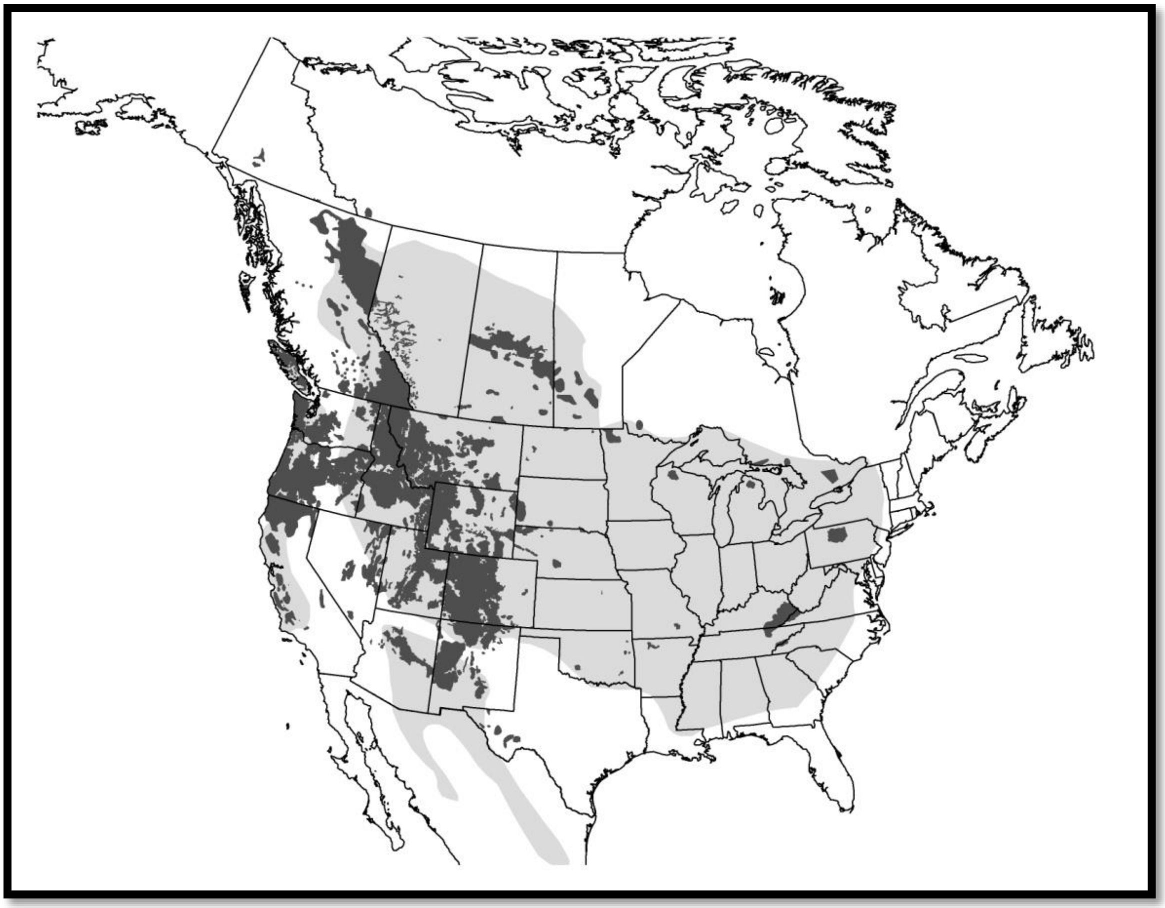


Fig 1. Historical (light grey) and current (dark grey) elk range in North America.

Reintroducing animals is a common conservation and management tool that has proven to work well for many species, especially native game species (Griffith et al. 1989), and reintroductions have occurred for over 100 years (Kleiman 1989). Since the extirpation of elk from the east, numerous reintroductions have been attempted with varying degrees of success and failure (O'Gara and Dundas 2002). Although many elk reintroductions have taken place since the early 1900s, sufficient monitoring has been lacking and related publications are sparse (Larkin et al. 2001). For example, the Pennsylvania elk herd was not studied until 60 years after its initial release (Eveland et al. 1979).

The objective of this chapter is to provide an overview of elk restoration attempts in eastern North America by reviewing the current literature and survey information obtained from regional elk managers. The goals are to examine major causes of mortality and to detail the trends in population growth by comparing rates of increase among regions.

Methods

In order to provide an overview of the population trends of elk reintroductions in eastern North America, survey questionnaires were e-mailed to primary elk managers in each respective region during September 2013. Pertinent literature and management reports were gathered as supplementary material. Eastern North America was defined as any province or state east of the Great Plains. On the basis of the information gathered from surveys, reports, and the literature, the exponential rates of increase ($r = \ln(N_{t+1}/N_t)$) were calculated using regression analysis which incorporated available population estimates since the time of reintroduction up to the most recent population estimate. A linear regression was used to examine the relationship between the number of elk released and the exponential rate of increase. Martin (2011) found that reintroduced elk in Ontario took 1-3 years to acclimate, or habituate to their environments based on spatial behaviours. Causes of mortality during the release years and/or within the first 3 years post-release (acclimation phase) were thus calculated for each elk population with available information. More recent major sources of post-acclimation mortality were also detailed for each elk population.

Reintroductions: An Overview

Approximately 40% of documented elk reintroductions in eastern North America have resulted in failure within 5-94 years (Table 1). Elk population declines have been attributed to a variety of factors including vehicle collisions, poor release conditions, lack of appropriate habitat, hunting or poaching, crop damage, disease and parasites, and less commonly poor management (Witmer 1990; O'Gara and Dundas 2002). More recent attempts have resulted in varying degrees of success. The rate of population change over time (*r*) for established reintroduced elk populations in eastern North America ranged from -0.05 to 0.13 (Table 1), with the populations from Kentucky, United States and Bancroft, Ontario increasing at the most rapid rates. The majority of populations have grown since reintroduction; however, the populations from Minnesota, United States and Lake of the Woods (LOW), Ontario, have decreased in size (Fig. 2; Table 1). Hunting seasons have been opened in several regions and contribute to population control and potentially account for slower rates of increase (i.e. Minnesota, United States); however, other populations have low growth rates or are declining without the presence of a legal hunt (i.e. Burwash, LOW, Ontario and Minnesota).

Table 1. Statistics on elk released in different regions of eastern North America. Failed attempts sourced from (O'Gara and Dundas 2002).

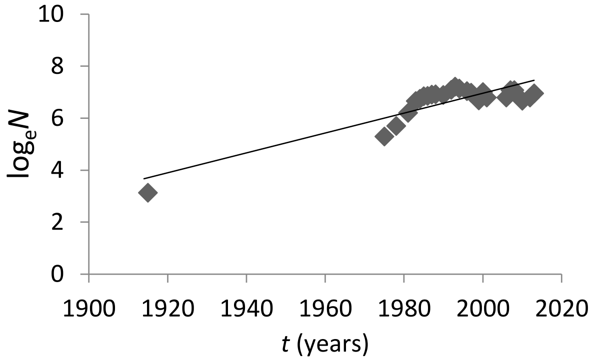
Region	**Total Released**	**Year(s) Released**	**2013 Estimate**	**Years Since Release**	***r***	**First Hunt**
Kentucky	1,547	1997-2002	10,000	11	0.13	2001
Bancroft, ON	120	2000-2001	500	12	0.13	2010
LH-NS, ON	47	2001	200	12	0.12	NA
Wisconsin	25	1995	154	18	0.12	NA
North Carolina	52	2001-2002	150	11	0.10	NA
Tennessee	201	2000-2003	400[a]	10	0.08	2009
Arkansas	112	1981-1985	617	28	0.06	1998
Michigan	23	1914-1915	1050	97	0.04	1920s
Pennsylvania	177	1913-1926	833	87	0.04	2001
Burwash, ON	172	1998-2001	145	12	0.03	NA
Minnesota[b]	56	1914	28	98	-0.01	1987
LOW, ON	104	2000-2001	60	12	-0.05	NA
Missouri	108	2011-2013	110	NA	NA	NA
Virginia	18	2012	24*	NA	NA	NA
Failed					**Extirpation Date**	
Alabama	55	1916	NA	5	1921	
Arkansas	11	1933	NA	~20	1950s	
Florida	6	1968	NA	5	1973	
Indiana	UNK	early 1960s	NA	UNK	UNK	
Louisiana	20	1916	NA	UNK	UNK	
Missouri	10	1951	NA	8	1959	
New Hampshire	12	1903	NA	94	1997	
New York	332	1893-1906	NA	60	1953	
Virginia	110-150	1917	NA	~50	1960s	
Ontario	UNK	Early/mid 1900s	NA	UNK	Trace remained	

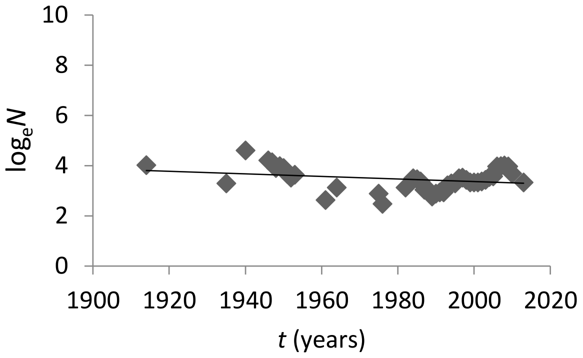
LH-NS, Lake Huron-North Shore; UNK, unknown; *r*, exponential rate of increase; NA, not applicable.
Failed attempts; source: O'Gara and Dundas (2002).

[a] 2012 estimate.

[b] Grygla herd.

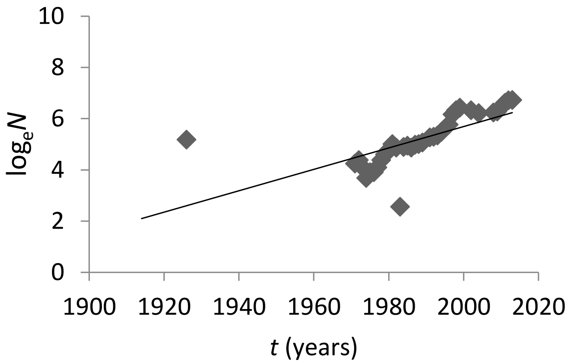
Early:





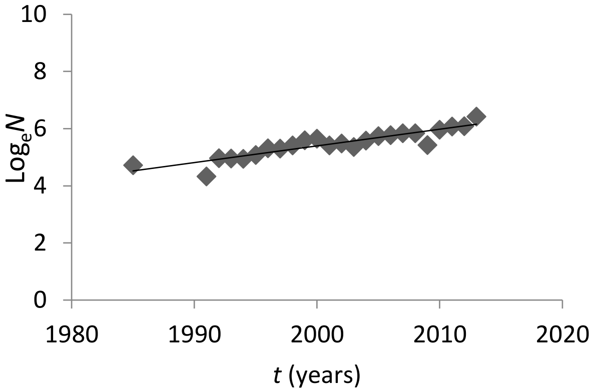
Michigan[1]

Minnesota[2]

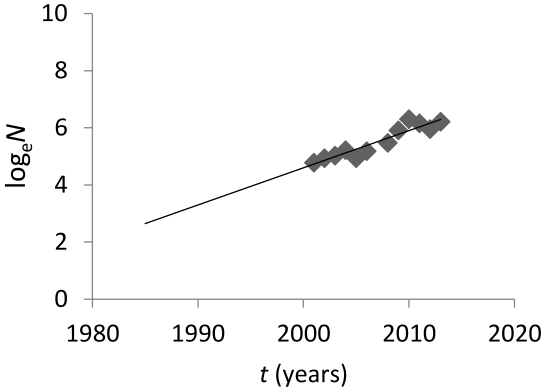


Pennsylvania[3]

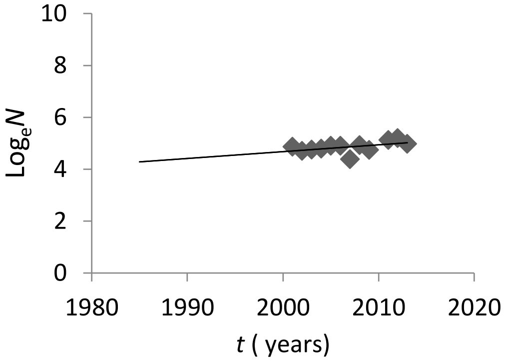
Late:



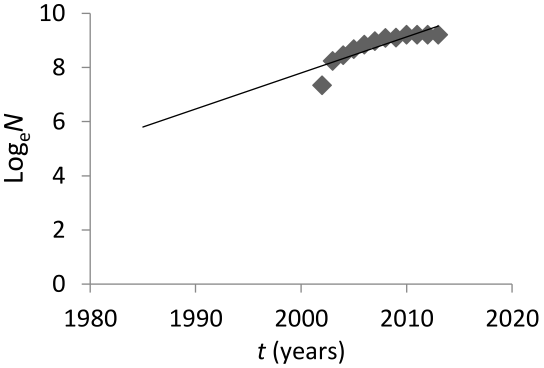
Arkansas



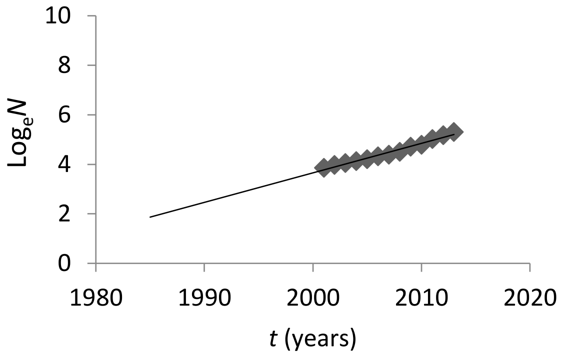
Bancroft, ON[4,5]

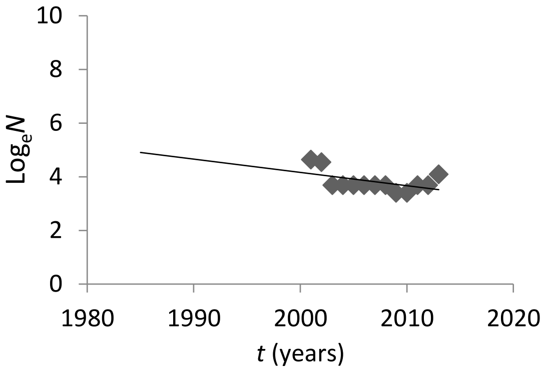


Burwash, ON[4]



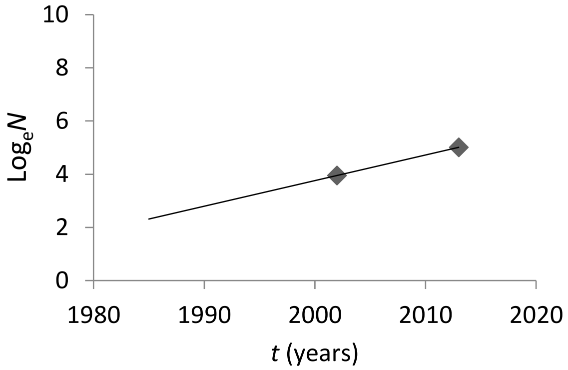
Kentucky

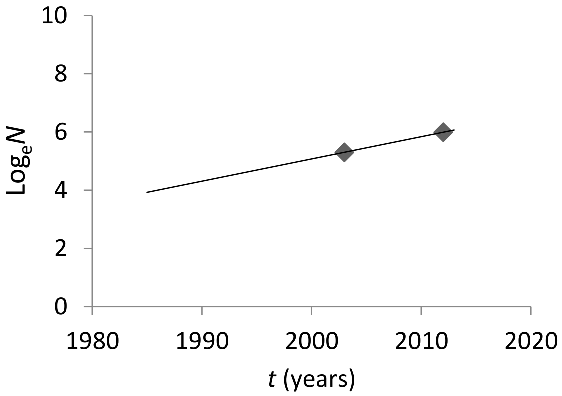




LH-NS, ON[a,4]

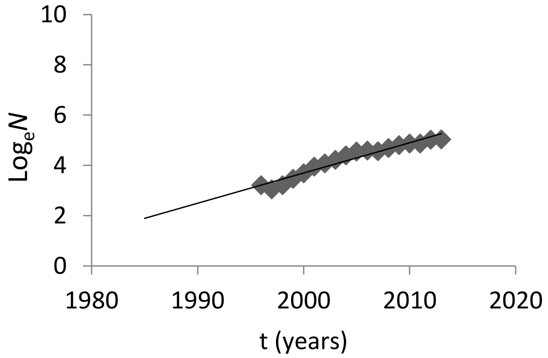
LOW, ON[b,4]





North Carolina

Tennessee



Wisconsin[6]

Fig 2. Estimates of elk population growth in different restoration regions across eastern North America.

[a]Lake Huron-North Shore, [b]Lake of the Woods.

[1]Michigan Department of Natural Resources. 2012. Michigan Elk Management Plan. Lansing, Michigan.

[2]Minnesota Department of Natural Resources. 2009. Strategic Management Plan for Elk Minnesota Department of Natural Resources November 2, 2009, Minnesota.

[3]Banfield, J., Perlock, E., and C. Rosenberry. 2013. Elk Research/Management. Pennsylvania Game Commission Bureau of Wildlife Management Project Annual Job Report; DeBerti, J.M. 2006. Management Plan for Elk in Pennsylvania 2006–2016. Northcentral Regional Office Pennsylvania Game Commission.

[4]Ontario Ministry of Natural Resources Annual Provincial Elk Status Updates.

[5]Rosatte, R. *In Press*. The Behaviour and Dynamics of a Restored Elk (*Cervus elpahus manitobensis*) Population in Southern Ontario, Canada: 5–12 Years Post Restoration. Canadian Wildlife Biology and Management.

[6]Stowell, L.R., Zickmeister, M., Jonas, K.W. Wallengang, K., Roepke, S.C., Gilbert, J., Eklund, D.A., Ginnett, T. Rolley, R., Wydeven, A., Dhuey, B., Babros, T., and K. Johansen. 2012. 2012 Clam Lake and Black River Elk Management Plan Amendment. Wisconsin Department of Natural Resources. Madison, Wisconsin.

Griffith et al. (1989) found that larger founding populations were more successful for large mammal reintroductions; however, this was true only up to 20–40 founders, after which there was little increase in success rate. Fischer and Lindenmayer (2000) found that reintroductions with more than 100 animals as a founding population in many species resulted in a greater chance of success. Kentucky's high rate of increase, with a current population of 10,000 elk, appears to be related to the high total number of elk released (Table 1); however, when Kentucky is removed from the analysis, there is no relationship between the number of elk released and the rate of increase for the remaining elk populations ($R^2 = 0.03$ without Kentucky; $R^2 = 0.10$ with Kentucky).

Irruptive growth is common in ungulates when the environment is not at carrying capacity and predators and diseases are absent (Riney 1964; Gogan and Barrett 1987). Larkin et al. (2003) suggested that Kentucky's irruptive population growth may eventually be followed by population decline. Irruptive growth has also been seen in other elk populations in Manitoba and Washington

State (Banfield 1949; McCorquodale et al. 1988); however, the Washington elk population subsequently declined and had reduced cow and calf survival (Eberhardt et al. 1996).

Small founder populations may affect more than population growth rates, as they often result in reduced genetic variability due to the founder effect and genetic drift (Conard et al. 2010). However, genetic variability in elk reintroduced across North America was not well explained by founding population size (Conard et al. 2010). Allee (1938) and Armstrong and Seddon (2008) suggested that genetic variability could decrease over time in small populations and initial population growth rates could be negative, as individuals may be too dispersed to find mates (the Allee effect). The distribution of potential mates may therefore be crucial to population growth. In Ontario, 50% of released elk dispersed more than 40 km from their release sites (Yott et al. 2011) and it has been suggested that reducing post-release dispersal of females would enhance calving rates (Larkin et al. 2002). Post-release dispersal can be reduced by holding elk for longer periods of time prior to release to acclimate them to release sites. This has been shown to result in greater post-release site fidelity in Ontario elk (Ryckman et al. 2010).

Pre-Acclimation Mortality

Prior to release, stress-induced mortality of introduced elk can be substantial. Rosatte et al. (2007) reported that 9% of the mortality in elk reintroduced into Ontario occurred in holding pens prior to release and most of these were related to transport injury and stress. Hunting and poaching played a large role with respect to pre-acclimation mortality, especially in the U.S. populations; however, disease, emaciation, injury, and accidents (classified as other), were the greatest causes of mortality in most cases (Table 2). Predation was more important in the northern populations. The adverse impact of stress is an important component to consider during reintroduction, as many attempts have failed due to stress-related mortality soon after release (Hamr 2001; Teixeira et al. 2007).

Table 2. Percent mortality by cause during release years and/or within the first 3 years after the final release (pre-acclimation phase).

Region	N	Hunting/ Poaching	Meningeal Worm	Vehicle/ Train	Predation	Other	Unknown	Source (*data from*)
Kentucky	410	38.7	45.3	16.0	-	-	-	Dan Crank (2013) (*2003-2005*)
Bancroft	43	20.9	-	14.0	2.3	62.8	-	Rosatte et al. 2007 (*2000-2001*)
LH-NS[1]	12	25.0	-	8.3	-	66.7	-	Rosatte et al. 2007 (*2001*)
Tennessee	62	17.7	8.1	12.9	-	19.4	41.9	Kindall et al. 2011 (*2000-2005*)
Arkansas[a]	20	35.0	10.0	5.0	-	35.0	15.0	Wes Wright (2013) (*1985-1989*)
Burwash	101	3.0	-	4.0	40.6	52.4	-	Rosatte et al. 2007 (*1998-2001*)
LOW	34	29.4	-	2.9	17.6	50.0	-	Rosatte et al. 2007 (*2000-2001*)

LH-NS, Lake Huron-North Shore.
Other: disease, emaciation, injury, drowning, accidents, and ‘other.’
[a]Mortality within the first 4 years post-release.

Meningeal or brain worm is a nematode that utilizes white-tailed deer (*Odocoileus virginianus*) as the reservoir host and causes no ill effects to this species. However, the worm causes lethal neurological disease in elk, moose (*Alces alces*), and caribou (*Rangifer tarandus*) (Anderson et al. 1966; Anderson 1972; Samuel et al. 1992). Susceptible ungulates become infected by accidentally ingesting gastropods with infective larvae (Anderson 1972). Mortality caused by meningeal worm (*Parelaphostrongylus tenuis*) accounted for 45.3% of reported deaths in Kentucky, 8.1% in Tennessee, and 10% in Arkansas during the pre-acclimation period (Table 2).

It has been suggested that past elk reintroduction efforts have failed because of meningeal worm (Raskevitz et al. 1991; O'Gara and Dundas 2002), and it has been predicted that future elk restorations would fail due to mortality caused by this nematode (Carpenter et al. 1973; Severinghaus and Darrow 1976; Bergerud and Mercer 1989; Raskevitz et al. 1991).

As meningeal worms rely on gastropods as their intermediate host, their prevalence may depend on habitats where gastropods are abundant, such as low-lying, damp forests (Anderson 1972). Much of eastern North America has a high density of white-tailed deer and when combined with wetter habitats, gastropods may thrive, thus increasing the prevalence of the nematode (Van Deelen et al. 1997). However, Raskevitz et al. (1991) reported that elk were most often found in habitats with the least number of gastropods. McIntosh et al. (2007) found that within the first few years after reintroduction in south-central Ontario, 59% of deceased elk were infected with *P. tenius*. Larkin et al. (2003) suggested that because of the high rate of meningeal worm related deaths, the Kentucky elk population would likely decline; however, this has not happened thus far. Bender et al. (2005) showed that elk populations can persist at high levels of productivity in the presence of meningeal worms. This may be because elk are known to survive low levels of meningeal worm infection (Larkin et al. 2003) and do not develop clinical signs in this condition (Samuel et al. 1992; McIntosh et al. 2007). The rate of infection in elk populations may be related to many factors associated with the elk range, such as the parasite prevalence in deer, the abundance of deer, the deer-elk range overlap, the age of infected elk, acquired immunity, and the ability to survive low level infections (McIntosh et al. 2007). Although meningeal worm has accounted for mortality in some recent elk reintroductions, the negative impact appears lower than initially suspected, indicating that further research of the meningeal worm–elk dynamics would be beneficial.

Vehicle and train collisions accounted for 2.9–16% of post-release elk mortality in eastern North America (Table 2). Although this rate accounts for less mortality than other factors, it deserves attention. Vehicle and train collisions result in alarming numbers of animal deaths every year (Jaren et al. 1991; Romin and Bissonette 1996; Bertwistle 2001; Andreassen et al. 2005). Between 1951 and 1999, 3,791 large animals were killed by vehicle and train collisions in Jasper National Park, of which elk and bighorn sheep made up 53% (Bertwistle 2001). Under these conditions, small populations have greater chances of getting even smaller in accordance with the extinction vortex theory (Gilpin and Soulé 1986). Therefore, in small populations such as reintroduced elk herds where the risk of extirpation is high, every death deserves attention. Developing vehicle and train collision mitigation strategies is likely an important component of ensuring elk restoration success.

Black bear, wolves, coyotes, and cougars are well known elk predators (Singer et al. 1997; Anderson et al. 2005; Barber-Meyer et al. 2008). While wolves tend to focus mainly on adult ungulates for prey (Arjo et al. 2002), black bear and coyotes primarily focus on calves (Carter 2006; Barber-Meyer et al. 2008; Murrow et al. 2009). Black bear predation was the leading cause of elk calf mortality in Great Smoky Mountains National Park after reintroduction (Murrow et al. 2009). In an environment containing elk, moose, and white-tailed deer, wolves in Riding Mountain National Park in Manitoba preferred elk over other prey, in proportion to their availability (Carbyn 1983). Predator species composition and abundance varied among release regions and predation was found to be a limiting factor in the Burwash and LOW populations of Ontario, accounting for 40.6 and 17.6% of the initial mortality, respectively. These populations have low or negative growth rates, suggesting that predation may be a strong factor influencing population growth. Frair et al. (2007) found that although wolves had an important negative effect on western elk survival during the first post-release winter, elk subsequently learned to mediate their mortality risk, regardless of previous predator experience.

Post-Acclimation Mortality

Major sources of post-acclimation mortality varied among populations (Table 3). Meningeal worm did not account for high mortality, with the exception of the Arkansas and North Carolina populations, which showed positive growth, regardless. From 1981 to 1994, 67–80 years post-release, meningeal worm caused only a small proportion of elk deaths (3% of all mortality) in Michigan (Bender et al. 2005).

Table 3. Recent major causes of elk mortality in eastern North American reintroductions based on manager surveys.

Region	Hunting/Poaching	Meningeal Worm	Vehicle/Train Collision	Predation	Accidental/Other
Kentucky	*				
Bancroft, ON	*		*		*
LH-NS, ON	*		*		*
Wisconsin			*	*	
North Carolina		*	*	*	
Tennessee[a]	*				*
Arkansas	*	*			*
Michigan	*		*		
Pennsylvania	*		*		*
Burwash, ON			*	*	*
Minnesota	*			*	*
LOW, ON				*	*

LH-NS, Lake Huron-North Shore.

[a] From 2000 to 2005 (Kindall et al. 2011).

Vehicle collisions are currently considered a source of high mortality in some regions. As populations increase, it is likely that more animals come into contact with roads and railways. Even for relatively small populations, collision mortality can have a large negative impact on population dynamics. In recent years, vehicle-wildlife collision mitigation strategies have been put in place for reintroduced elk populations in some areas. For example, in Wisconsin signs along roads that light up when elk are in the vicinity (based on response to radio-collars) have been used. Wisconsin also cut back roadside vegetation to try to allow for early detection of animals close to the road. In Burwash, Ontario, fencing along a major highway was put up in conjunction with a highway wildlife overpass and highway underpasses, the first of their kind in eastern Canada.

Predation appears to be associated mainly with reintroduced elk populations that have lower rates of increase (Table 2). However, some populations seem to maintain positive rates of increase in spite of predator presence. For example, it has been suggested that in Pennsylvania, elk calves have 80% chance of surviving to 1 year, possibly due to high quality habitat that ensures elk are in top physical condition (DeVivo et al. 2011). McClafferty and Parkurst (2001) state that elk restoration must be based on specific information about the species' historic range, habitat requirements, interspecific relations, socioeconomics, public relations and management, in order to be successful. Conard et al. (2010) suggests that maximizing post-restoration population size, reducing annual variability, and maintaining positive growth rates should assist in promoting the retention of genetic variability. Calf recruitment, an important driver of large herbivore population dynamics (Pimlott 1967; Raithel et al. 2007), is likely influenced by many variables including habitat quality, elk density, predation, and adult male age structure (Gratson and Zager 1998). Larkin et al. (2004) suggested that reintroduction efforts should be focussed on habitats with high levels of open forest edge and limited human disturbance. Areas dominated by a single cover type should be avoided, as they will likely result in lower reintroduction success. Differences among major habitat types in each release location are apparent. For example, Wisconsin's elk range is comprised mainly of unbroken forest (Anderson et al. 2005), while Burwash, Ontario (Popp et al. 2013) and Michigan (Bender et al. 2002) elk ranges consist primarily of forest interspersed with agricultural land and openings.

Elk reintroductions are often poorly documented (Fischer and Lindenmayer 2000), and many programs are plagued with low success and researchers have failed to deliver a scientific framework to managers, which would assist in improving reintroduction success (Deredec and

Courchamp 2007). A thorough investigation of factors influencing elk population dynamics in different parts of the continent is needed in order to obtain a clearer understanding of their cumulative effects and to identify those most strongly associated with the success and/or failure of reintroductions (Popp in preparation).

Elk reintroductions have had varying degrees of success in eastern North America; however, more positive results have been displayed during recent years. As can be seen from the varying rates of population growth among recent reintroduction populations, research is still needed to improve on success. In order to address the current lack of knowledge and obtain a better understanding of elk reintroduction dynamics, managers should collaborate and exchange information, post-release monitoring should be intensified, failures should be reported and analyzed, and associated research should continue. Better knowledge should further contribute to the success of elk restoration across the species' former range in eastern North America.

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Chapter 3

Factors influencing population growth of reintroduced elk in eastern North America

Abstract

Attempts to reintroduce wildlife populations have often resulted in failure. Identification of factors that influence reintroduction success is fundamental to guiding future attempts. Studies of reintroduced species often have been limited to the examination of single populations; however, important additional knowledge can be acquired through across-population investigations. I aimed to demonstrate the importance of among-population analyses by examining factors that influence growth rates of reintroduced elk populations in eastern North America. I hypothesized that land use composition, initial population size, snow depth, disease, the presence of predators, and the presence of competitors would influence elk population growth rates among ten reintroduced populations. I used a model-selection approach, incorporating several covariates to determine which factors best explained variation in rates of increase among populations. The most prominent factor explaining variation in reintroduced elk population growth rates was an inverse relation to the percentage of coniferous forest within elk range. Landscapes dominated by coniferous forests in eastern North America likely represent sub-optimal elk habitat as reintroduced elk population growth rates decline when ranges are associated with greater proportions of coniferous forest in the landscape. Future elk reintroductions in eastern North America should avoid targeting areas dominated by coniferous forest. My study emphasizes the

value of using across-population approaches when assessing factors affecting the demographics of reintroduced wildlife populations.

Introduction

Reintroductions are intended translocations of a species to part of their historical range where they have been extirpated (International Union for Conservation of Nature/Species Survival Commission 2013). Although a management tool for at least a century (Kleiman 1989; Popp et al. 2014), reintroduction biology only recently has become a field of research, developed partially in response to poor success rates (Armstrong and Seddon 2007; Seddon et al. 2007). Fischer and Lindemayer (2000) reviewed 116 published reintroduction studies and found that of those with known outcomes only 49% were successful. Pérez et al. (2012) assessed published and unpublished translocation projects and found that most addressed less than 50% of basic translocation criteria and were inadequately designed to guarantee success.

Reintroductions can be costly (Lindburg 1992; Converse et al. 2013), and often are a last resort in the recovery of a species. Understanding the mechanisms that influence the outcome of previous reintroductions can provide valuable insight to future efforts which may prevent waste of conservation funding and effort. Because of this, there has been increased interest in determining factors that influence reintroduction success, with studies often categorizing species into groups; for example, by different food habits (i.e.: carnivore, herbivore, omnivore), or other category types (Griffith et al. 1989; Wolf et al. 1996; 1998). Although this approach has merit, it may fail to identify the causal factors of success or failure, because different species and taxa are pooled in such analyses and species- or taxon- specific responses may be overlooked. For example, Griffith et al. (1989) determined that overall 86% of native game reintroductions resulted in success, but Popp et al. (2014) determined that elk (*Cervus elaphus*), a native ungulate in eastern North America, only had a 60% reintroduction success rate. Along with the need for estimates of reintroduction success, managers need to identify specific environmental factors related to success to assist in decision making and management approaches. Studies that address species-specific questions may better reveal factors that influence reintroduced populations compared to those that use a multi-species approach.

Multiple reintroductions of elk in eastern North America provide an opportunity to examine aspects associated with reintroduction success and failure across multiple populations. The range of elk has decreased by 74 % over its historic distribution (Laliberte and Ripple 2004) mainly due to overexploitation and habitat loss (O'Gara and Dundas 2002), especially in eastern North America (Popp et al. 2014). Many factors are known to influence reintroduction success including founding population size (Griffith et al. 1989), site fidelity (Larkin et al. 2002), stress (Hamr 2001; Teixeira et al. 2007), poor-quality habitats, excessive or illegal harvest, as well as parasites and disease (Witmer 1990; Thorne et al. 2002). Meningeal or brain worm (*Parelaphostrongylus tenuis*), a nematode carried by white-tailed deer (*Odocoileus virginianus*), causes lethal neurological disease in other ungulates including elk (Anderson et al. 1966; Anderson 1972). Many early historical elk reintroduction efforts appear to have resulted in failure because of this parasite (Raskevitz et al. 1991; O'Gara and Dundas 2002). The most common reason described for early elk reintroduction failure in the eastern United States was a lack of appropriate habitats resulting from either low habitat quality, quantity or both (Witmer 1990). Regardless of what factors contributed to past reintroduction failures, studies of existing elk populations can provide important insight into future reintroduction efforts.

In this study, I provide an example of the importance of multi-population analyses associated with reintroduction biology. Elk have been reintroduced throughout eastern North America for over a century (Popp et al. 2014), and with several reintroductions and associated demographic data, this species provides an opportunity to identify factors influencing population growth, and ultimately, reintroduction success. The purpose of this study was to identify factors that most influence elk population growth rates while demonstrating the importance of among-population analyses when assessing the potential of success for future elk reintroductions by examining factors that influence growth rates of extant populations. i used annual population estimates from 10 reintroduced populations of elk in eastern North America to calculate expomemtial rates of increase. Based on factors known to influence elk population dynamics, I incorporated several covariates and used a model-selection approach to determine which factors best explained variation in rates of population increase among populations.

Methods

In 2013, I mailed a survey questionnaire to elk managers across eastern North America requesting annual population estimates and the extent of population ranges. I also gathered management reports and pertinent literature that could aid in evaluating population characteristics. For this study, I defined eastern North America as any state or province east of the Great Plains. Although there are currently 14 elk populations that have been established through reintroduction in eastern North America (Popp et al. 2014), sufficient data were only obtained for 10 (approx. 70% of all populations). Each of these populations were the result of reintroductions that occurred at varying times throughout the past century (Popp et al. 2014; Table 1). These populations included Arkansas (AR), Kentucky (KY), Michigan (MI), Minnesota (MN), Pennsylvania (PA), Wisconsin (WI), and 4 populations in Ontario: Bancroft (BAN), Burwash (BUR), Lake Huron-North Shore (LHNS), and Lake of the Woods (LOW) (Fig. 1). The majority of the assessed populations occupied the Type I Northern Forest ecoregion (BAN, BUR, LHNS, LOW, MI, MN, PA, WI), but two populations (AR, KY) occupied the Type I Eastern Temperate Forest ecoregion (Commission for Environmental Cooperation 2006).

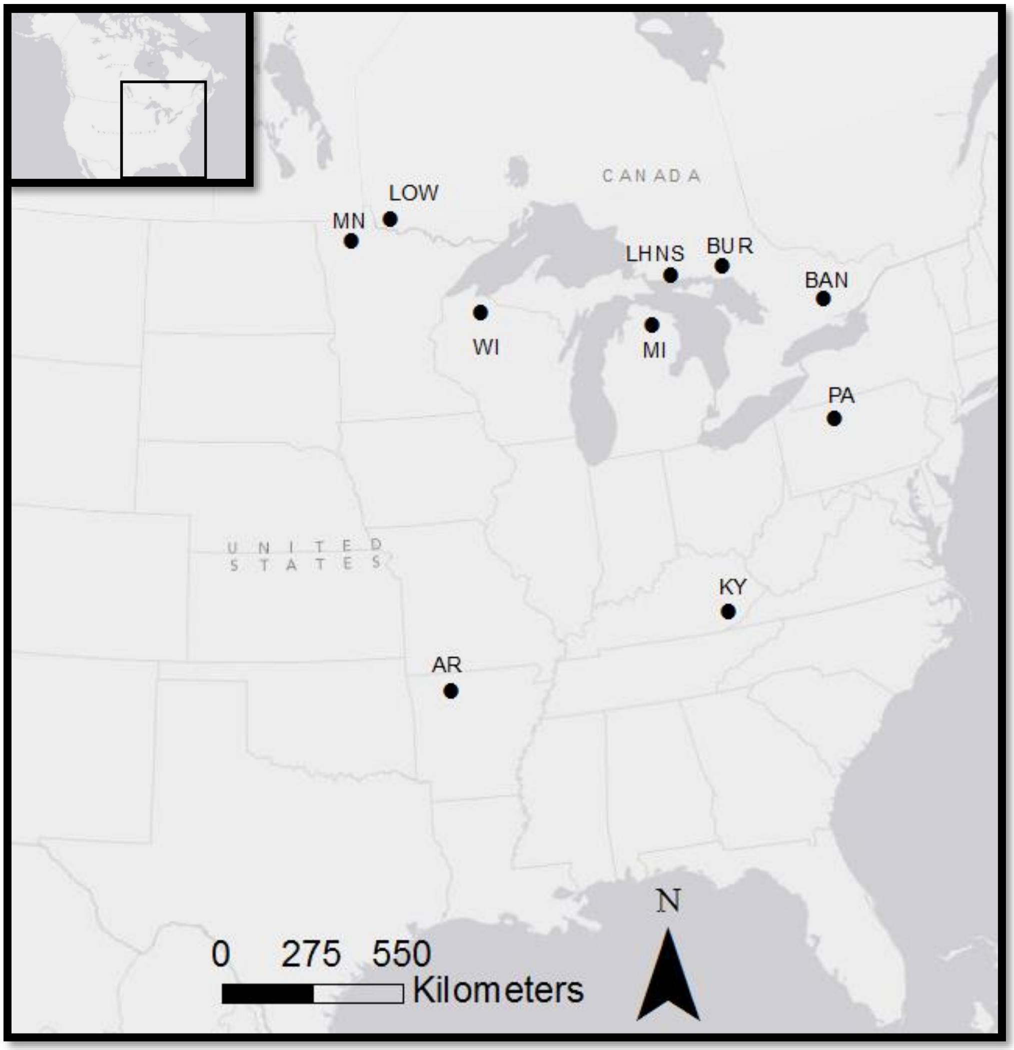


Fig 1. Distribution map for ten reintroduced elk populations in eastern North America. AR = Arkansas; BAN = Bancroft; BUR = Burwash, KY = Kentucky; LHNS = Lake Huron-North Shore; LOW = Lake of the Woods; MI = Michigan; MN = Minnesota; PA = Pennsylvania; WI = Wisconsin.

Table 1. Elk populations and corresponding release years, exponential rates of increase (r) and covariate data used in model selection analysis.

Population	Release Yrs	r	Initial	Deer[2]	Moose[2]	Wolf	NPP	Snow[3]	Decid[4]	Grass-Crop[4]	Conif[4]
KY	1997-2002	0.16	1547	4.0	0.00	0	999	0.8	94	3	3
BAN	2000-2001	0.13	120	3.5	0.15	1	772	12.0	69	5	2
LHNS	2001	0.12	47	3.5	0.25	1	760	33.5	41	10	6
WI	1995	0.09	52	8.0	0.01	1	724	38.9	35	0	55
AR	1981-1985	0.06	226	9.5	0.00	0	1051	0.8	99	1	0
PA	1913-1926	0.04	560	7.0	0.00	0	831	5.0	98	1	0
BUR	1998-2001	0.03	129	3.5	0.35	1	725	28.0	21	6	19
MN[1]	1914	0.03	28	8.0	0.01	1	740	42.0	19	71	0
MI	1914-1915	-0.02	900	15.0	0.00	0	795	22.0	39	4	42
LOW	2000-2001	-0.05	104	3.5	0.35	1	781	30.7	0	1	76

[1]Grylga Herd. [2]Density (/km^2) (median value if data was collected as a range); [3]Depth (cm); [4]Percent of elk population range. AR = Arkansas; BAN = Bancroft; BUR = Burwash, KY = Kentucky; LHNS = Lake Huron-North Shore; LOW = Lake of the Woods; MI = Michigan; MN = Minnesota; PA = Pennsylvania WI = Wisconsin.

I calculated exponential rates of increase for each elk population using the annual population estimates provided by regional elk managers. As elk populations were reintroduced, density-dependence was not expected over the time frames considered. Exponential rates of increase ($r = \ln[(N_{t+1} + H_t)/N_t]$: where N_t is population size at time t, N_{t+1} is the population size at time $t+1$ and H_t is the number of elk harvested at time t) were calculated using the slope of the line after plotting the natural logarithm population estimates over time. Population estimates were of elk in their core range from 2001 or 2002 to 2013. Five of the 10 populations had final reintroductions in 2001 or 2002 whereas the remaining populations were reintroduced prior to that time (Table 1). To note, 6 populations were legally harvested during the assessment period, including AR, BAN, KY, MI, MN, and PA.

I used the calculated exponential growth rate over time (one value for each population; $N = 10$) as my dependent variable. I evaluated the possible role of several covariates based on literature reviews that I hypothesized could explain variation in population growth rate. Model selection of linear models using AIC_c (Burnham and Anderson 2002) was used to identify the most important predictor variable(s). Specifically, I hypothesized that land use composition, initial population size, snow depth, parasitism, the presence of predators, and the presence of competitors would influence elk population growth rates (Table 1).

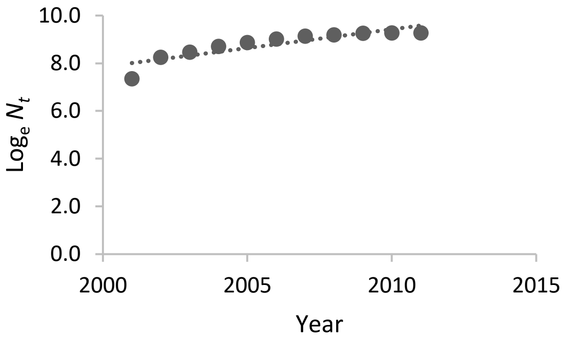
I incorporated habitat variables known to be selected for or avoided by elk and overlapped the range of each elk population onto a Land Cover Map of North America for the year 2000 (GLC 2000-NCA) with 1 km resolution (Latifovic et al. 2002; 2004) to determine the proportions of cover types in each range. Elk are known to select for deciduous forest habitats (Bobek et al. 1984; McCorquodale 2003; Jenkins et al. 2007; Popp et al. 2013) as well as areas abundant with forbs and grass (Collins and Urness 1983; McIntosh 2003; Anderson et al. 2005; Creel et al. 2005). Based on this, I hypothesized that these cover types (deciduous forest, grasslands and croplands) would positively influence elk population growth rates. The land cover covariates Ianticipated would have a positive effect on elk population growth rate included (1) percent range in broadleaved deciduous forest (Decid); and (2) percent grassland with or without a sparse tree layer combined with mosaics of cropland or other natural vegetation which I combined as one covariate because the grassland cover class alone only comprised 0-2% of each elk herd range (Grass-Crop). Additionally, because elk in eastern North America use coniferous habitats significantly less than expected (Popp et al. 2013; McGeachy 2014) as well as forage on coniferous species significantly less than expected (Jost et al. 1999; Jenkins et al. 2007), I predicted that (3) percent coniferous forests (Conif) would negatively affect elk population growth rates. I also predicted that (4) summed annual Net Primary Productivity (NPP) would have a positive influence on population growth rate. As such, NPP was included as a covariate. I used data from the year 2000 GloPEM (Global Production Efficiency Model) with 8 km resolution (Prince 2003) to calculate the mean pixel values of the raster file for each elk range. As predation is a leading cause of mortality in several reintroduced eastern elk populations (Popp et al. 2014), I incorporated (5) the presence or absence of wolves *Canis lupus* (Wolf) (density estimates not available). Additionally, although the degree of competition between moose (*Alces alces)* and elk has been suggested to be minimal, there is some habitat selection overlap in winter (OMNR 2010). Thus I hypothesized that (6) moose density (Moose) would influence elk population growth rates through direct or indirect competition (Data sources: USA: regional elk managers; Canada: OMNR 2007 Combined Harvest Data). Where density estimates were given as a range (ie: ±), the median values were used in my analysis. White-tailed deer, *Odocoileus virginianus*, are competitors with elk, especially during mild winters (Jenkins et al. 2007), as well as reservoir hosts for meningeal worm, a parasite that causes lethal neurological disease in elk (Anderson et al. 1966; Anderson 1972) which has been suggested as the cause of many early elk reintroduction failures (Raskevitz et al. 1991; O'Gara and Dundas 2002). I incorporated (7) white-tailed deer density (Deer) (Data sources: USA: regional elk managers; Canada: OMNR 2009 Cervid Ecological Framework). Because severe winters are well known to influence ungulate survival (Singer et al. 1997; Smith et al. 2003; Evans et al. 2006), I incorporated (8) average seasonal (December to February) snow depth (Snow) from 1980 to 2010 (Data sources: USA: National Weather Service; Canada: Environment Canada). Finally, because founding population size is known to affect reintroduction success (Griffith et al. 1989), I used (9) the initial elk population size (Initial) in year 2001 (or 2002 if data for 2001 was not available).

Predictor variables with positive or negative correlation ($|r| > 0.50$) were not used in the same candidate model. I limited the number of variables in each candidate model to 1-2 due to small sample size. The software “R” was used to perform statistical analysis by linear models using the function “lm”. In addition, I calculated the coefficient of determination for the top linear model. Because I incorporated 5 elk populations that had reintroductions completed in 2001 or 2002 (BAN, BUR, KY, LHNS, LOW) with 5 populations that were reintroduced prior to that (AR, MI, MN, PA, WI), I also calculated the coefficient of determination for the top model using only the 5 recent reintroductions for comparison purposes. In addition, because there was variation among ecoregions in the assessed populations, after identifying the top candidate model I calculated the coefficient of determination for populations that occupied the Northern Forest ecoregions (BAN, BUR, LHNS, LOW, MI, MN, PA, and WI). All 10 populations were maintained in the majority of analyses to improve sample size.

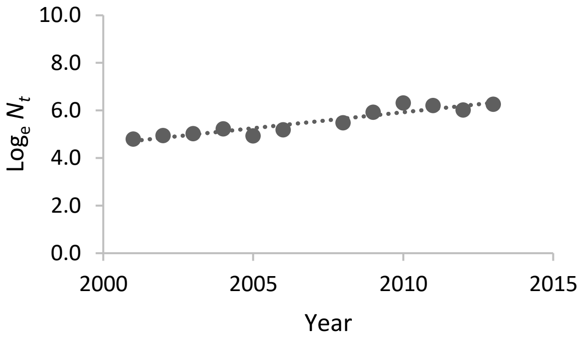
Results

The exponential rates of increase from 2001 (or 2002) to 2013 varied from -0.05 to 0.16 (Table 1; Fig 2). The model that best explained elk population growth rates among populations was the “Conif” candidate model where a negative relationship was found between population growth rate and the percentage of coniferous forest within elk range (Table 2; Fig. 3). The “Conif” candidate model was 1.3 times (0.31/0.24) more likely than the candidate model with the second highest weight, deciduous forest, and approximately 3.4 times more likely than the model ranked 3rd, deer density, which had considerably less support ($\Delta i > 2$).

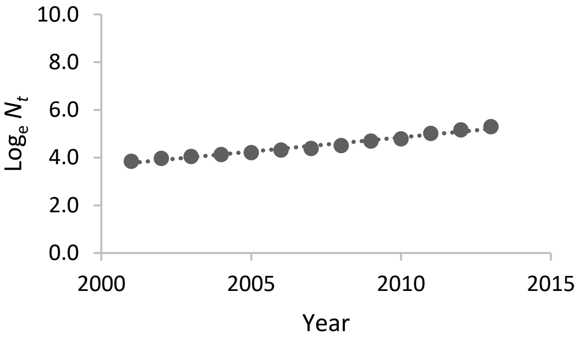
KY



BAN



LHNS



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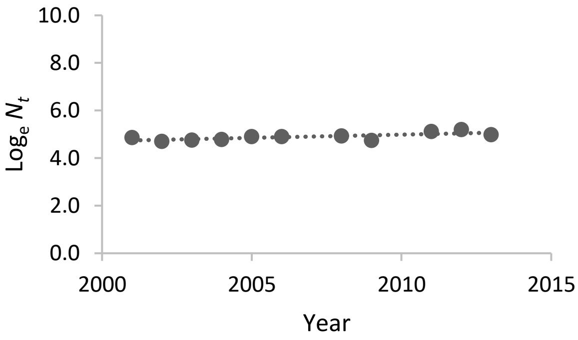
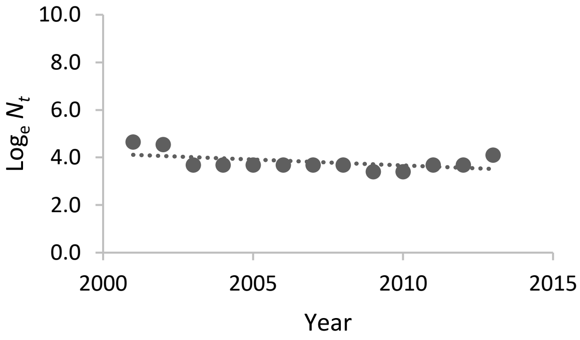
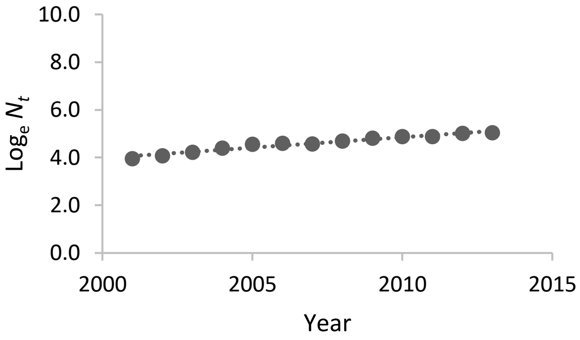


LOW



WI



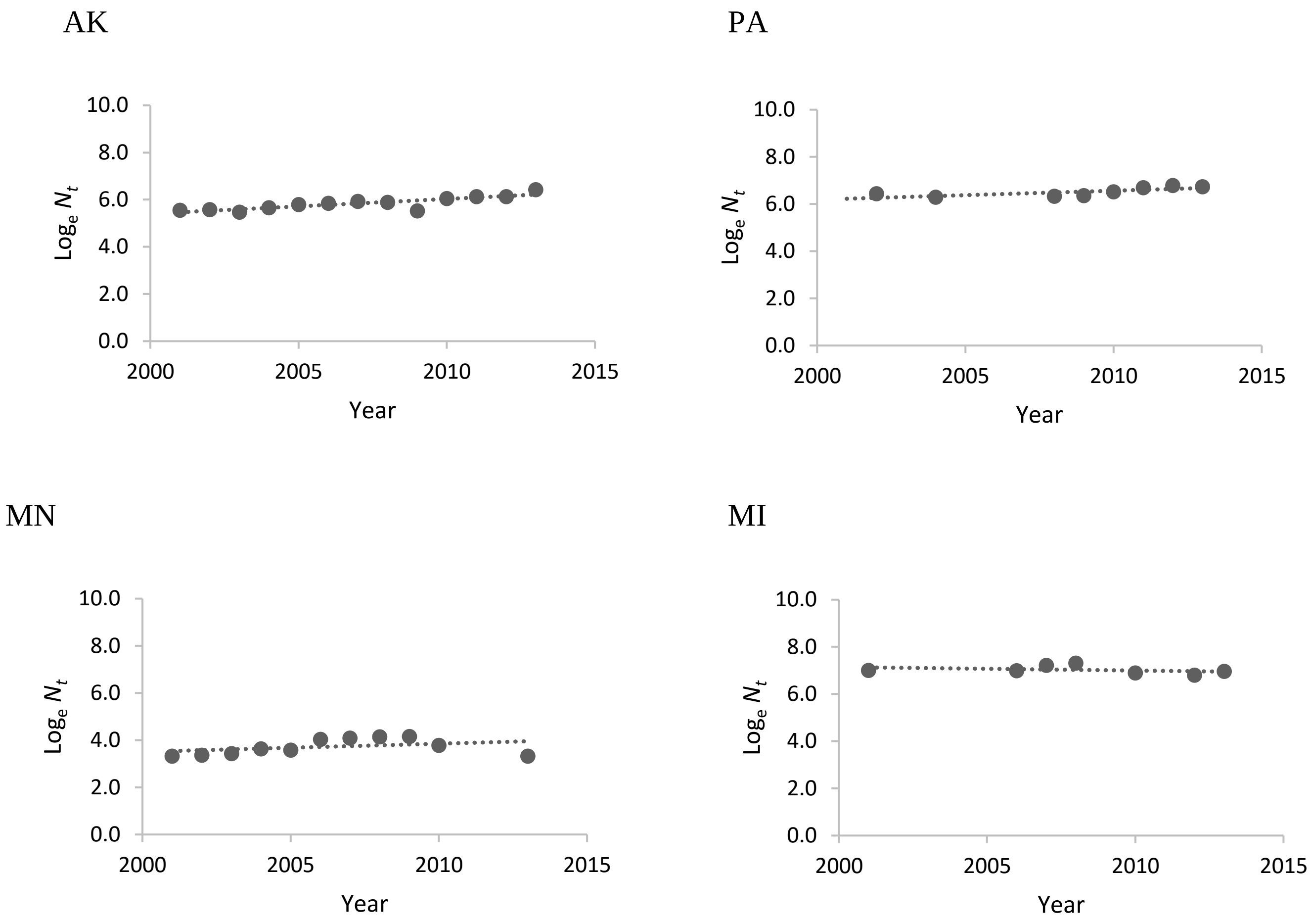


Fig 2. Natural logarithm of reintroduced elk populations estimates in eastern North America during from 2001 (or 2002) to 2013. AR = Arkansas; BAN = Bancroft; BUR = Burwash, KY = Kentucky; LHNS = Lake Huron-North Shore; LOW = Lake of the Woods; MI = Michigan; MN = Minnesota; PA = Pennsylvania; WI = Wisconsin. **NB: Figures adapted from Popp et al. (2014).*

Although elk populations occupied two major ecoregions in my study, the Northern Forest ecoregion (8 of 10 populations) and the Eastern Temperate Forest ecoregion (2 of 10 populations) (Commission for Environmental Cooperation 2006), and plant species data were not available in the coniferous forest class, the relationship of this forest type with elk population growth rates was similar when comparing populations that occupied the Northern Forest ecoregion (BAN, BUR, LHNS, LOW, MI, MN, PA, WI; R^2 = - 0.31) and all populations (R^2 = - 0.33).

Although the confidence intervals for the "Conif" model slightly overlapped zero (Table 2), when I compared the 5 populations that were recently reintroduced (2001 or 2002) to all of the elk populations with available data, I found that the inverse relationship between elk population growth rate and coniferous forest was much stronger (R^2 = - 0.86).

Table 2. Relative support for all candidate models tested with model-averaged coefficients and statistics of covariates explaining variation in population growth rates for reintroduced elk in eastern North America.

							95% Confidence Intervals	
Model Description	K	AIC_c	Δi	w_i	β	Standard Error	Lower	Upper
$\beta_0 + \beta_1$(Conif)	3	-20.94	0.00	0.31	-0.0014	0.0007	-0.0030	0.0002
$\beta_0 + \beta_1$(Decid)	3	-20.46	0.48	0.24	0.0010	0.0005	-0.0002	0.0023
$\beta_0 + \beta_1$(Deer)	3	-18.57	2.37	0.09	-0.0071	0.0057	-0.0200	0.0059
$\beta_0 + \beta_1$(Snow)	3	-17.90	3.04	0.07	-0.0012	0.0015	-0.0045	0.0022
$\beta_0 + \beta_1$(NPP)	3	-17.64	3.30	0.06	0.0002	0.0002	-0.0003	0.0006
$\beta_0 + \beta_1$(Moose)	3	-17.44	3.50	0.05	-0.1093	0.1516	-0.4522	0.2336
$\beta_0 + \beta_1$(Initial)	3	-17.41	3.53	0.05	0.0000	0.0000	-0.0001	0.0001
$\beta_0 + \beta_1$(Crop-Grass)	3	-16.96	3.97	0.04	0.0002	0.0011	-0.0023	0.0027
$\beta_0 + \beta_1$(Wolf)	3	-16.82	4.12	0.04	-0.0017	0.0457	-0.1050	0.1017
$\beta_0 + \beta_1$(Conif) + β_2 (Initial)	4	-15.29	5.65	0.02				
$\beta_0 + \beta_1$(Conif) + β_2 (Snow)	4	-14.99	5.95	0.02				
$\beta_0 + \beta_1$(Crop-Grass) + β_2 (Deciduous)	4	-14.54	6.40	0.01				

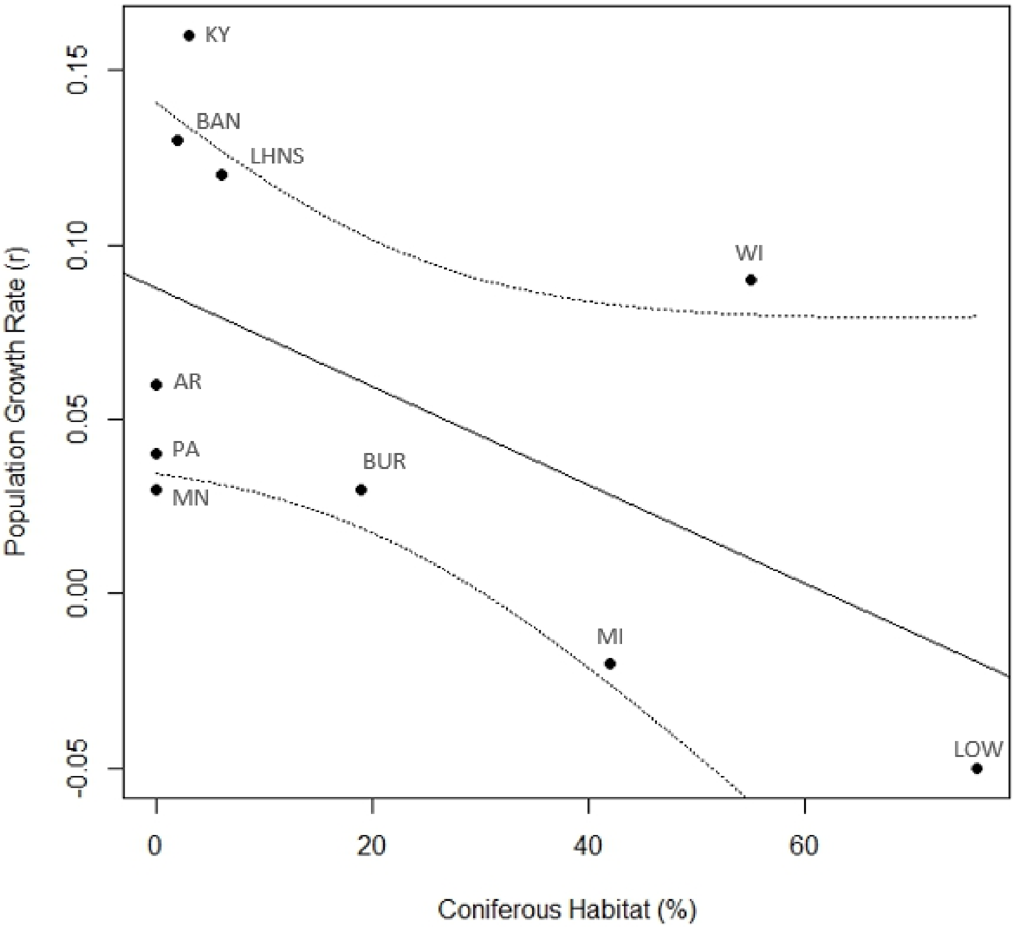


Fig 3. Exponential rates of increase of reintroduced elk populations in eastern North America (*N* = 10) in relation to the percentage of coniferous forest habitat in each elk regional range. Dashed lines are 95% confidence intervals. AR = Arkansas; BAN = Bancroft; BUR = Burwash, KY = Kentucky; LHNS = Lake Huron-North Shore; LOW = Lake of the Woods; MI = Michigan; MN = Minnesota; PA = Pennsylvania; WI = Wisconsin.

Discussion

The importance of maintaining positive population growth rates ($r > 0$) during animal restorations has been reported previously (Conard et al. 2010). Small populations are at greater risk of becoming even smaller because a myriad of stochastic events can significantly reduce population viability (Boyce 1992). Therefore, increasing small founding population size as quickly as possible may be a vital component of reintroduction success. My analyses revealed that coniferous forest had the most important inverse relationship to reintroduced elk population growth rates in eastern North America. This relationship was even stronger when I examined only recently reintroduced populations, suggesting that sub-optimal habitat also influences elk during the first years following reintroduction.

Several past attempts to reintroduce elk to portions of eastern North America resulted in failure apparently due in part to lack of appropriate habitat (Witmer 1990), however, no empirical studies have been conducted to support this suggestion. Elk often select deciduous forest communities (Bobek et al. 1984; Schroer et al. 1993; Jenkins et al. 2007; Popp et al. 2013) within close proximity of other plant communities such as meadows and grasslands (Collins and Urness 1983; Peck and Peek 1991; Anderson et al. 2005; McGeachy 2014). Similar to western populations, elk populations in eastern North America primarily graze on forbs, grasses, and sedges, but browse from deciduous trees and shrubs are also important dietary components especially when herbaceous vegetation becomes unpalatable or unavailable due to snow accumulation or other changes in environmental conditions or seasons (Jost et al. 1999; Schneider et al. 2006; Jenkins et al. 2007). In winter, Jenkins et al. (2007) found that quaking aspen (*Populus tremuloides*) was most preferred in south central Ontario, while Jost et al. (1999) found that big-tooth aspen (*Populus grandidenta*), white birch (*Betula papyrifera*), red maple (*Acer rubrum),* pin cherry (*Prunus pensylvanica*), willow (*Salix* spp.), bush honeysuckle (*Diervilla lonicera*), and beaked hazel (*Corylus cornuta*) were consumed significantly more than available in north central Ontario. In Kentucky, the most important browse species were flowering dogwood (*Cornus florida*), autumn-olive (*Elaeagnus umbellate*), black locust (*Robinia pseudoacacia*) and maple (*Acer* sp) (Schneider et al. 2006). In Pennsylvania, elk also selected quaking aspen, autumn-olive, and flowering dogwood as forage in addition to eastern hemlock (*Tsuga canadensis*), willow (*Salix* sp), and oak (*Quercus* sp) (Heffernan 2009). In contrast to deciduous forests, reintroduced elk in eastern North America used coniferous forest habitats such as stands dominated by red (*Pinus resinosa*) and white pine (*Pinus strobus*) significantly less than expected (Popp et al. 2013; McGeachy 2014), and foraged on coniferous plant species less than expected based on availability (Jost et al. 1999; Jenkins et al. 2007). Jenkins et al. (2007) found these selective patterns in elk during the two years immediately following reintroduction illustrating non-random behaviour in a novel environment.

While my analyses revealed an inverse effect of coniferous forest on elk population growth rate, it is important to recognise that the availability of some forests and shrubland communities are known to benefit elk. For example, wooded areas are used by elk for protective cover and rest sites (Creel et al. 2005; Marcum 1975; Irwin and Peek 1983) and it is well known that edge habitat is important to elk (Skovlin et al. 2002). Elk population dynamics, predator composition, landscapes and habitats, and causes of elk mortality differ substantially between eastern and western North America (Keller et al. 2015) and in light of this, the importance of coniferous forests for elk across landscapes may differ. Thus, although coniferous forest may provide some benefits to elk, large patches comprising large proportions of elk ranges in eastern North America may reduce foraging opportunities, which is thought to be the most important driver of elk habitat selection (Beck et al. 2006). Future elk reintroductions in eastern North America should avoid targeting areas dominated by coniferous forest.

Griffith et al. (1989) found that if animals were reintroduced into areas with good to excellent habitat, 69-84% of reintroductions succeeded, whereas if released into poor-quality habitats, only 38% succeeded. Although Witmer (1990) suggested that elk reintroductions in the east were less successful than in the west because there was less high-quality habitat and higher human densities, Michigan elk calves had the highest recorded survival rates in North America and it was suggested that habitat, not predators, had greater influence on recruitment (Bender et al. 2002). Good habitat may lead to better physical condition of elk (DeVivo et al. 2011), resulting in higher survival rates and if elk cannot find adequate forage, the effects on productivity and survival could be detrimental (Cook et al. 2002; Noyes et al. 2002). Poor-quality habitats have been shown to negatively affect other ungulate species also. For example, with decreasing forage quality and/or quantity in sub-optimal habitat, woodland caribou (*Rangifer tarandus caribou*) may not sustain the required levels of body fat to be able to conceive, maintain embryos or sustain adequate lactation (Brown and Mallory 2007).

Although studies of reintroduction success using a single population approach contribute to viable management strategies, the comparison of factors related to growth rates of multiple populations can be helpful for understanding factors that influence success rates. In support of past suggestions, I found that habitat was the most important predictor of elk population growth, where an increase in sub-optimal habitat (coniferous forest) led to decreased elk population growth rates. Armstrong and Seddon (2007) suggested that meta-analyses should play a significant role in future restoration ecology research involving assessments of reintroduction success and my study supports this conclusion. The growing need for species restoration and presently available results of various reintroduction studies warrant the use of multi-population studies and meta-analyses to enhance management strategies and future reintroduction efforts.

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Chapter 4

Railway Ecology: Underrepresented in Science?*

Abstract

Over the past two decades, the effects of roads on wildlife have been extensively studied. Theoretically, railways cause similar effects as well, yet ecologists do not understand the magnitude of these effects. Despite the field of road ecology rapidly expanding and the large footprint created by railways, there is a prominent lack of research related to railways and their effects on wildlife. To emphasize gaps between road and railway wildlife studies, I performed a thorough systematic review of 14 peer-reviewed journals in which ecologists and conservation biologists commonly publish. I found a clear underrepresentation of railway studies despite the potential negative ecological effects associated with this important anthropogenic feature. I found 259 road-wildlife articles and only 17 railway-wildlife articles in the journals I assessed with the majority of road studies focused in North America and the majority of railway studies in Europe. Although road-wildlife studies have increased through time, railway-wildlife studies have remained stagnant. In my opinion, the development of research pertaining to 'Railway Ecology' is long overdue.

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Introduction

Over the past two decades the effects of roads on ecological processes have been extensively studied (Rytwinski and Fahrig 2015). Roads have been identified as a substantial threat to mammals (Benítez-López et al. 2010; Beyer et al. 2013), birds (Benítez-López et al. 2010; Kociolek et al 2011), herpetofauna (Beebee 2013; Gibbs and Shriver 2005), pollinators (Baxter-Gilbert, et al. 2015), non-pollinating insects and other invertebrates (Muñoz et al. 2014), as well as plants (Lee et al. 2012). Roads affect fauna directly through habitat fragmentation (Jackson and Fahrig 2011) and road mortality (Beebee 2013; Jackson and Fahrig 2011), as well as indirectly via noise (McClure et al. 2013; Ware et al 2015), light (Gaston et al. 2013) and chemical pollution (Dananay et al. 2015), fluctuation in stress response (Owen et al. 2014), and even as a source of microevolution (Brown and Bomberger Brown 2013). Railways have also been shown to cause some of these effects (Waller and Servheen 2005; Bartoszek and Greenwald 2009; Dorsey 2011); however, a very limited understanding exists in relation to the magnitude of such effects.

Habitat loss and degradation are considered leading causes of wildlife population decline (Brooks et al. 2002; Gibbons et al. 2000). The effects of roads however are far greater than the habitat loss associated solely with its sizable footprint. When adjacent road-effect zones are included into models, the ~4 million km linear footprint of roads in the United States is dwarfed by the approximately 2.1 million km^2 of habitat (22% of the contiguous United States) which is directly affected by roads (Forman 2000). This effect is stronger in rural areas versus developed areas (Forman 2000), suggesting that wildlife would experience disproportionately large effects, despite lower traffic volume (Laurance et al. 2014). As such, I argue that the construction of linear features such as roads and railways represent one of the most significant anthropogenic alterations to the planet's ecosystems. Worldwide, there are approximately 42 million km of paved roads (Dulac 2013). Recent research interest in this area has led to the creation of a relatively new field of biology known as "Road Ecology" (Forman 2003) with focus not only on the effects of roads on wildlife but the mitigation of those effects. Railways have an approximately 1 million km footprint worldwide, and although road length is substantially greater, the railway footprint is estimated to rise 45%, while paved roads are expected to increase by only 36% by 2050 (Dulac 2013). That being said, the underrepresentation or importance of railway-wildlife research in science should not be decided based upon differences between the linear footprints of railways and roads, but based on the apparent lack of railway ecology research in general, especially since the magnitude of railway effects are not yet understood.

Just as roads have been documented to, railways are likely to influence many species of wildlife. Many species have been identified as victims of wildlife-train-collisions including birds, reptiles, and mammals (van der Grift 1999; Dorsey 2011; Heske 2015). Wildlife-train-collisions can cause substantial declines in populations. For example, in Alaska there was a 35% reduction of a moose (*Alces alces*) population due to several factors including poor winter survival, car collisions and hunting, but train collisions accounted for more than 60% of mortalities during the winter of 1989 to 1990 (Becker and Grauvogal 1991). In Norway, a rate of 0.36 moose per year per km were killed on a 240 km stretch of railway totalling 86 moose per year (Gunderson and Andreassen 1998). Rea et al. (2010) suggested that moose are trapped by deep snow along railbanks and therefore cannot easily escape pursuing trains. The effects of wildlife-train-collision mortalities can be amplified even further if wildlife species that are gregarious in nature travel along a railway. For example, elk (*Cervus elaphus*), a reintroduced species in eastern North America, were monitored from 2002 to 2015 in Ontario and were often killed by trains during the winter where several animals travelling together died in one instance (Popp, *in prep*; Fig. 1). To compound this threat, high-speed rail networks are expected to increase (Dulac 2013), which may lead to an increased rate of collision, further putting wildlife populations at risk.

In addition, significant economic loss can be associated with wildlife-train-collisions. As proposed with roads, the economic loss associated with a deer-vehicle-collision, excluding automobile-specific costs (eg: vehicle damage and insurance), can be approximately $2000 USD (Huijser et al. 2008) and in Norway, the benefit of preventing a single moose-train-collision is approximately $3170 USD including train-specific costs (Jaren et al. 1991). Although these costs are not directly comparable because automobile-specific costs are considerably more expensive, these figures demonstrate significant economic value in preventing wildlife-vehicle collisions, with respect to both automobiles and trains. Further, these numbers are likely conservative as they do not represent the ecosystem services provided by these animals, a metric which is undetermined for many species.

Fig. 1. Train collision induced elk mortalities (Photo credit: D.N.C. McGeachy).

Despite the field of road ecology being rapidly expanded (van der Ree et al. 2011) the recognition for the need of rigorous study designs (Lesbarrères and Fahrig 2012), as well as the development of global road building strategies (Laurance et al. 2014), railways, which affect wildlife in similar and sometimes more impactful ways, receive limited attention from researchers (Dorsey et al. 2015). While both roads and railways have the ability to serve as barriers and sources of mortality to wildlife, the strength of effects on wildlife may differ between infrastructure types. Road surfaces are very different than railway surfaces. Such differences may result in species-specific attractions or repulsions. Similarly, the sound and scent emanating from each form of infrastructure cannot be considered equal. In addition, traffic volume and speed likely differ among roads and railways. Behavioural differences among wildlife species in proximity to either roads or railways could account for variation in mortality rates and landscape connectivity patterns. While it may seem simple to group linear infrastructure together, especially those that produce similar effects, doing so will not provide an accurate representation of said effects. The objective of this article is to highlight the lack of railway-wildlife research in science as well as to identify the gaps between road and railway wildlife studies. In my opinion, the development of research pertaining to '*Railway Ecology*' as a branch of Transportation Ecology, is long overdue.

Methods

To emphasize the lack of research with focus on railways in comparison to roads, as well as to identify gaps among road and railway studies, I performed a thorough systematic review (using both publisher websites and Google Scholar) of 14 peer-reviewed journals where ecologists and conservation biologists commonly publish with a wide scope of impact factors (ISI Impact Factor range (2014): 1.61 – 5.06), and in my opinion, representative samples, namely: Animal Conservation, Basic and Applied Ecology, Biological Conservation, Conservation Biology, Ecography, Ecological Applications, Ecological Modelling, Ecology and Society, Journal of Applied Ecology, Journal of Environmental Management, Journal of Wildlife Management, Landscape Ecology, PlosONE, and Transportation Research Part D: Transport and Environment. I used the keyword search terms: “railroad*”, “railway*”, “road*” and “highway*” and I only included articles published between 1990 and 2014. Prior to 1990, while several important pieces of research exist (Mader 1984; McLellan and Shackleton 1988), publications rates for both road and railway ecology were relatively low and thus for the sake of this review were excluded. The resulting articles were reviewed to ensure relevance as unrelated research articles were often produced by the search engines. I only included articles in which research was related to the effect of a road or railway on wildlife or research related to the mitigation of road or railway effects on wildlife. Taxa included in the search were restricted to herpetofauna, mammals, and birds, as these were most abundant in a preliminary review of the literature. Geographic location (continent and/or country) of the study site was also noted. The focus and main finding of each railway related article was also noted. Reviews as well as studies that focussed on the potential and unexamined effects of roads or railways were not included.

Results

In total there were 259 road-wildlife articles and 17 railway-wildlife articles which represents approximately 15 times more road than railway studies published. Of the 14 journals I reviewed, Biological Conservation and the Journal of Wildlife Management yielded the greatest number of publications (Fig. 2). While the number of studies focused on roads has steadily increased since 1990, the number of studies investigating the effects of railways has remained stagnant (Fig. 3). Roads or railways were most studied with respect to their effects on mammals (53.3% and 68.4% respectively), followed by herpetofauna (24.9% and 15.8% respectively) and birds (21.8% and 15.8% respectively) (Table 1). The majority of mammal studies were focused on large mammals, mainly ungulates and bears. The continent with the most road site publications was North America while Europe (Spain) produced the most railway publications (Table 2). It should however be noted that all journals that I assessed, although international, may represent a biased sample. Smaller national journals or journals not published in English may have road and railway specific research published in them at rates differing from the data I present here. Approximately 24% of railway studies and 15% of road studies focused on mitigating negative effects on wildlife, while the remainder gathered baseline information about the effects of roads or railways on wildlife with the study focus area and main findings varying substantially among articles (Table 3). Although the railway-wildlife studies included in my survey had a broad range of focus areas encompassing both basic and applied (ie mitigation) science, each area was poorly represented. Because a minimal number of railway-wildlife studies existed in general, specific focus areas lacked substantial attention.

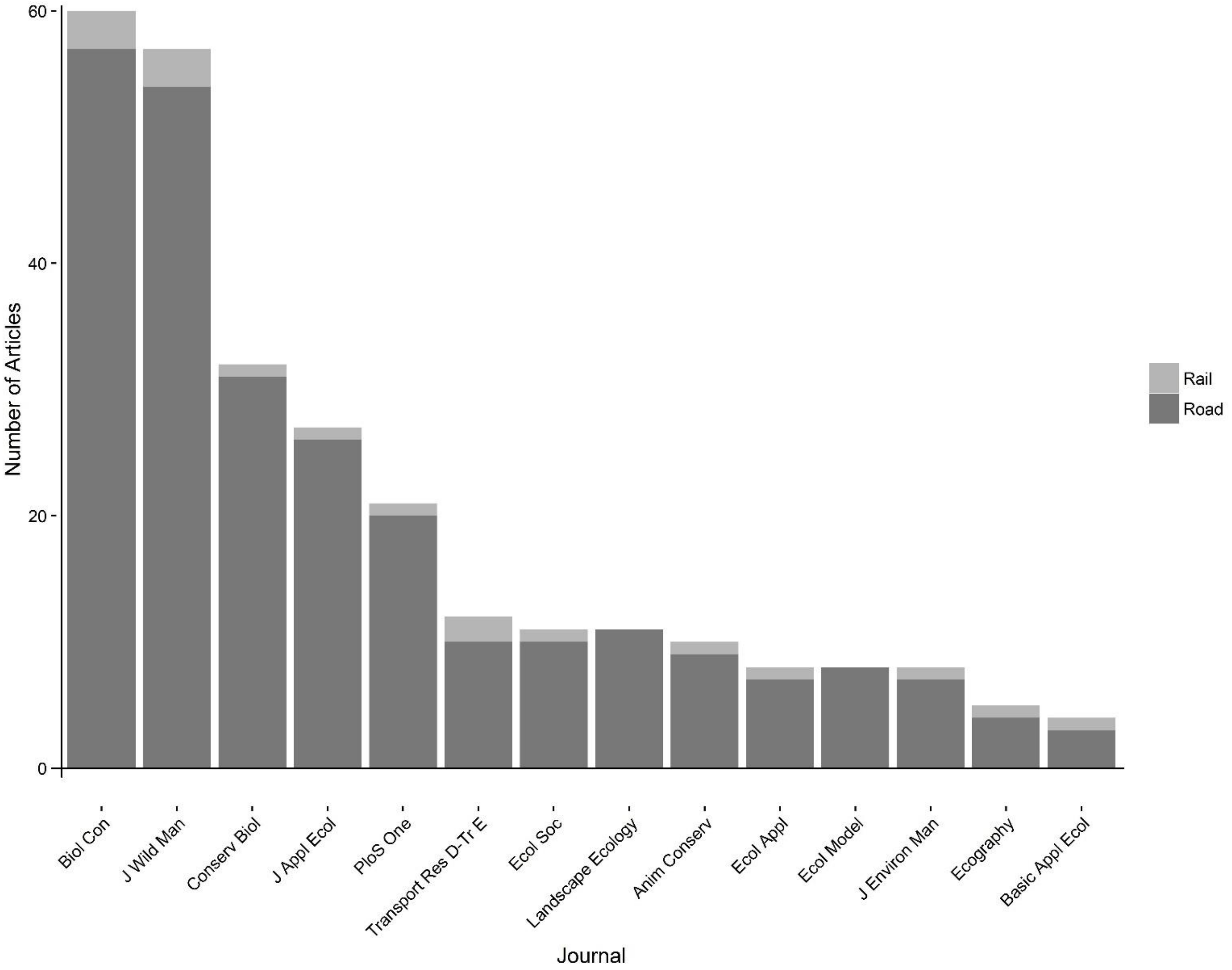

Fig. 2. The number of railway and road related research articles published in each of 14 ecology and conservation journals from 1990 to 2014.

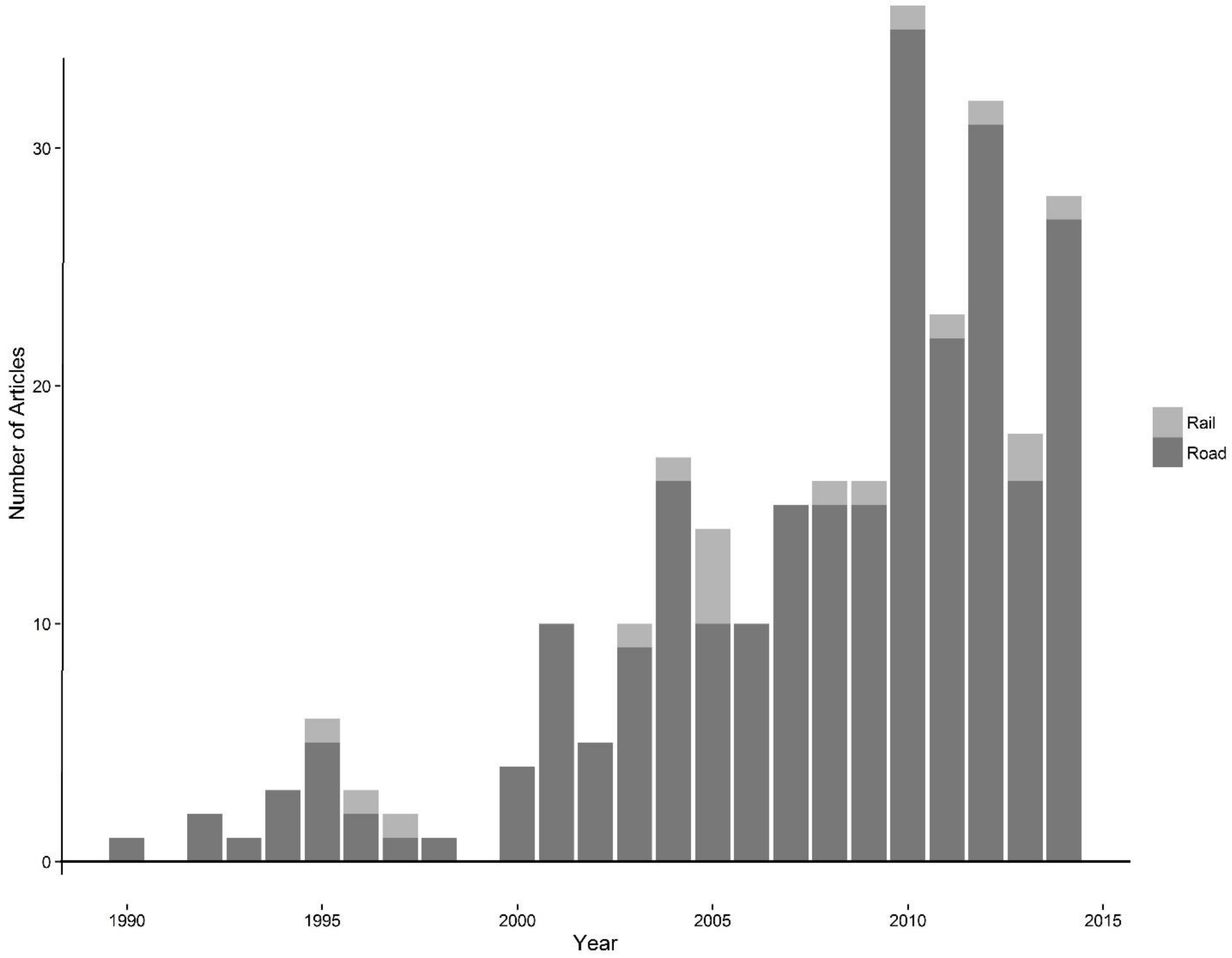

Fig. 3. The number of railway and road related research articles published in 14 ecology and conservation journals per year from 1990 to 2014.

Table 1. The number of road (railway) related research articles published with respect to taxon focus. *NB. Some articles had a multi-taxa focus.*

	Taxa			
Journal	Mammals	Birds	Herps	*Total*
Anim Conserv	3 (1)	3 (0)	4 (0)	*10 (1)*
Basic Appl Ecol	3 (1)	0 (0)	0 (0)	*3 (1)*
Biol Conserv	31 (2)	16 (0)	18 (1)	*57 (2)*
Conserv Biol	14 (1)	12 (0)	12 (0)	*31 (1)*
Ecography	3 (1)	0 (0)	1 (0)	*4 (1)*
Ecol Appl	3 (1)	1 (0)	3 (0)	*7 (1)*
Ecol Model	7(0)	1(0)	0(0)	*8(0)*
Ecol Soc	5(1)	1(0)	4(0)	*10(1)*
J Appl Ecol	14 (1)	8 (1)	4 (1)	*26 (2)*
J Environ Manage	4 (0)	1 (0)	3 (1)	*7 (1)*
J Wildl Manage	38 (3)	5 (0)	13 (0)	*54 (3)*
Landscape Ecol	7 (0)	2 (0)	2 (0)	*12 (0)*
PLoS One	13 (1)	6 (0)	3 (0)	*20 (1)*
Transport Res D-Tr E	7 (0)	6 (2)	4 (0)	*10 (2)*
Total	*152 (13)*	*62 (3)*	*71 (3)*	*259 (17)*

***Total column represents the number of articles without duplication.*

Table 2. The number of road and railway research articles with respect to study continent and country (if greater than 3 publications). **NB. One article focused on Canada and USA.*

Continent	Country	Road	Railway
Africa	Other	3	0
Asia	Other	7	5
Australia	Australia	20	0
Europe	Spain	16	4
	Netherlands	9	0
	France	6	1
	Norway	6	1
	United Kingdom	5	0
	Other	27	2
North America	USA	96	1
	Canada	54	3
	Other	2	0
South America	Other	8	0

Table 3. Outline of the focus and main findings of each railway-wildlife ecology research article included in my survey.

Authors	Year	Taxa	Focus	Main finding
Mateo-Sánchez et al.	2014	Mammals	Landscape connectivity	Landscape features highly constrain connectivity
Ito et al.	2013	Mammals	Landscape connectivity	Railways and international borders act as barriers to ungulates
Clauzel, Girardet, & Foltête	2013	Herpetofauna	Railway effect zone	Largest impacts seen within 500 m of railway, but smaller impacts detected up to 3500 m away
Hepenstrick et al.	2012	Mammals	Genetic connectivity	Unfenced railways have no effect on genetic connectivity
Ge, Li, Li, & Huang	2011	Birds	Effects on vigilance	Railway and highway affects bird vigilance behaviour
Li et al.	2010	Birds	Species richness and abundance	Bird species richness and abundance were greater closer to railway and highway than further away
Tremblay & St. Clair	2009	Birds	Landscape connectivity	Railways are the most permeable of linear features tested for songbirds
Ito et al.	2008	Mammals	Mortality rates	Mortality rates vary between side of tracks as well as regionally
Ito et al.	2005	Mammals	Landscape connectivity	Railways act as a barrier despite higher quality habitat
Andreassan et al.	2005	Mammals	Reducing railway mortality	Forest clearing and supplemental feeding reduce railway mortality
Waller & Servheen	2005	Mammals	Crossing rates	Railway crossing rates are higher when traffic volume is higher
Whittington, St. Clair, & Mercer	2005	Mammals	Movement ecology	Wolves select areas within 25 m of roads, trails and rails
Whittington St. Clair, & Mercer	2004	Mammals	Movement ecology	Wolves cross roads and rails less than expected by random, and have higher avoidance for high volume trails

Kaczensky et al.	2003	Mammals	Landscape connectivity; Mortality	Transportation features are a boundary but not an absolute barrier; Road and railway related mortality
Rodriguez, Crema, & Delibes	1997	Mammals	Crossing structure usage (not designed for wildlife)	Cover in and around the entrance of crossing structures related to increases in wildlife use
Rodriguez, Crema, & Delibes	1996	Mammals + Herpetofauna	Crossing structure usage (not designed for wildlife)	Structure location with respect to habitat was most influential factor associated with wildlife usage
Yanes, Velasco, & Suarez	1995	Mammals + Herpetofauna	Culvert usage	Properly designed culverts can aid conservation

Discussion

Railways: an underappreciated threat?

The linear footprint of railways is relatively small in comparison to roads (~1:42; Dulac 2013); however, situations exist in which roads have been shown to be more ecologically damaging than railways, and vice versa. For example, wildlife road mortality has been shown to be greater on both roads (Heske 2015) and railways (Becker and Grauvogal 1991). Further, the size of the global railway network is expected to increase due to its reduced requirement for carbon based energy sources (Dulac 2013). While environmentally this may prove to be valuable, we still know very little about the effects railways have on wildlife. Both basic and applied research regarding the effects of railways on wildlife exist; however, among the journals assessed, only 6% of road- and railway-wildlife studies were focused on railways. Among the small number of railway-wildlife articles, study focus areas differed substantially, suggesting that although some progress is being made in this branch of ecology, abundant information is lacking with respect to all ecological areas. With respect to railways, applied research has focussed on assessing mitigation of wildlife-train-collisions with strategies consisting of wildlife crossing structures, supplemental feeding stations, altered habitat, exclusion systems, and train speed reduction (Dorsey et al. 2015). While mitigation of wildlife-train-collision is important, other negative effects may exist and the gap in my knowledge regarding basic ecology hampers my ability to mitigate these potential threats effectively. Movement ecology and landscape connectivity are better represented than other fields, but research focussed on mitigation and especially on population level effects are very limited. Due to this limited scope of research, my general understanding of complex interactions occurring across the landscape is hindered.

In my review, mammals were the most studied taxon with respect to both roads and railways followed by birds and herpetofauna. Other taxa, although not included in this study, would likely demonstrate similar trends regarding road and railway wildlife research. The majority of railway related mammal studies were focussed on ungulates (33%) (Andreassan et al. 2005; Hepenstrick et al. 2012; Ito et al. 2005, 2008, 2013) and bears (25%) (Kaczensky et al. 2003; Mateo-Sánchez 2014; Waller and Servheen 2005). Many large mammal species have economic importance as tourist attractions or harvestable resources; however human safety has undoubtedly played a role in the proliferation of road ecology research on mammals (Huijser et al. 2008). In comparison to wildlife-vehicle-collisions, human injuries are likely to occur much less frequently in wildlife-train-collisions which may contribute to the lack of railway ecology research.

In contrast to large mammals, small mammals and other taxa have received relatively little attention in terms of wildlife-railway research (but see van der Grift 1999). Railways have been noted to trap and potentially lead to overheating of smaller vertebrates between the tracks (Kornilev et al. 2006). Railways may also act as an ecological trap if mortality occurs, as for example, several species of freshwater turtle are attracted to railway beds in order to nest (Ernst and Lovich 2009). During ecological surveys, small animals are likely less detectable than large mammals due to their size, the potential for deflection into the adjacent habitat, and because they are likely more easily removed by scavengers. These potential limitations likely contribute to the relative rarity of railway studies involving small animals. The effects of railways can be evaluated using techniques other than visual monitoring, which could be especially helpful in relation to small mammal research. For example, the use of telemetry, genetics, and adjacent habitat surveys can inform my understanding of the spatial ecology, population diversity and demographics, as well as sub-lethal effects associated with railways. Studies that focus on smaller taxa, especially those that are species at risk, or have important ecological roles, may be critical to conservation initiatives.

Investigating the effects of railways on multiple species or taxa is especially important because as with roads (Carr and Fahrig 2001; van der Grift et al. 2013), the effects of railways should not be generalized among species. For example, railways have been shown to act as barriers to some species of wildlife (i.e.: Marbled salamanders (Bartoszek and Greenwald 2009); Mongolian gazelles (Ito et al. 2013)), while others utilize railways as corridors, especially during seasonal migration when snow depths increase (i.e.: moose (Andreassan et al. 2005); moose, elk, deer (Rea et al. 2010)).

Advancing railway ecology

Due to the theoretical overlap between road and railway ecology, many of the lessons learned by road ecologists can be applied to railway research. The development of baseline understanding is critical for mitigation success (Lesbarrères and Fahrig 2012; Rytwinski et al. 2015). Railway Ecology poses several unique difficulties which need to be overcome in order to advance as a branch of Transportation Ecology. Railway studies are under-developed likely due in part to a lack of related available funding (Dorsey et al. 2015). As stated previously, the desire to ensure human safety in the event of wildlife-vehicle collisions likely warrants additional funding for road related research (Huijser et al. 2008). In addition, due to railway locations often being uneasily accessed, railway mortalities are rarely viewed by the public, reducing the potential for public concern, and thus political will. Further, the difficult to access nature of many railways increases the difficulty of data collection. Many monitoring methods used by road ecologists can be readily adapted to railway studies. For example, trail cameras (Mann et al. 2015; Rowcliffe and Carbone 2008; Rowcliffe et al. 2014) or snow-tracking are reliable methods used to observe mammal distributions in road ecology projects (Alexander et al. 2005; Alexander 2008). To access more remote regions of railways, collaboration with railway companies may allow for transportation arrangements (e.g.: hi-rail passenger railway vehicle).

Arguably the most important step in advancing railway ecology is to engage cooperation with railway companies or owners as permission and safety training is often required to access railway properties. Access to private lands is not an uncommon consideration when designing experiments in nature. The difficulty arises when experiments are directly aimed (or are perceived to aim) at identifying negative effects of private landowner activities, because such studies could lead to increased environmental regulation and eventual loss of income. Benefit to public image may be enough in some situations to warrant cooperation with companies, especially in highly lucrative endeavours (i.e. resource extraction). However, in areas where public image is not necessarily an important factor (i.e. railways), strategies for conservation based on incentives for private landowners to set independent conservation practices have been a popular approach (Merenlender et al. 2004). It is critical to the advancement of railway ecology that as scientists we use the scientific method properly. Vilifying the effects of railways may be counterproductive to increasing research along railways in situations where landowners want to avoid additional regulations. Rather, investigating effects, whether good or bad (roads have been shown to benefit some wildlife – see: Rytwinski and Fahrig 2012, 2013), and developing an understanding of the complex interactions railways have with wildlife should be the main goal.

Conclusion

Railways facilitate a well-established mode of transportation and will have a substantially increased world-wide footprint in the near future. The effects of railways on wildlife are poorly understood. Although lessons learned from road ecology can shed some light on the form these effects may take, their magnitude remains uncertain. The underrepresentation of railways in both basic and applied research has given rise to only a limited understanding of the baseline ecology of wildlife near railways. This vague baseline makes the planning and implementation of responsible and informed development including mitigation, much more difficult. The inability to address such effects may have profound repercussion on wildlife populations, especially in relation to species in need of conservation. Although ecologists may be faced with many challenges in developing wildlife-railway research programs, it is essential, and possible, that these issues are overcome. By further developing '*Railway Ecology*' ecologists can focus on this immense worldwide footprint and potentially enormous magnitude of impacts on wildlife. In my opinion, it is time we start addressing this issue.

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Chapter 5

Railway mortality of reintroduced elk: an assessment of spatial, temporal, and environmental influences

Abstract

Human infrastructure affects wildlife in many ways and has led to world-wide habitat loss and degradation, which are leading causes of wildlife population decline. Understanding the effects of railways on wildlife, an aspect of ecology that is highly underrepresented in science, is a crucial component of the development of management and conservation strategies. Wildlife-train collisions have resulted in the deaths of many species and gathering baseline information is imperative to the development of effective mitigation, especially for at-risk or small reintroduced populations such as elk in eastern North America. Train collisions are the greatest known source of mortality for a small isolated elk population in Ontario, Canada. I used a combination of radio-telemetry and remote camera surveys to investigate spatial relationships between railways and elk. Elk were closer to the railway in winter than in any other season. Cows (with or without calves) and yearlings of both sexes were found directly on the railway in most seasons, but utilized the railway most frequently during the spring and fall. Bulls were only found on the railway during summer. Elk-train collisions were highly site-specific, significantly closer to the apex of bends in the railway than random locations along the railway, and collision rates were positively related to snow depth. Railways may be perceived by elk as easy travel corridors, and deep snow likely prohibits escape from oncoming trains. My study gathered important

information about an under-studied aspect of wildlife-human conflicts and provides a basis for the investigation of other species that may be affected by railways.

Introduction

Global areas that harbour significant regions of species diversity are often favoured by humans, creating land use conflict, one of the most important challenges for conservation biologists today (Balmford et al. 2001a,b; Luck et al. 2004). Human infrastructure affects wildlife in several ways and has led to population declines of many species world-wide through habitat loss and degradation (Gibbons et al. 2000; Brooks et al. 2002). Direct and indirect effects of human infrastructure can have a variety of influences on many species of wildlife. For example, in addition to roads directly affecting wildlife through fragmenting habitat (Jackson and Fahrig 2011), vehicle collision mortality is common (Beebee 2013; Jackson and Fahrig 2011). Indirect effects of roads on wildlife are extensive and include examples such as noise (McClure et al. 2013; Ware et al. 2015), chemical (Dannay et al. 2015), and light pollution (Gaston et al. 2013).

Of the many human infrastructures known to adversely affect wildlife populations, impacts associated with railways are one of the least studied, especially in comparison to the effects of roads on wildlife (Popp and Boyle 2017). Railways have a worldwide footprint of approximately 1 million km which is predicted to rise 45% by 2050 (Dulac 2013). It is important that ecologists increase their focus on investigating the potential effects of railways on wildlife in order to ensure adequate management and conservation, especially for species at risk or small populations.

Many species of wildlife have been victims of train collisions while using railways (Gundersen and Andreassen 1998; van der Grift 1999; Bertwhistle 2001; Andreassen et al. 2005; Iosif 2012; Kusta et al. 2014; Dasgupta and Ghosh 2015). Such mortalities can have severe impacts on animal populations. For example, during the winter of 1989-1990 the moose (*Alces alces*) population in lower Susitna Valley, Alaska, was reduced by 35% due to a combination of poor winter survival, car collisions, hunting, and railway mortalities, where train collisions alone accounted for approximately 60% of investigated mortalities (Becker and Grauvogel 1991). Railway effects on wildlife can be highly species-specific. For example, railways can be beneficial to some species such as moose, allowing for easier travel, especially in winters with great snow depth (Andreassan et al. 2005; Rea et al. 2010), while for other species such as Marbled salamanders or Mongolian gazelles, railways can act as a barrier to movement (Baroszek and Greenwald 2009; Ito et al. 2013).

Although not yet investigated, reintroduced species may be particularly vulnerable to the effects of railways. Translocations are often restricted to a small number of individuals, which may become at risk if further reduced in size, potentially leading to significant impacts of stochastic events (Gilpin and Soulé 1986). Monitoring programs that identify and quantify causes of mortality for small populations are necessary in order to gather baseline information and to design mitigation strategies for ensuring that population sizes increase to sustainable levels. Given the impacts railways may have on wildlife, as apparent from the limited number of studies available, further monitoring the effects of railways on wildlife populations is warranted.

Elk are a native species in North America, which were extirpated from most of their range during the 19th century, and have since been reintroduced in several locations over the past century (Popp et al. 2014). Although several reintroduced elk populations thrive, others are struggling to increase growth rates (Popp et al. 2014). The Burwash elk population in Ontario, Canada was first reintroduced in the 1930's (Ranta 1979). A remnant population of 40-50 animals was boosted by 172 elk imported from Elk Island National Park, Alberta between 1998 and 2001 (Popp et al. 2014, Rosatte et al. 2007). The current population estimate is approximately 150 individuals and train collisions are one of the leading causes of mortality (Popp et al. 2014). It is not well understood under what conditions and how frequently elk use railways throughout the year. The timing and locations of elk-train collisions are also of interest.

I investigated the effects of railways on elk to better understand how this human-based infrastructure impacts local populations and to develop science-based recommendation for mitigating elk-train collisions. I focused on the spatial, temporal, and environmental components related to the effects of railways on elk by investigating 1) the importance of railways as a source of mortality for elk; 2) the influence of season on the proximity of elk to the railway; 3) the existence of elk-train collision spatial hotspots; and 4) the effects of weather and topography on collision rates.

Methods

Study area

The study area consisted of the Burwash elk core population range in Ontario, Canada, which encompassed approximately 20 km of railway. The area was situated in the Great Lakes-St. Lawrence Ecotonal Forest Region (Rowe 1972) comprised mainly of mixed conifer-hardwood forest (Chambers et al. 1996). Topography was characteristic of Precambrian Shield and included rugged outcrops, valleys, and many water bodies including marshes, swamps, and bogs/fens (Popp et al. 2013). In addition, open abandoned fields; remnants of a historical correctional facility/industrial farm were present throughout the study area. Climate in the region was continental with average winter snow depth of 28 cm (Environment Canada Historical data: mean of December to February 1981-2010).

Elk mortality

Annual causes of elk mortalities were documented from 2002 to 2015 for elk fitted with VHF radio-collars (Lotek Engineering LMRT 4 with motion sensitive mortality sensors) and for non-collared elk, documented opportunistically. In addition, every March or April from 2002 to 2015, subsequent to snow thaw, winter elk-train collision mortalities were counted and the locations recorded along a 20 km stretch of railway that bisects the elk core population range. During the survey, observers walked the railway and recorded new carcasses or body parts found. In addition, railway workers randomly called in mortalities that had been discovered opportunistically. In total, 189 elk mortalities from all investigated sources were recorded over 14 years.

Elk seasonal proximity to railway

In order to determine if elk proximity to the railway differed among seasons, 12 female elk previously fitted with VHF radio-collars (Lotek Engineering LMRT 4 with motion sensitive mortality sensors) were tracked 1 – 3 times per week from 2012 to 2014 from the ground with a Lotek SRX 400 telemetry receiver. To reduce triangulation error, at least three compass bearings were obtained for each elk location from various high points within the elk population range (White and Garrot 1990). Because elk are gregarious in nature, I used the software "Association" (Weber et al. 2001) to ensure individual movements were independent from each other. Parameters were set to consider females associated (or non-independent) if they spent more than 60% of their time within 250 m of one another. Seasons were defined based on elk behaviour where "Winter" included the months of January to March, "Spring" included April to June, "Summer" included July to September, and "Fall" included October to December (Popp et al. 2013). I calculated the mean distance of each elk during each season to the railway using ArcGIS v.10.1. I used a repeated measures ANOVA and a post-hoc Tukey HSD test to determine if elk were significantly closer to the railway in any particular season.

Elk railway usage

From the beginning of July 2015 to the end of June 2016, 10 trail cameras were placed along the 20 km stretch of railway bisecting the elk range, one every 2 km, attached to trees growing alongside the railway and directly facing the railway. Cameras were set to record a burst of 3 images when motion was detected and were set to stop recording images for 5 minutes after the initial burst to prevent an excess of train photos. Camera batteries and cards were replaced every 1-3 months depending on the season. Because elk are gregarious in nature, regardless of the number of elk in an image, one photo was considered a single elk capture event and the total number of bull or cow (with or without calves or yearlings) capture events were documented per season. To reduce the chance of resampling the same animals, capture events within one hour from the initial capture were not included.

Elk-train collisions: mortality hotspots, topography, and weather

I used the program SIRIEMA v 1.1.0 (SIREMA 2011) and elk-train collision data from 2002-2015 to conduct Linear Hotspot Identification analyses using Ripley K-Statistics to identify elk-train collision hotspots (areas where collisions occurred more often than expected). This software, has been used for road hotspot identification (Coelho et al. 2012; Teixeira et al. 2013), but has not yet been applied to railway hotspots to my knowledge. I examined the number of hotspots using two approaches: 1) Kill Events: all elk mortalities involved in a specific incident were reported as a single event for analytical purposes (gregarious nature predisposes elk to multiple kills at one location), and 2) Number of Kills (Kills): the number of elk mortalities arising from each event at a particular location were used to gain a better understanding of where single-event losses would most impact the elk population.

From personal observations over time, elk kill events appeared to cluster around bends in the railway, therefore a t-test was performed to determine if elk kill events were significantly closer to the apex of bends of <135 degrees than an equal number of random points along the railway (N = 44). Because trains travel only in a north-to-south direction along this section of railway, the distance to the northernmost bend apex was calculated.

To determine if elk-train mortality was correlated with winter weather conditions, the number of elk mortality events was related to the mean monthly snow depth and the mean temperature over the months of December to February (Environment Canada Historical Data) using regression analyses. All statistical analyses were conducted using the ‘R’ statistical software v.3.0.1 (R Core Team 2013).

Results

Elk mortality

The greatest source of elk mortality since the most recent reintroduction were train collisions. Although the proportion of mortality due to train collisions ranged from 0 to 100% of annual losses, the mean percentage of train collisions was greatest in comparison to all other causes of mortality (Table 1).

Table 1. The percentage of cause-specific mortalities in the Burwash elk population from 2002 to 2015 and the total number of investigated elk mortalities (N).

Year	Drown	Train	Vehicle	Predation	Other	N
2002	0	44	11	44	0	18
2003	0	0	0	40	60	5
2004	33	0	0	67	0	3
2005	67	0	0	0	33	3
2006	48	39	4	4	4	23
2007	33	33	0	17	17	6
2008	0	100	0	0	0	1
2009	7	73	0	10	10	30
2010	18	36	18	18	9	11
2011	0	38	25	25	13	8
2012	18	18	27	27	9	11
2013	0	70	10	15	5	20
2014	0	60	7	20	13	15
2015	9	18	0	27	45	11
Mean (SE)	17 (6.1)	39 (8.5)	8 (2.7)	22 (5.3)	13 (4.6)	

Elk seasonal proximity to railway

None of the 12 tracked, radio-collared elk had associated movements with one another at the set parameters (250 m, 60% of the time) so all were utilized in subsequent analysis with their movements considered independent. Elk proximity to the railway varied significantly among seasons ($F_{3, 33} = 31.06$, $p = 0.001$). In winter, elk were significantly closer to the railway than in summer, spring, or fall (All seasons: $p < 0.001$) (Fig 1).

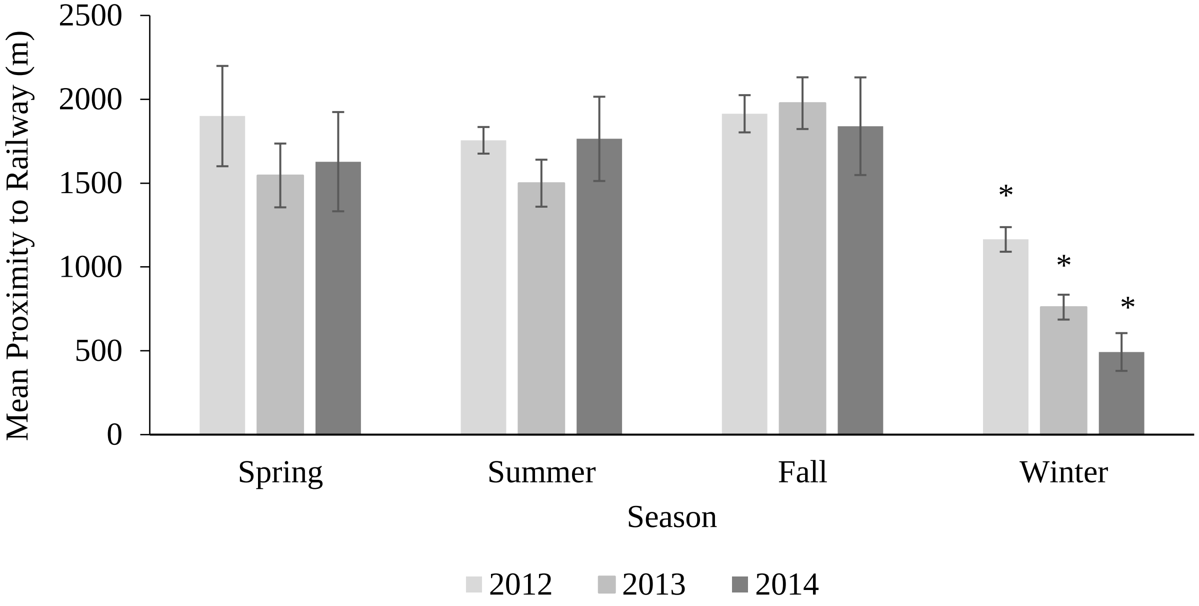


Fig 1. Mean seasonal and annual distances (m) of elk to the railway (+/- standard error).

**Represents significant difference from all other seasons in respective year.*

Elk railway usage

Elk were captured on the railway by digital trail cameras 17 times. Elk used the railway in all seasons; however, most instances were documented in the spring and fall (Table 2). The majority of captured usage events were of cows (with or without calves) or yearlings (N= 15 of 17); however, bulls utilized the railway as well (N = 2 of 17) in the summer. There were no instances of elk appearing on more than one camera in the same day.

Table 2. Total number of cow (with or without calves or yearlings) and bull trail camera capture events from 10 cameras set up along a 20 km stretch of railway bisecting the elk range.

Sex	Spring	Summer	Fall	Winter
Bull	0	2	0	0
Cow	7	0	7	1
All	7	2	7	1

Elk-train collisions: mortality hotspots, topography, and weather

In total, 67 elk-train collision mortalities (Kills) were recorded over the 14-year survey period, resulting in 44 mortality event locations (Kill Events) that varied geographically (Fig 2). Upon examining elk kill events, I found 5 hotspots, most adjacent to each other and within a 2 km span of one another (Fig 3a). When considering the number of elk that died during each kill event (Kill Events), I found 7 hotspots spread over approximately 5 km (Fig 3b) with the majority of "Kills" hotspots overlapping the "Kill Event" hotspots (Fig 2). The majority of hotspots were located along bends in the railway section that was monitored (Fig 2). "Kill Event" locations were significantly closer (1358 m +/- 186 m) to the apex of bends ($\leq$135 degrees) than were random locations (3800 m +/- 627 m) along the railway ($p < 0.001$).

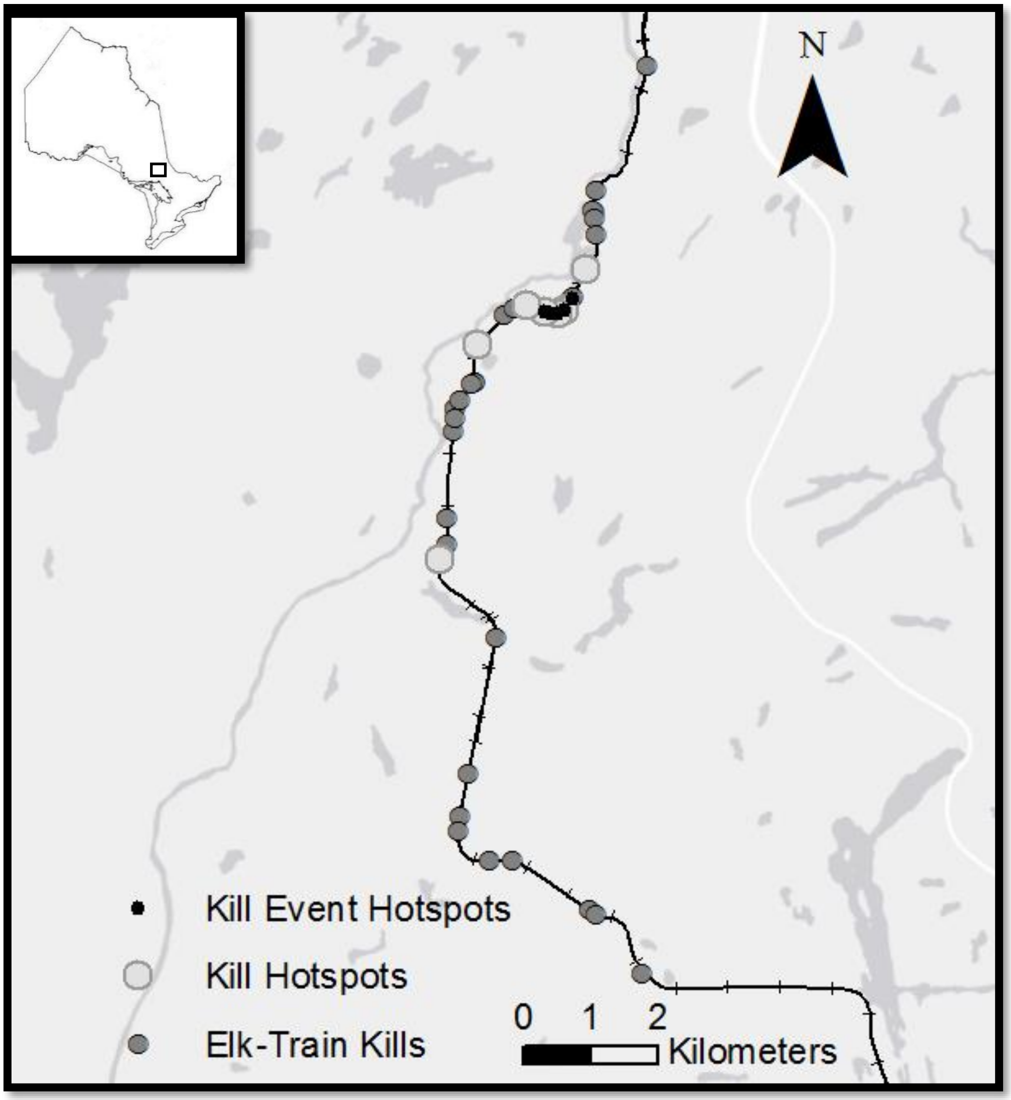
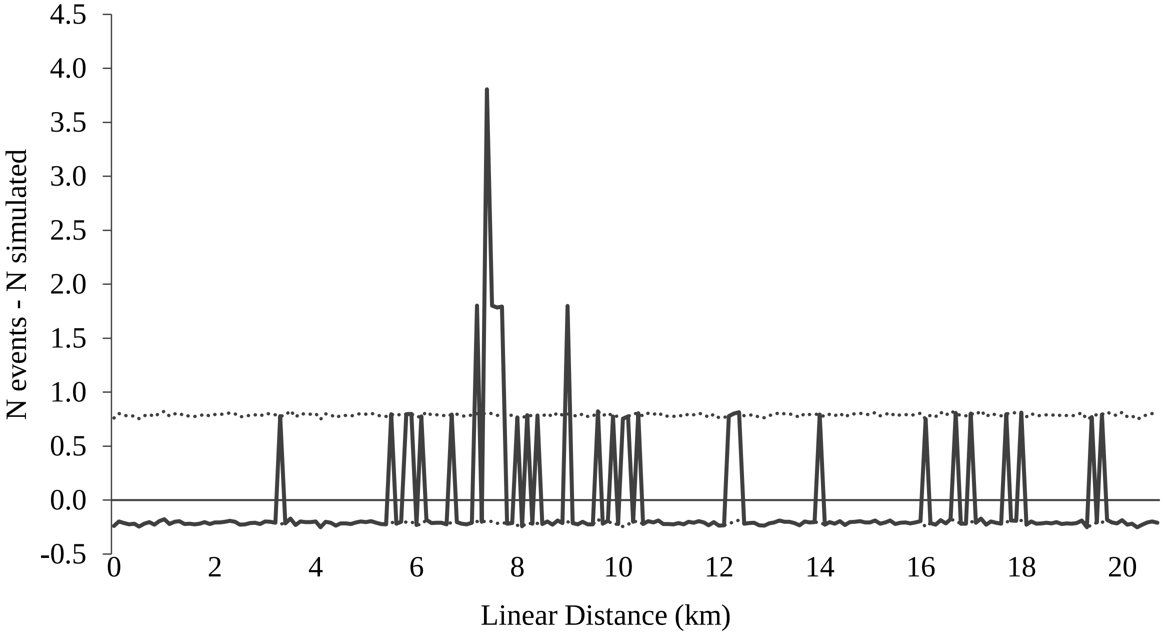


Fig 2. Elk-train kill sites, "Kill Event Hotspots", and "Kill Hotspots" (includes number of elk that died during each event) locations from 2002 to 2015 along the railway bisecting the Burwash, Ontario elk core range (n = 67 mortalities, 44 mortality events).

a)



b)

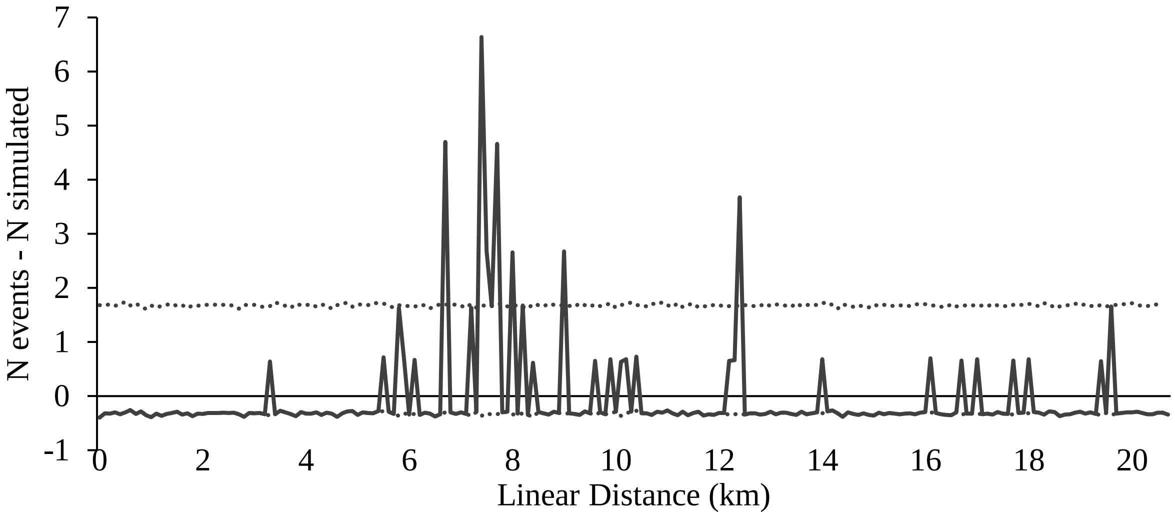


Fig 3. Location of elk-train collision mortality hotspots at various distances from the northern end of the studied railway section (approx. 20 km) using a) elk-train kill event locations (Kill Events) and b) elk-train kill locations (Kill: includes number of elk that died during each kill event). Dashed lines are 95% confidence intervals.

There was no correlation found between the mean winter temperature and the number of elk train-kill events over 14 years ($R^2 = 0.009$, $p = 0.75$); however, there was a strong polynomial relationship found between the mean snow depth (December to February) and the number of elk train-kill events per year ($R^2 = 0.71$, $p = 0.001$; Fig 4) where "Number of Kill Events = 4.52 - 0.56 (Mean Snow Depth) + 0.023 (Mean Snow Depth)^2".

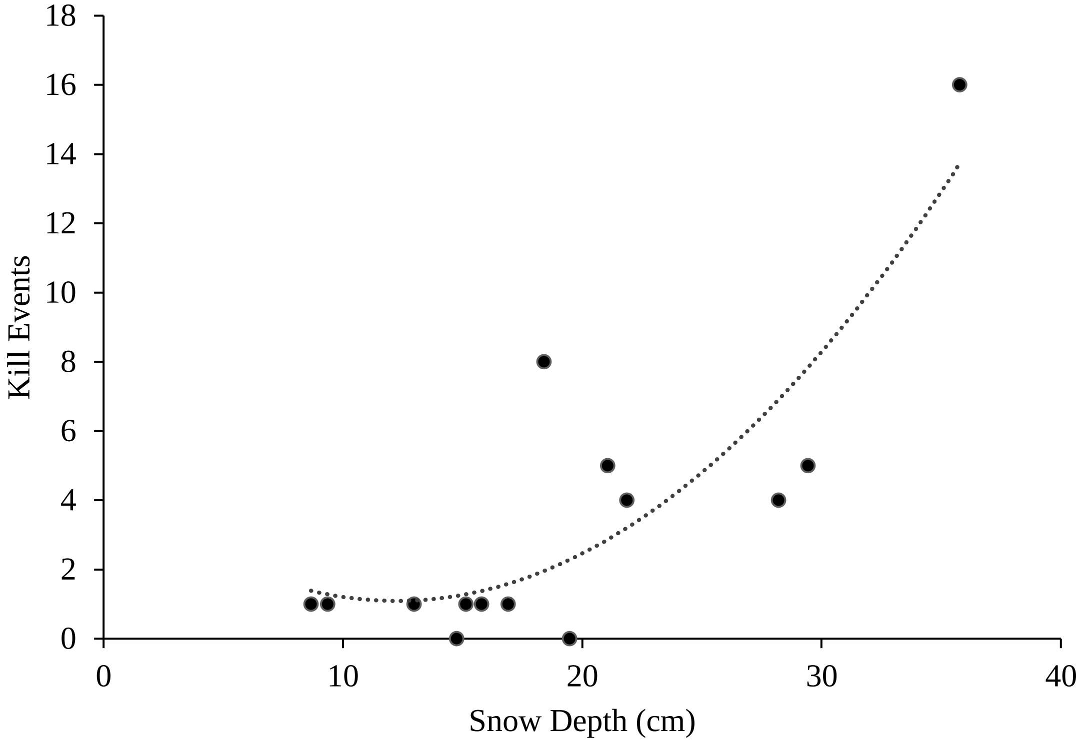


Fig 4. The number of elk-train collision kill events per year (n = 14 years) in relation to the mean snow depth (cm) (December to February) along a 20 km stretch of railway bisecting the Burwash, Ontario elk core population range.

Discussion

Train collisions were the greatest source of mortality for the Burwash elk population since the recent reintroduction 15 years ago. I found prominent trends in temporal, spatial, and environmental factors in relation to elk-railway usage, proximity, and elk-train collisions rates. Female elk were significantly closer to the railway in winter than in any other season and were found utilizing the railway most during the spring and fall. The close proximity to the railway in winter is likely an artifact of the close location of their wintering grounds to the railway. The shift in usage rates of the railway coincides with seasonal movements of elk between summer and winter ranges in the spring and fall. Similarly, in Norway, moose-train collisions occurred mainly in winter when moose migrated to winter ranges that were close to the railway (Jaren et al. 1991; Gundersen et al. 1998). Bertwhistle (2001) found that collision rates increased when other large mammals migrated to winter ranges that were adjacent to transportation corridors (i.e.: roads and railways). When migration occurs in winter and snow depths may impede movement, animals may use railways as travel routes with less physical resistance (i.e.: shallow snow) in accordance with Zipf's (1949) Law of Least Effort. Although the majority of elk I found utilizing the railway were cows (with or without calves) or yearlings, bulls were also found on the railway during the summer. Bull elk in the Burwash population utilize different regions than cows during seasons outside of the rut. My study focused on cow elk, which may explain why bulls were seldom captured on the monitored portion of railway.

Although I found elk utilizing the railway mostly in the spring and fall, I did not have the capacity to survey every section of railway and likely did not capture every usage event. In addition, my camera data were restricted to one year of sampling. Over 14 years of railway mortality monitoring, I found that the number of elk-train collisions were highly correlated with snow depth. Increased train collision rates in deeper snow conditions has been a pattern also found for moose (Gunderson and Andreassen 1998; Gundersen et al. 1998). Because I found elk utilizing railways during all seasons, I suspect that deep snow along the railway augmented by railway plowing, may discourage elk from leaving the railway when trains approach. This is a trend that has also been identified with moose (Child 1983; Muzzi and Bisset 1990). Railway footage has shown that moose followed by trains appear to be trapped by deep snow banks along the railway sides (Rea 2010).

It is well documented that elk mortality rates increase and recruitment rates and population growth decrease when snow depths increase (Garrot et al. 2003; Hebblewhite et al. 2002; Creel and Creel 2009; Johnson et al. 2013). Greater snow depths allow more opportunity for predators with light foot-loads when prey movement is restricted (Telefer and Kelsall 1984), especially when prey animals are in poor nutritional condition due to increased energy expenditure (Gese and Grothe 1995). Coupled with limited forage opportunities in winter, increased energy expenditure due to restriction of movement in deep snow is likely to leave elk seeking easy travel corridors. Increased forage opportunities along railways may also be related to increased winter train collision rates. When animal movement becomes restricted and energy expenditure approaches high levels, obtaining adequate calories is essential to survival. Jaren et al. (1991)

suggested that forage along railways seemed to attract moose, causing them to stay longer and closer to the railway.

Train collisions have been site-specific in moose (Gundersen et al. 1998) and in turtles (Iosif 2012). Elk-train collisions were highly site-specific in my study resulting in several “hotspots” generated by examining kill event locations and by including the number of elk killed during each event. There were more hotspots identified when the numbers of elk killed in each event were included. This may suggest that elk travelling in groups are sometimes restricted from escaping the railway when trains appear in certain areas. I also found that elk-train collision sites were significantly closer than random locations to the northernmost apex of bends of < 135 degrees in the railway. Because very little information exists with respect to the effects of railways on wildlife in general, we can only speculate on some of the relationships between the two. If elk using the railway are close to a bend in the railway, oncoming train detection may be limited and could potentially be the cause for the increased number of collisions that were found close to bends. By understanding where animals are likely to be affected most by trains, researchers can further investigate factors influencing kill rates and develop appropriate mitigation strategies. Having a focal point with relative predictive certainty of use would facilitate testing and speed up the development of various mitigation measures.

I highly recommend that train collision mortality be considered in all studies of factors influencing the population dynamics of wildlife. Because different species are likely to display a variety of responses to railways, I recommend species-specific studies, especially when considering species at risk or small reintroduced populations. As displayed by my example with elk, it is important to consider temporal, spatial, and various environmental aspects of railway relationships to wildlife. By determining how railways influence the dynamics of a wildlife populations and identifying factors that are related to such effects, appropriate mitigation strategies can be developed and tested.

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Chapter 6

Black bear (*Ursus americanus*) and wolf (*Canis* spp.) summer diet composition and ungulate prey selectivity in Ontario, Canada

Abstract

Understanding predator-prey dynamics is an important component of management strategy development for at-risk or declining populations that are directly affected by predation. Ungulates often serve as a significant source of prey for many large mammals, and patterns of predation are known to influence ungulate population dynamics. Although black bear and wolf diets have been investigated extensively, prey selectivity has been less commonly examined, especially in relation to ungulate juveniles. Understanding predator selectivity for ungulate species can enhance the ability of managers to develop appropriate conservation strategies for declining ungulate prey populations, as well as contribute to the general understanding of predator-prey relationships. I examined black bear (*Ursus americanus*) and wolf (*Canis* spp.) prey selectivity in Ontario based on the availability of 3 ungulate species; elk (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) within the range of the declining reintroduced Burwash elk population in Ontario. I analyzed the presence of prey items in black bear and wolf scats collected over 3 years by examining prey hair cuticular scale patterns. I related predator diet composition to the availability of ungulates, determined by fecal pellet transect surveys. In addition, non-ungulate diet items were identified to obtain full diet composition profiles for wolves and black bear. I found that black bear were opportunistic and did not select for particular ungulate species. Although moose were the more abundant ungulate

prey species in the study area, wolves selected for elk and used moose less than expected. White-tailed deer were used slightly more or less than expected depending on the predicted presence in the study area over winter.

Introduction

Understanding predator-prey relationships is important for identifying focal points for management of at-risk or declining prey populations. Although predation is considered one of the leading causes of mortality in many ungulate populations in North America (Schlegel 1976; Nelson and Mech 1986; Gasaway et al. 1992; Kunkel and Mech 1994; Murrow et al. 2009), information regarding key predator species is not always readily available to managers. When predator-prey relationships are poorly understood, uninformed management strategies may lead to wasted time and money, and potentially to unnecessary pressures on other species of wildlife. For example, in Yellowstone National Park, wolves were extirpated in the 1930s; however, in 1995 to 1996, 31 wolves were reintroduced into the park (Weaver 1978). Elk counts declined 80% within a decade of wolf reintroduction (White and Garrot 2005), a correlation with the potential to lead to negative wolf management. However, with further investigation, Barber-Meyer et al. (2008) found that bear accounted for the greatest proportion of elk calf deaths and with the incidental increase in bear numbers since wolf restoration, it was suggested that elk declines were not the result of wolf restoration alone.

Black bear (*Ursus americanus*) and wolves (*Canis lupus*) are well known as major ungulate predators across North America (Bergerud and Page 1986; Gasaway et al. 1992; Kunkel and Mech 1994; Barber-Meyer et al. 2008; Yarkovich et al. 2011; Wiwchar and Mallory 2012; Patterson et al. 2013). Although wolves have been identified as having selective diets (Fuller and Keith 1980; Carbyn 1983; Potvin et al. 1987; Wiwchar and Mallory 2012), bears in general are most often recognized as opportunistic (Bastille-Rousseau et al 2011). However, grizzly bear actively sought out elk neonates in Yellowstone National Park (Gunther and Renkin 1990). Black bear are increasingly recognized as important predators of juvenile elk (Schlegel 1976; Smith and Anderson 1998; Barber-Meyer et al. 2008; Murrow et al. 2009), moose (Franzmann et al. 1980; Ballard 1992), caribou (Mahoney et al. 1990) and deer (Conger and Guisti 1992; Vreeland et al. 2004). Diet composition has been well documented for both wolves (Fuller and Keith 1980; Potvin et al. 1987; Paquet 1992; Barja 2009; Wiwchar and Mallory 2012) and black bear (Graber and White 1983; Raine and Kansas 1990; Bull and Torgensen 2001; Mosnier et al. 2008); however, it is apparent that diet composition changes among geographical regions and with differing prey species abundances (Lamothe and Parker 1989; Wiwchar and Mallory 2012; Newsome et al. 2016). Although several studies have investigated wolf prey selection, few studies have investigated ungulate prey selection by black bear, especially in relation to juvenile ungulates. Ungulate juvenile survival is often limited by predation, with bears having large impacts during the first few weeks following parturition (Ballard et al. 1981; Adams et al. 1995; Murrow et al. 2009). Juvenile survival and recruitment are the main drivers of large herbivore population dynamics due to their inherent variability in relation to adult survival (Pimlott 1967, Galliard et al. 1998; Gaillard et al. 2000, Raithel et al 2007). Based on the large contribution of juvenile survival to ungulate population trajectories, it is crucial that wildlife managers acquire reliable information, especially before the initiation of extreme management strategies such as predator management (Barber-Meyer et al. 2008).

Elk, a common prey species for both wolves and black bear (Carbyn 1983; Mathews and Porter 1988; Barber-Meyer 2008; Murrow et al. 2009; White et al. 2010), have been reintroduced across eastern North America over the past century after being extirpated in the late 19th century (Popp et al. 2014; Hamr et al. 2016). Several of these populations have declined since reintroduction, with predation considered one of the leading causes of mortality (Popp et al. 2014). The consideration of predator-prey relationships among bears, wolves, and their prey species is an important component for developing conservation strategies for declining ungulate populations elsewhere (Barber-Meyer et al. 2008). As such, understanding predator-prey relationships for declining elk populations in eastern North America should help guide management, and also contribute to the general understanding of predator-prey relationships.

I aimed to gain insight regarding predator-prey relations within a multiple predator prey system in the Burwash region of Ontario, Canada. This region hosts a reintroduced elk population that has been in decline for several years (Popp et al. 2014). The goal of this study was to determine if black bear or wolves displayed prey selectivity based on the availability of 3 ungulate species; elk (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginanus*). I related the relative availability of the three ungulate prey species within my study area to the composition of ungulate prey in wolf and black bear diets. Additionally, non-ungulate diet items were also identified to construct more comprehensive diet composition profiles for black bear and wolves.

Methods

Study area

Elk were reintroduced into the Burwash area approximately 30 km south of Sudbury, Ontario in the 1930s and again between 1998 and 2001 (Rosatte et al. 2007; Popp et al. 2014; Hamr et al. 2016). My study area was based on the core range of the reintroduced population, which I determined by creating a minimum convex polygon around all radio telemetry locations of 23 adult females. The locations of each radio-collared female had been recorded approximately once per week from 2008 to 2011, resulting in an approximately 450 km^2 study area.

The study area consisted mainly of mixed conifer-hardwood forest of the Great Lakes-St. Lawrence Ecotonal Forest Region (Rowe 1972; Chambers et al. 1996). Topography included rugged rock outcrops, valleys, marshes, swamps, and bogs/fens typical of the Precambrian Shield (Popp et al. 2013) and maximum elevations of 300 m (Jost et al. 1999). Approximately 4000 ha of abandoned agricultural fields were present throughout the study area, along with several tertiary roads used for logging or recreational purposes. Regional climate is continental (Ranta 1979) where July, the warmest month of the year, has a 15°C mean temperature (Vankat 1979) and in January, the coldest month of the year, has a -12.5°C mean temperature (Chambers et al. 1996). The average seasonal (December to February) snow depth in the area was 28 cm from 1980 to 2010 (Environment Canada). Populations of three ungulate species were known to exist within the study area including elk, moose, and white-tailed deer. The two most common ungulate predators within my study area were black bear and wolves. Due to the "*Canis* soup" in the upper Great Lakes region (Wilson et al. 2009), it was difficult to distinguish between wolves and their coyote hybrids. In light of this, I used the term "wolves" to describe the large canids and their hybrids that populated my study area. It was estimated that there were 0.2 to 0.3 wolves per 10 km^2 (Kittle et al. 2008) and 2.4 black bear per 10 km^2 (OMNR 2014) in the study area.

Predator scat collection

I collected black bear and wolf scats annually from May 1 to August 31, 2013 to 2015. The spring/summer season was selected as the collection period because of the high sightability of scats during this time as it was the core period of black bear activity, but also because ungulate calves are born during this period. I used an ATV to search for scats along approximately 65 km of unimproved roads that were used for logging and/or recreation that were distributed throughout the study area. ATV driving speeds were maintained at 10-15 km/hour to ensure consistent detectability of predator scats. Each road was sampled following two week intervals and as fresh scats (< 2 weeks old) were collected, the entire scat was removed to eliminate resampling. Scats were identified and recorded by the same observer to remove bias (Spaulding et al. 2000). I placed each scat sample in an individually labeled re-sealable plastic bag, and stored the in a walk-in freezer until processed to identify dietary contents.

Hair scale pattern analysis

Identification of prey hair found in predator scat is a common, non-invasive approach used to investigate mammal diet composition of bears (Graber and White 1983; Raine and Kansas 1990; Bull and Torgensen 2001), wolves (Fuller and Keith 1980; Potvin et al. 1987; Lamothe and Parker 1989; Carter 2006; Barja 2009) and many other species (García Alaniz et al. 2010a, 2010b). I removed each scat sample from the freezer approximately 12 hours prior to processing to allow thawing. Once thawed, I rinsed each scat with water over fine sieves to allow the retention of coarse organic material; primarily bone fragments and animal hair. Three randomly selected clusters of hair were pulled from each scat and dried for approximately 12 – 24 hours. To reduce observer bias, only one person macroscopically assessed the size and colour of individual dried hairs as well as microscopically by observing hair cuticular scale patterns. To examine cuticular scale patterns, I applied a thin layer of clear nail polish on a microscope slide and then placed 3-10 individual guard hairs onto the slide to create an imprint of the hair scales (Adorian and Kolenosky 1969). Unknown hair scale slides were compared to reference slides made from guard hairs of museum mammal species known to occur in Ontario and followed Adorian and Kolenosky's (1969) guide to further confirm prey species, as well as to differentiate between adult and juvenile ungulates.

Prey availability

In order to determine the relative prey availability of elk, moose, and white-tailed deer, a fecal pellet survey was employed (Smith et al. 1969; Forsyth 2005). Fecal pellet counts are useful indices for determining the relative abundance of ungulates in concealing habitats (Forsyth et al

2007), and yield reliable data under most field conditions (Neff 1968). They are commonly used in North America to estimate ungulate population sizes (Ripple et al. 2001; Patterson et al. 2002; Hebblewhite et al. 2005). I conducted four fecal pellet transect surveys in the study area over 3 years including: (1) 30 random transects sampled in the fall of 2013; (2) 30 random transects sampled in the fall of 2014; (3) 30 random transects sampled in the spring of 2014; and (4) 100 random transects sampled in the spring of 2015. It is generally agreed that long narrow fecal pellet survey plots provide superior results compared to shorter and wider plots (Neff 1968). As such, I conducted pellet counts along 150 m long transects that began at pre-determined random locations which were calculated using a range of geographical coordinates in Excel. At each random transect location, a pre-determined random compass bearing was selected and walked for the entire 150 m and every 5 m the area within a 1 m radius was examined for ungulate pellets (Forsyth 2005). Each of the four fecal survey bouts were completed within a 30-day period. I estimated the date of leaf-off for each transect year to be November 1. I used mean defecation rates for each ungulate species to determine relative abundances (Neff 1968). The mean defecation rates per animal per day for white-tailed deer, moose, and elk were 13.20, 13.00, and 11.76 respectively (Neff 1968). The mean defecation rate for elk was determined by calculating the mean of the two values given in Neff (1968) ((11+12.52)/2). I calculated mean relative abundances of each ungulate species for each survey using the methodology outlined in Smith et al. (1969), and used them for subsequent analysis. In addition, because ungulate abundance calculations assume animals are present in the study area for the entire duration since leaf-off, and because white-tailed deer (deer) often migrate to winter ranges outside of my study area and migration timing is unknown but related to snow depth, I calculated the relative abundance of deer in my study area using two extremes of occurrence; (1) by predicting that deer were present in the study area during the entire study period, and (2) by predicting that deer were completely absent from the study area every year between January 1 and April 1 (winter).

Data analysis

Carnivores consume fewer hairs of prey items with larger biomass, which may lead to bias in scat results related to larger mammalian prey (Weaver 1993). Although the frequency of occurrence of prey items is the most highly utilized metric in predator diet research, results can be misleading and are often of low ecological significance (Klare et al. 2011). Biomass calculations using correction factors are the best approximation of true diets according to Klare et al. (2011). To reduce bias, I applied the Weaver et al. (1993) correction factor to my occurrence data using the equation: $y = 0.439 + 0.008x$, where y is the mass of prey per collectable scat and x is the average body mass of each prey item, which enabled us to determine the frequency of relative total weight of each prey species in both black bear and wolf diets. Average prey mass was calculated using the median of ranges given for each mammal species (except juveniles) following Eder (2002). To determine mass of juvenile ungulates, I used the median between the average birth mass and median adult mass (Eder 2002) (White-tailed deer: Verme 1969; Elk: Johnson 1951; Moose: Keech et al. 1999). I performed Chi-squared tests to determine if black bear and wolves utilized ungulate adult or juvenile prey species significantly more or less than expected. Prey selection is commonly calculated using the Jacobs' Index (Hayward 2006; 2012; Lyngdoh et al. 2014), which I utilized for both black bear and wolves in relation to ungulate adult and juvenile prey species using the following equation (Jacobs 1974):

$$D = \frac{(r_i - p_i)}{(r_i + p_i - 2r_i p_i)}$$

where, r_i is the proportion of species *i* found among all scat collected for each predator species and p_i is the proportion of ungulate species *i* available in the study area. Jacobs' Index values range from a maximum preference of +1 to a minimum preference of −1 (Boitani and Powell 2012).

Results

Relative abundances

The relative abundances of deer, elk, and moose varied among survey periods (Table 1). Deer had the lowest relative abundance when predicted to be present within my study area throughout the year, followed by elk, then moose. However, when deer were assumed not to be present in the study area from January 1 to April 1, elk had the lowest relative abundance, followed by deer, then moose.

Table 1. Relative abundances (#/km^2) for 3 ungulate species in the Burwash region of Ontario, Canada. Deer estimates were based on the presence of deer in the study area throughout the four time periods assessed (All-Year) and also based on their seasonal absence from the study area between January 1 and April 1 (Part-Year).

	White-tailed deer		Elk	Moose
	All-Year	Part-Year		
Fall 2013	1.12	1.58	1.08	1.95
Spring 2014	1.91	3.51	1.23	3.75
Fall 2014	0.08	0.12	1.03	1.19
Spring 2015	0.04	0.07	1.36	1.11
Mean (SE)	0.79 (0.45)	1.32 (0.81)	1.17 (0.07)	2.00 (0.61)

Black bear diets

I collected and examined a total of 503 black bear scat samples. Black bear diets in my study area were comprised of approximately 87% vegetation based on the frequency of the relative total weight of diet items found in scat (Table 2). Mammals comprised approximately 13% of the total black bear diet. The relative total weight of the mammal portion in black bear diets was comprised of 53% juvenile ungulates, 33 % of adult ungulates, and 14 % non-ungulates. Similar to the trend seen in ungulate abundance, moose adults and juveniles accounted for the greatest proportion of ungulate prey species in the mammal portion of black bear diet followed by elk, then white-tailed deer. In relation to ungulate availability, black bear did not exhibit significant prey selectivity among all species of juveniles (deer present in winter: $X^2 = 0.53$; df = 2; $p > 0.05$; deer absent in winter: $X^2 = 3.45$; df = 2; $p > 0.05$) nor adults (deer present in winter: $X^2 = 0.16$; df = 2; $p > 0.05$; deer absent in winter: $X^2 = 0.40$; df = 2; $p > 0.05$). The black bear prey selectivity indices for all ungulate species (adults and juveniles) were close to what was expected when deer were predicted to be within my study area during the entire study period (Fig. 1).

Similarly, when deer were assumed to be absent annually from January 1 to April 1, prey selectivity indices for each juvenile and ungulate species were close to what was expected; however, deer juvenile and adult selection indices were less than those for moose and elk (Fig. 2).

Table 2. The number of black bear scat samples (N=503) in which various diet items were detected, the frequency of occurrence for each item, and frequency of relative total weight of each item.

Diet Item	n	Freq. of Occurrence	Freq. of Relative Total Weight
Small mammal	5	0.99	0.42
Muskrat	5	0.99	0.43
Beaver	8	1.59	0.96
Juvenile Deer	7	1.39	1.00
Adult Deer	5	0.99	0.99
Juvenile Elk	6	1.19	2.14
Adult Elk	2	0.40	1.22
Juvenile Moose	9	1.79	3.55
Adult Moose	3	0.60	2.03
Vegetation	453	90.06	87.25

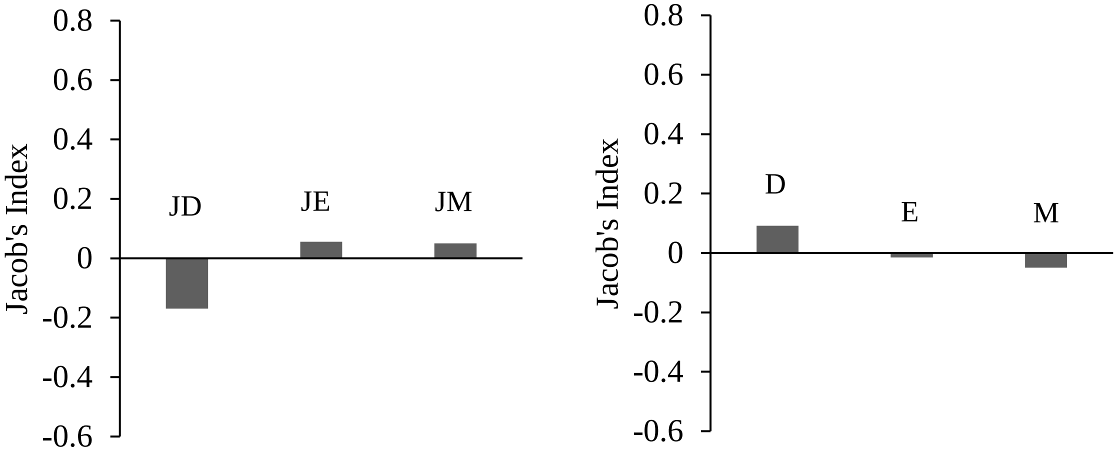
Wolf diets

I collected and examined a total of 247 wolf scat samples. Wolf diets in my study area were comprised entirely of mammals (Table 3). The relative total weight of mammals in wolf diets was comprised of 44% juvenile ungulates, 29% of adult ungulates, and 27% non-ungulates including muskrat (*Ondatra zibethica*) and beaver (*Castor canadensis*). Wolves used juvenile and adult ungulate prey species significantly more or less than expected; juvenile ungulates (deer present in winter: $X^2 = 6.04$; df = 2; $p < 0.05$; deer absent in winter: $X^2 = 7.19$; df = 2; $p < 0.05$) and adult ungulates (deer present in winter: $X^2 = 11.71$; df = 2; $p < 0.005$; deer absent in winter: $X^2 = 16.05$; df = 2; $p < 0.001$). Wolf prey selection indices were greatest for both juvenile and adult elk and least for juvenile and adult moose (Fig. 1 and 2).

Table 3. The number of wolf scat samples (N=247) in which various diet items were detected, the frequency of occurrence for each item, and frequency of relative total weight of each item.

Prey Species	n	Freq. of Occur.	Freq. of Rel. Total Wt.
Small mammals	22	8.91	3.73
Muskrat	49	19.84	8.47
Beaver	61	24.70	14.64
Juvenile Deer	37	14.98	10.61
Adult Deer	15	6.07	5.91
Juvenile Elk	23	9.31	16.43
Adult Elk	11	4.45	13.38
Juvenile Moose	22	8.91	17.35
Adult Moose	7	2.83	9.49

a) Black bear



b) Wolves

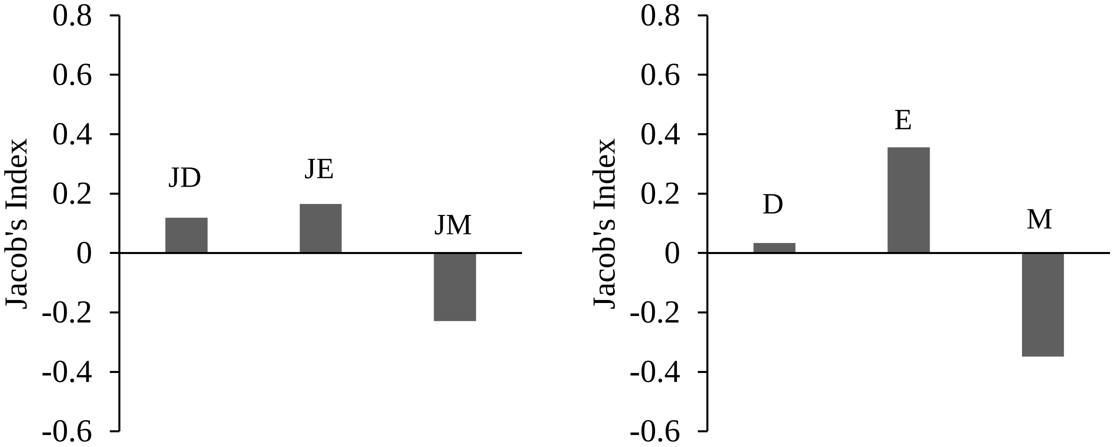
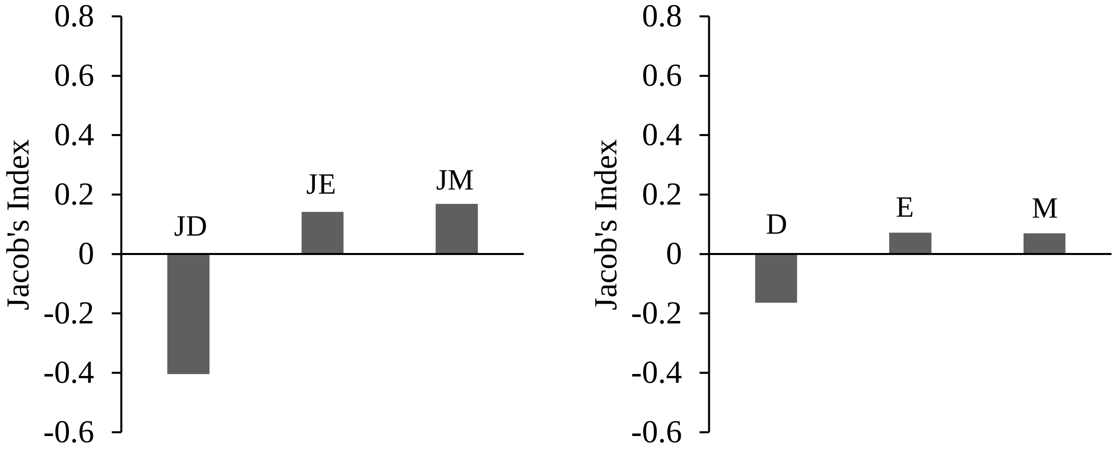


Fig 1. Prey selectivity indices (Jacob's Index) of black bear (a) and wolves (b) for juvenile (JD) and adult (D) white-tailed deer, juvenile (JE) and adult (E) elk, and juvenile (JM) and adult (M) moose, when white-tailed deer were assumed as present in the study area all year.

a) Black bear



b) Wolves

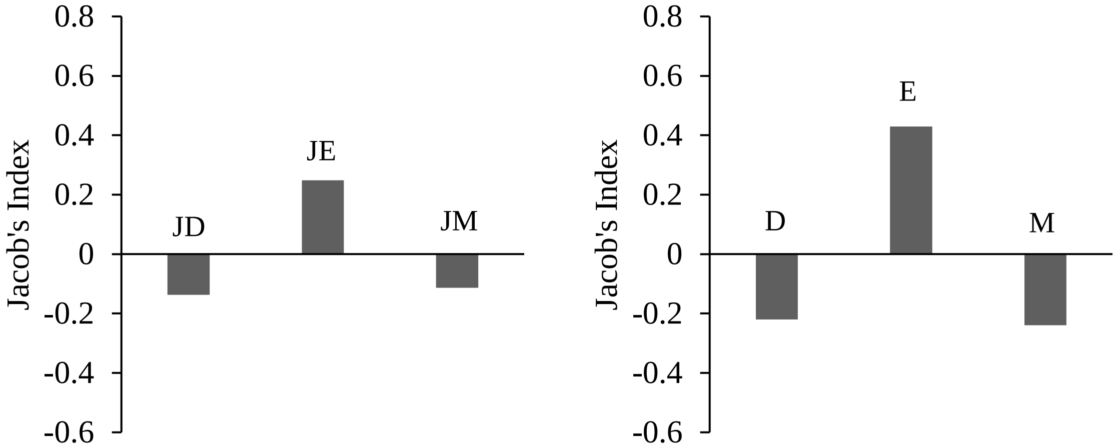


Fig 2. Prey selectivity indices (Jacob's Index) of black bear (a) and wolves (b) for juvenile (JD) and adult (D) white-tailed deer, juvenile (JE) and adult (E) elk, and juvenile (JM) and adult (M) moose, when white-tailed deer were assumed as absent in the study area annually between January 1 to April 1.

Discussion

My study revealed differential use of ungulates as prey items by wolves and black bear in the Burwash region of Ontario. Although black bear in my study area utilized a variety of mammal species including all 3 of the available ungulate species, their selectivity for ungulates was not apparent. Vegetation comprised approximately 87 % of the relative total weight of black bear diet in my study, with the remaining 23 % comprised of mammals, most of which were ungulates. Similarly, in Quebec, Canada, an area without elk, black bear diet consisted of 90 % vegetation with moose being the second most important diet item during the spring and summer (Mosnier et al. 2008). In Yosemite National Park, USA, black bear diet was comprised of 75 % vegetation, with mule deer (*Odocoileus hemionus*) being the only common vertebrate food item (Graeber and White 1983). In Oregon, USA, animal remains accounted for only 10 % of black bear diet and diet composition varied among seasons, with ungulates being most important during the spring and fall (Bull and Torgensen 2001). Although it is widely acknowledged that black bears are opportunistic, black bear predation has been reported to be the primary cause of juvenile ungulate population decline in some regions (Lewis et al. 2016). I did not find evidence of ungulate adult or juvenile prey use more than was expected in black bear diet during the summer months, supporting the theory that black bear consume ungulate prey opportunistically. The ungulate component of black bear diet in my study did however consist of more juveniles than adults (~61 % of ungulates). Because wolves rarely use all of elk or moose carcasses (Paquet 1992) and ungulates die due to non-predator related events such as road-kill, scavenging opportunities may have been created for black bear, especially later in the summer when juveniles are more mobile. As such, it is important to recognize that the ungulate items I detected in black bear scats may have been from predation or scavenging behaviour. Regardless, all three ungulate species collectively made up a rather small component of bear summer diets.

Unlike black bear, summer diets of wolves in my study area were comprised largely of ungulates (73 % of all items detected). This finding is consistent with other studies that have examined wolf diets (Mech et al. 2001; Arjo et al. 2002; Barja 2009). Wolves also exhibited selection for ungulate prey species in my study, whereby juvenile and adult elk were consistently consumed more than expected and juvenile and adult moose were utilized less than expected. The majority (63 %) of the ungulate items detected in my wolf scat samples were from juveniles, which is not surprising given my scat collection coincided with all three ungulate species calving/fawning seasons. Wolves elsewhere are known to disproportionately kill younger, older, and likely more debilitated ungulates than prime adults (Fuller and Keith 1980; Huggard 1993b; Christianson and Creel 2014). Higher rates of predation on juvenile ungulates compared to adults have been documented in other studies and are suggested to be due to the increased vulnerability of juveniles in comparison to adults (Ballard et al. 1987, Salvador and Abad 1987, Jedrzejewski et al. 1992).

North American wolf diets are dominated by large ungulates and medium-sized mammals (Newsome et al. 2016). Prey use by wolves is thought to be dependent on prey availability (Paquet and Carbyn 2003; Newsome et al. 2016). Wolves most often consume prey species that are the most abundant and may change their diet in response to changes in prey availability

(Barja 2009; Wiwchar and Mallory 2012). Although moose are larger than elk and were the most abundant ungulate in my study area, elk were the ungulate prey item of choice for wolves. Deer were used as or less than expected by wolves and may not have been selected for due to their relatively low abundance and seasonality. Similar to my results, elk were consumed by wolves 15 times more often that moose despite elk only being 2.4 times more abundant than moose in Riding Mountain National Park, Canada (Carbyn 1983). Paquet (1992) further confirmed that wolves in the Riding Mountain National Park preyed primarily on elk and white-tailed deer, rather than moose. In Yellowstone National Park, elk, the most abundant ungulate in the park, comprised 91 % of wolf diet; however, mule deer (*Odocoileush emionus*), bison (*Bison bison*), moose (*Alces alces),* bighorn sheep (*Ovis canadensis*), and pronghorns (*Antilo-capra americana*), were also available (Mech et al. 2001). Interestingly, both elk (Johnson 1951; Geist 2002) and white-tailed deer (Carl and Robbins 1988) use "the hider" anti-predator strategy during the first weeks of life leaving calves relatively unprotected should a predator discover them. Conversely, moose do not use "the hider" strategy; rather mothers stay close to their young as neonates utilize "the follower" anti-predator strategy (Bogomolova et al. 1992). The difference in anti-predator strategies between moose and elk may in part explain the observed selection for elk by wolves (an easier, non-protected target). Encounters with protective large ungulates such as a moose can be very risky for wolves and have been documented to lead to wolf deaths (Mech and Nelson 1990; Weaver et al. 1992). In addition, in systems with a variety of large and small bodied ungulate species, wolves tend to prey primarily upon smaller species (Carbyn 1983; Paquet 1992; Kunkel et al. 1999; Smith et al. 2000)

Other factors influence the selection of a prey species including prey density, predator density, prey size, alternative prey densities, predator characteristics, and prey behavior (Pimlott 1967). Both juvenile and adult elk were the most selected ungulate by wolves in my study area. Elk live in both small and large herds which change seasonally, wolves encounter and kill more elk than expected from larger groups (Hebblewhite and Pletcher 2002). Grouping behaviour is a common anti-predator strategy of many species (Bertram 1978; Pulliam and Caraco 1984) which may benefit the prey through the dilution effect (Hamilton 1971; Bertram 1978). With increased group size, predator detection probability may also increase (Triesman 1975), which may result in increased encounter and predation rates. In addition, larger groups may be more spatially predictable (Huggard 1993a) as well as more likely to contain weak individuals (Bertram 1978). Because elk are such a gregarious species, they may be more predictable in space, providing easier targets for wolves in my study area. This grouping anti-predator behaviour may be responsible for wolves selecting more juvenile and adult elk than moose or deer (less gregarious than elk in summer months) in my study.

As many factors influence predator-prey dynamics, careful consideration should be taken before applying predator-prey results to the development of management strategies. Factors that vary among regions may influence predator-prey population dynamics (Ballard et al. 1987; Mech and Peterson 2003). My study was limited to periods between May and August, but predator diets have been demonstrated to vary among seasons for both wolves (Pimlott 1967; Potvin et al 1987; Barja 2009) and black bear (Raine and Kansas 1990; Bull and Torgensen 2001). My results indicate that for the calving and summer period, black bear had little apparent impact on elk in my study area, whereas wolves heavily utilized ungulates during the summer with, both juvenile and adult elk preferred over moose and white-tailed deer.

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Chapter 7

Population-specific responses to climate by restored elk in eastern North America

Abstract

The effects of climate on wildlife population dynamics have been investigated extensively; however, relationships can be very complex, often indirect, and in many cases, not well understood. Wildlife responses to changes in weather are often population-specific, indicating that generalizations should be carefully considered. The effects of climate on elk in North America has been studied; however, little is known about population growth rate responses of restored elk in eastern North America. To determine if restored elk have population-specific responses to climate, I compared annual population rates of increase using time series for 7 reintroduced elk populations in eastern North America. I used a model selection approach with five climatic variables and found that population-specific responses existed. Three of the 7 populations displayed significant responses to climate variables. Two populations responded negatively to increased snow depths, while one population responded negatively to increased summer temperatures. Our study contributes to the understanding of the complex relationship among wildlife population dynamics and climate.

Introduction

Climate can directly and indirectly influence large herbivore population dynamics through differences in precipitation, temperature, wind, and winter severity (Coughenour and Singer 1996, Creel and Creel 2009, Hegel et al. 2010; Owen-Smith 2010). Weather can have direct effects on wildlife such as cold or heat stress (Owen-Smith 2010), as well as indirect effects on forage production and availability (Bo and Hjeljord 1991; Finstad et al. 2000; Raedeke et al. 2002; Melis et al. 2009; Owen-Smith 2010), energy expenditure due to locomotion restriction (i.e.: deep snow) (Telfer and Kelsall 1984; Owen-Smith and Marshal 2010), and predator-prey processes (Post et al. 1999; Hebblewhite et al. 2002; Melis et al. 2009).

Responses to climate may differ among ungulate populations of the same species. For example, in western North America, Griffin et al. (2011) found that weather conditions affected neonatal elk survival differently among populations, and response variation was found to be related to differences in predator species diversity among the elk populations. Hegel et al. (2010) found variation in herd recruitment response to weather among mountain-dwelling caribou (*Rangifer tarandus*) populations. It has been suggested that herd- or population- specific characteristics such as terrain or predator densities should be incorporated when investigating the complex relationships between ungulate population dynamics and climate (Hegel et al. 2010).

The effects of climate on wildlife population dynamics are governed by several factors and these relationships can be very complex and most often indirect (Owen-Smith 2010). Factors that are well known to govern population response to climate include population density (Clutton-Brock et al. 2004; Owen-Smith and Marshal 2010), age class composition (Clutton-Brock et al. 2004), sex ratio (Owen-Smith and Marshal 2010), body condition (Raedeke et al. 2002), and the presence of predators (Griffin et al. 2011). There are likely several other factors that influence responses of wildlife populations to climate and identifying them would greatly enhance our understanding of causal agents associated with population-specific responses.

Elk survival has been linked to changes in temperature, precipitation, and more commonly, snowpack or winter severity (Picton 1984, Coughenour and Singer 1996, Post and Stenseth 1999, Taper and Gogan 2002, Garrot et al. 2003, Creel and Creel 2009). In western North America, high summer temperatures are known to negatively influence population growth rates of elk (Wang et al. 2002), while spring or summer precipitation tends to improve population growth rates, as well as recruitment (Coughenour and Singer 1996; Taper and Gogan 2002; Wang et al. 2002), but not for all populations. For example, Creel and Creel (2009) found that summer precipitation was not a strong predictor of elk population growth rate in Rocky Mountain National Park. Several studied elk populations were shown to respond negatively to increased snowpack and severe winter weather (Huggard 1993; Raedeke et al. 2002; Garrot et al. 2003; Smith et al. 2003; Evans et al. 2006; Creel and Creel 2009; Brodie et al. 2013); however, other populations were not significantly affected (Coughenour and Singer 1996; Singer et al. 1997; Johnson et al. 2013).

Elk were extirpated in eastern North America in the 19th century; however, over the past century, reintroductions have become prevalent (O’Gara 2002; Popp et al. 2014). Restoration attempts have resulted in success, failure and a wide degree of variation among population growth rates

(Popp et al. 2014). Factors related to the variation in population dynamics of elk reintroductions in eastern North America are critical to the success of established and future populations. Although some research has been done in this area, the effects of climate on reintroduced elk populations in eastern North America has not yet been investigated in depth.

Reintroductions are often initiated with small populations, which are far below carrying capacity, providing opportunity to study the effects of climate in the absence of density dependent influences. Although Picton (1984) identified significant climatic effects on elk populations at carrying capacity, to my knowledge, investigations of responses to climate in recently reintroduced ungulate populations have not been documented. I used annual estimates from 10 populations of eastern North American reintroduced elk to examine the effects of several climatic variables on population growth rates, and anticipated that responses would be population-specific.

Methods

Annual elk population estimates and harvest data were collected from regional managers of 7 populations in eastern North America including Burwash, Ontario (BUR) Lake Huron-North Shore, Ontario (LHNS); Bancroft, Ontario; Wisconsin; Minnesota; Michigan; and Pennsylvania (Fig. 1). Data were available from the time elk were reintroduced to 11 to 17 years post-introduction in 4 populations: BUR, LHNS, Bancroft, and Wisconsin; and in 3 populations more than 48 years after they were reintroduced (Minnesota – 72 years; Michigan – 68 years;

Pennsylvania – 48 years) with 13 to 37 years of data following. Population survey methods were indicated as consistent among years by managers in all populations except Michigan and Pennsylvania where several methods were used throughout the time-frame.

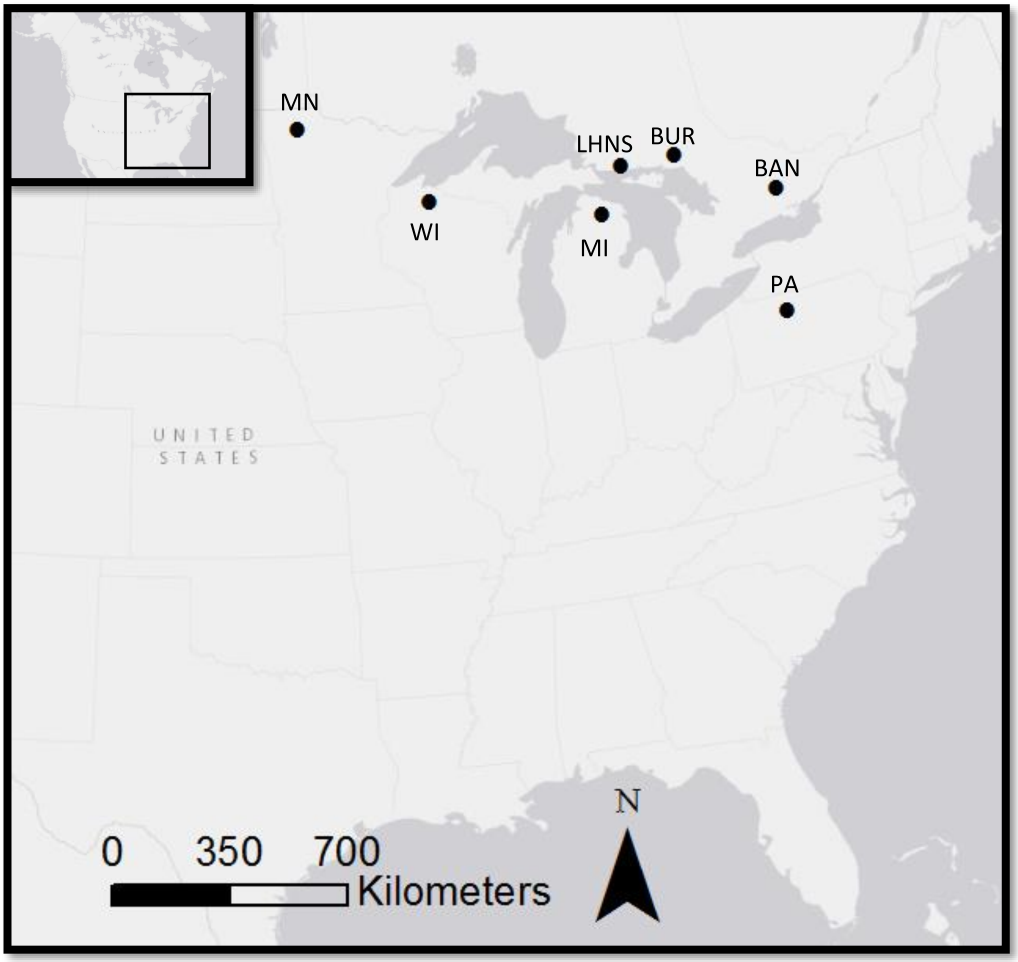


Fig 1. Distribution for 7 restored elk populations in eastern North America.

BAN = Bancroft; BUR = Burwash; LHNS = Lake Huron-North Shore; MI = Michigan; MN = Minnesota; PA = Pennsylvania; WI = Wisconsin.

I modeled abundance time series from each population using a Bayesian state-space model (BSS), which has two components: a model of the underlying population processes (the process model) producing abundance changes over time, and a model of the observation process (the observation model) relating abundance estimates to inferred true abundance (de Valpine and Hastings 2002; Buckland et al. 2004). The state-space model partitions variation within time series into process variance (σ^2_{proc}) and variance caused by observation error (σ^2_{obs}). Failure to account for observation error bias estimates of density dependence and decreases power to detect effects of environmental covariates (Freckleton et al. 2006). My process model is the discrete time stochastic Gompertz model (Dennis et al. 2006):

$$N_t = N_{t-1}\exp(a + b\ln N_{t-1} + E_t)$$

where N_t is the imperfectly-observed true abundance at each survey occasion and E_t is unexplained process variation distributed as $E_t \sim \mathrm{N}\left(0, \sigma^2_{proc}\right)$. Parameter *a* is a constant and parameter *b* controls the strength of density dependence. The stochastic Gompertz model is simple and is well supported for abundance time series across a variety of taxa (Brook and Bradshaw 2006). It has been employed in previous analyses of ungulate populations, including elk (Creel and Creel 2009; Ahrestani et al. 2013). I accounted for any harvest that occurred prior to each population survey by including a harvest term:

$$N_t + H_{t-1} = N_{t-1}\exp(a + b\ln N_{t-1} + E_t)$$

The observation model assumes that errors inherent to imperfectly observing abundance are log-normally distributed about the true abundances (Dennis et al. 2006). On the log scale, where $Y_t = \ln(Est._t)$ and $Est._t$ are the raw estimates of abundance, the observation model is:

$$Y_t \sim \mathrm{N}(\ln N_t, \sigma^2_{obs})$$

Models were fitted by Markov Chain Monte Carlo (MCMC) using a Gibbs sampler implemented in Program JAGS (Plummer 2013) run through the R package R2jags (R Development Core Team 2014; Su and Yajima 2014). Population annual growth rates r_t were estimated from BSS log abundance estimates, which accounted for observation error. The distribution of each r_t was calculated by MCMC, as a derived parameter of the BSS according to the relationship:

$$r_t = \ln((N_t + H_{t-1})/N_{t-1})$$

Mean estimates of $\overline{r_t}$ were regressed onto 12 combinations of environmental covariates. Covariate models were compared within each site using $\mathrm{AIC_c}$ for multi-model inference to select top models (Burnham and Anderson 2002). Based on the potential effects of climate variables on elk population growth through literature review, several candidate models were formed each with a maximum of 2 covariates due to the restrictions of small sample size. Climate variables that were correlated (Pearson's correlation coefficient > 0.70) were not used together in any given model. The same candidate models were used for each of the 7 elk populations to determine which model best explained the variation in population growth rates among years.

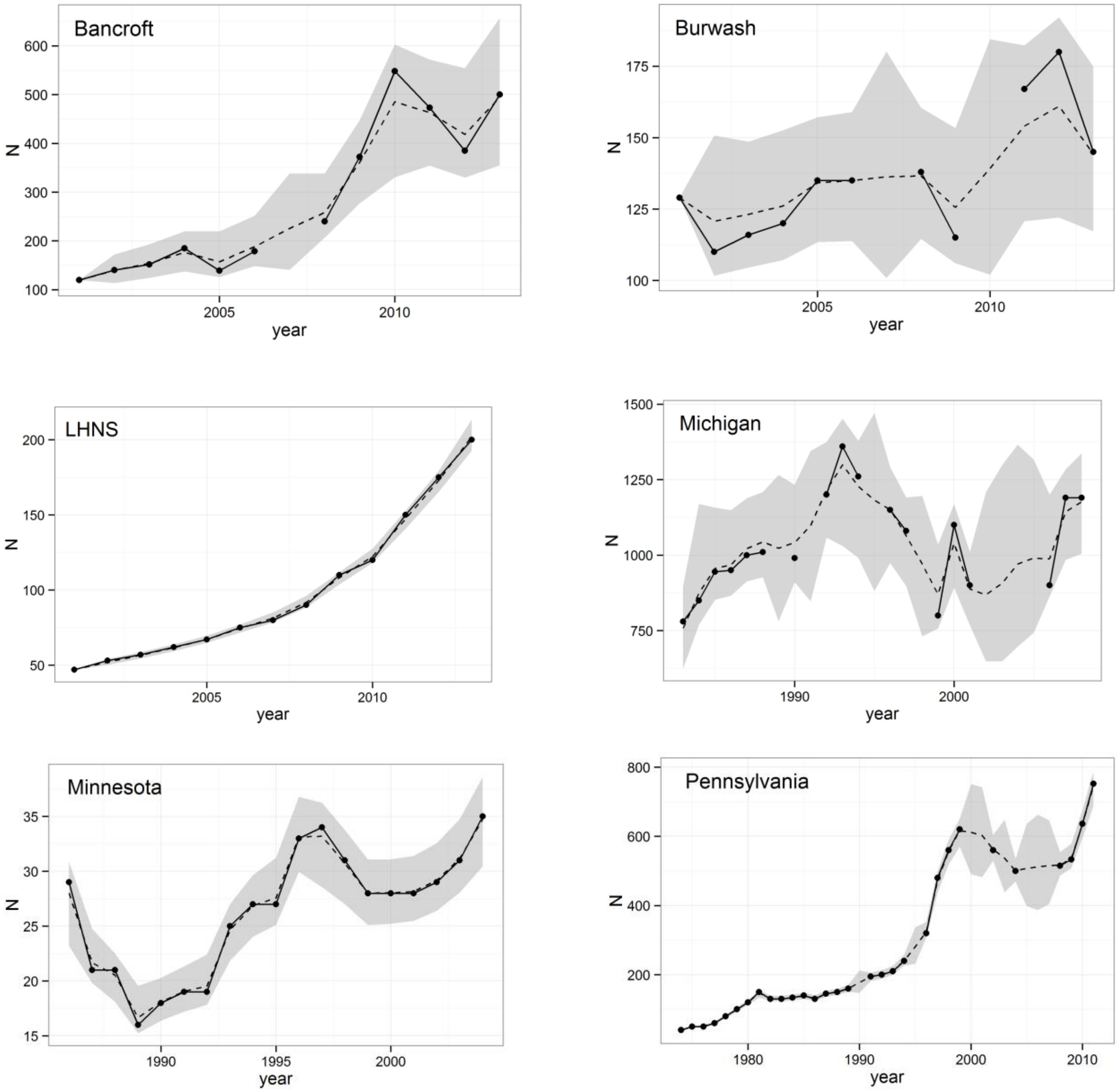
Several climate covariates were used (Table 1) and carryover effects were considered as populations can respond to past weather conditions (Owen-Smith 2010). Covariates included $\mathrm{SummerPrecip}_{(t-1)}$ - summer precipitation (mean precipitation from May to August in the year prior to the population survey); $\mathrm{SummerTemp}_{(t-1)}$ - summer temperature (mean maximum temperature from May to August in the year prior to the population survey); $\mathrm{WinterTemp}_{(t-1)}$ - winter temperature (mean maximum temperature from January to February in the year prior to the population survey; $\mathrm{WinterTemp}_{(t)}$ – winter temperature during the year of the population survey; and $\mathrm{LengthGrowth}_{(t-1)}$ - length of the growth season in the year prior to the population survey (McKenney et al. 2006; 2011). The mean total snow fall from January to February was also used from the year of the population survey ($\mathrm{Snow}_{(t)}$): as well as the year prior ($\mathrm{Snow}_{(t-1)}$) (*Snow Data Sources:* Canada - Environment Canada Historical Weather; USA – National Oceanic and Atmospheric Administration (NOAA).

Table 1. Description of restored elk population growth rate models with explanation of climate covariates.

Model Description	Covariate Justification	Reference
$\beta_0 + \beta_1(\text{SummerPrecip}_{(t-1)})$	Precipitation positively influenced elk survival, population growth rate, and juvenile recruitment	Coughenour and Singer 1996; Taper and Gogan 2002; Johnson 2013
$\beta_0 + \beta_1(\text{SummerTemp}_{(t-1)})$	Warmer temperatures resulted in heavier red deer calves/ and decreased elk survival	Albon et al. 1987/Wang et al. 2002; Griffin et al. 2010
$\beta_0 + \beta_1(\text{WinterTemp}_{(t)})$	Harsh winters related to elk mortality	Singer et al. 1997; Raedeke et al. 2002; Smith et al. 2003; Evans et al. 2006
$\beta_0 + \beta_1(\text{WinterTemp}_{(t-1)})$	Harsh winters related to elk mortality	Singer et al. 1997; Raedeke et al. 2002; Smith et al. 2003; Evans et al. 2006
$\beta_0 + \beta_1(\text{LengthGrowth}_{(t-1)})$	Local plant phenology can influence body condition of herbivores	Mysterud et al. 2001
$\beta_0 + \beta_1(\text{Snow}_{(t)})$	Harsh winters related to elk mortality	Singer et al. 1997; Raedeke et al. 2002; Smith et al. 2003; Evans et al. 2006
$\beta_0 + \beta_1(\text{Snow}_{(t-1)})$	Harsh winters related to elk mortality	Singer et al. 1997; Raedeke et al. 2002; Smith et al. 2003; Evans et al. 2006
$\beta_0 + \beta_1(\text{LengthGrowth}_{(t)}) + \beta_2(\text{Snow}_{(t-1)})$		
$\beta_0 + \beta_1(\text{LengthGrowth}_{(t)}) + \beta_2(\text{Snow}_{(t)})$		
$\beta_0 + \beta_1(\text{LengthGrowth}_{(t)}) + \beta_2(\text{SummerPrecip}_{(t-1)})$		
$\beta_0 + \beta_1(\text{LengthGrowth}_{(t)}) + \beta_2(\text{SummerTemp}_{(t-1)})$		
$\beta_0 + \beta_1(\text{Snow}_{(t)}) + \beta_2(\text{Snow}_{(t-1)})$		

Results

The Bayesian state-space abundance time series for each elk population had various credible intervals (CRI), with larger CRI's in years when population estimate data were missing due to the lack of annual population survey results (Fig 2).



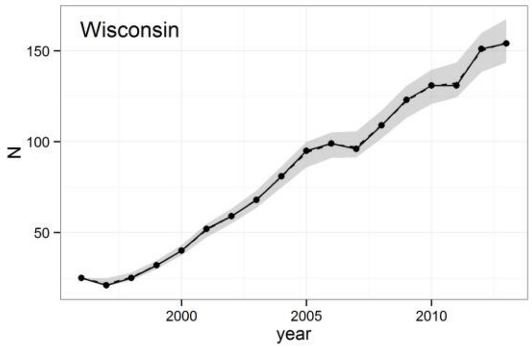


Fig 2. Bayesian state-space abundance time series for each elk population assessed. Points and solid line indicate observed population estimates, dashed line indicates estimated true abundance (N_t), the shaded region is the 95% CRI of N_t.

Only 3 of the 7 elk populations were significantly influenced by the climate according to the models I assessed (Table 2). Snowfall negatively influenced recently reintroduced BUR and LHNS population growth rates, where the BUR elk population growth rates decreased as snowfall increased both in the year of, and the year prior to, the population survey. LHNS elk responded negatively only to increased snowfall in the year prior to the population survey. In contrast, the Minnesota elk population responded negatively to increasing summer temperatures.

Table 2. Relative support with model-averaged coefficients for the top 3 candidate models explaining variation in population growth rates for 7 restored elk populations in eastern North America.

								95% Confidence Intervals$_1$				95% Confidence Intervals$_2$	
Population	Model Description	K	AIC$_c$	Δi	w_i	β_1	S.E.$_1$	Lower	Upper	β_2	S.E.$_2$	Lower	Upper
Bancroft	$\beta_0 + \beta_1(\text{Snow}_{(t)}) + \beta_2(\text{Snow}_{(t-1)})$	4	-6.63	0.00	0.15	0.006	0.005	-0.0050	0.0170	0.007	0.005	-0.0045	0.0175
	$\beta_0 + \beta_1(\text{Snow}_{(t-1)})$	3	-6.59	0.04	0.15	0.007	0.005	-0.0045	0.0175	-	-	-	-
	$\beta_0 + \beta_1(\text{WinterTemp}_{(t-1)})$	3	-6.57	0.05	0.15	0.018	0.021	-0.0282	0.0642	-	-	-	-
Burwash	$\beta_0 + \beta_1(\text{Snow}_{(t)}) + \beta_2(\text{Snow}_{(t-1)})$	4	-27.23	0.00	0.32	**-0.002**	**0.001**	**-0.0038**	**-0.0002**	-0.002	0.001	-0.0038	-0.0002
	$\beta_0 + \beta_1(\text{Snow}_{(t-1)})$	3	-26.69	0.53	0.24	-0.002	0.001	-0.0035	0.0005	-	-	-	-
	$\beta_0 + \beta_1(\text{WinterTemp}_{(t-1)})$	3	-25.69	1.53	0.15	-0.017	0.010	-0.0390	0.0050	-	-	-	-
LH-NS	$\beta_0 + \beta_1(\text{Snow}_{(t-1)})$	3	-34.78	0.00	0.51	**-0.001**	**0.000**	**-0.0019**	**-0.0001**	-	-	-	-
	$\beta_0 + \beta_1(\text{LengthGrowth}_{(t-1)})$	3	-31.77	3.01	0.11	0.001	0.001	-0.0005	0.0025	-	-	-	-
	$\beta_0 + \beta_1(\text{LengthGrowth}_{(t-1)}) + \beta_2(\text{Snow}_{(t-1)})$	4	-31.73	3.05	0.11	0.001	0.001	-0.0009	0.0021	**-0.001**	**0.000**	**-0.0019**	**-0.0001**
Wisconsin	$\beta_0 + \beta_1(\text{SummerPrecip}_{(t-1)})$	3	-25.52	0.00	0.22	0.002	0.001	-0.0005	0.0037	-	-	-	-
	$\beta_0 + \beta_1(\text{Snow}_{(t-1)})$	3	-25.15	0.37	0.19	0.003	0.002	-0.0015	0.0069	-	-	-	-
	$\beta_0 + \beta_1(\text{WinterTemp}_{(t)})$	3	-24.57	0.95	0.14	0.012	0.010	-0.0090	0.0330	-	-	-	-
Minnesota	$\beta_0 + \beta_1(\text{SummerTemp}_{(t-1)})$	3	-17.17	0.00	0.55	**-0.049**	**0.020**	**-0.0926**	**-0.0054**	-	-	-	-
	$\beta_0 + \beta_1(\text{Snow}_{(t-1)})$	3	-13.81	3.36	0.10	0.003	0.003	-0.0033	0.0093	-	-	-	-
	$\beta_0 + \beta_1(\text{LengthGrowth}_{(t-1)}) + \beta_2(\text{SummerTemp}_{(t-1)})$	4	-13.25	3.93	0.08	-0.002	0.003	-0.0083	0.0043	**-0.049**	**0.020**	**-0.0926**	**-0.0054**
Michigan	$\beta_0 + \beta_1(\text{WinterTemp}_{(t-1)})$	3	-68.78	0.00	0.28	0.010	0.006	-0.0016	0.0212	-	-	-	-
	$\beta_0 + \beta_1(\text{SummerTemp}_{(t-1)})$	3	-67.37	1.41	0.14	0.010	0.010	-0.0106	0.0306	-	-	-	-
	$\beta_0 + \beta_1(\text{LengthGrowth}_{(t-1)})$	3	-66.88	1.90	0.11	0.001	0.001	-0.0007	0.0022	-	-	-	-
Pennsylvania	$\beta_0 + \beta_1(\text{Snow}_{(t)})$	3	-42.66	0.00	0.31	0.002	0.001	0.0000	0.0040	-	-	-	-
	$\beta_0 + \beta_1(\text{WinterTemp}_{(t-1)})$	3	-41.51	1.15	0.18	-0.018	0.012	-0.0402	0.0042	-	-	-	-
	$\beta_0 + \beta_1(\text{Snow}_{(t)}) + \beta_2(\text{Snow}_{(t-1)})$	4	-40.07	2.59	0.09	0.002	0.001	0.0000	0.0040	0.001	0.001	-0.0014	0.0026

Number of parameters in each model (K), Akaike's information criterion adjusted for small sample size (AICc), the change in AICc (Δ), Akaike weight for each model (*w*), Beta coefficient (β), Standard error (S.E.), 95% Confidence Interval (95% C.I.). Confidence intervals that do not overlap 0.00 are bolded.

Discussion

The restored elk populations I assessed in eastern North America displayed population-specific responses to climate. Severe winter weather is well known to negatively impact ungulate population dynamics (Mech et al. 1987; Peterson 1999; Forchammer et al. 2001; Solberg et al. 2001; Owen-Smith and Marshal 2010), including elk (Singer et al. 1997; Raedke et al. 2002; Garrot et al. 2003; Smith et al. 2003; Evans et al. 2006; Creel and Creel 2009; Brodie et al. 2013); however, the effects are not consistent among populations (Hegel et al. 2010; Griffin et al. 2011). Of the populations I examined, 5 of the 7 were not significantly influenced by snowfall or winter temperatures; whereas the remaining 2 populations had population growth rates that decreased in response to increased snowfall. Snow can have both direct and indirect effects on ungulates. Snow accumulation can decrease the accessibility of food (Finstad et al. 2000) and lead to locomotion restrictions (Telfer and Kelsall 1984) and both factors may restrict dietary intake and nutrition, ultimately leading to the depletion of body reserves, and thus influencing survival, reproduction, and recruitment (Garrot et al. 2003). Both the Burwash and LHNS populations responded negatively to the previous year's snowfall, while only the Burwash population responded negatively to both the current and previous year's snowfall. Snow depths can have carryover effects, for example, following severe winter conditions, elk calves can be born later and lighter, ultimately decreasing their chances for survival (Singer et al. 1997).

Winter climate can also influence ungulate population dynamics through predator-prey processes (Post et al. 1999; Hebblewhite et al. 2002). For example, high snow depth was responsible for increased wolf predation on white-tailed deer in Minnesota (Nelson and Mech 1986), elk in

Banff National Park (Huggard 1993), and moose on Isle Royale (Post et al. 1999). Ungulate kill rates by wolves can increase substantially in the presence of snow (Nelson and Mech 1986; Huggard 1993), as deep snow can hinder ungulate movement, while wolves with lighter foot-loads (Telfer and Kelsall 1984) can travel more easily on top of snow with crusts (Peterson 1977) making ungulates, especially juveniles and older adults, more accessible to the predator (Mech et al. 1987; Garrot et al. 2003; Owen-smith 2010). Although I could not obtain wolf density estimates in each of the elk population ranges, wolves were absent in Minnesota, Michigan and Pennsylvania, but were present in the Burwash, Bancroft, LHNS, and Wisconsin elk population ranges. Thus, under certain conditions, interaction of predation and climate can result in lower population growth and vital rates in ungulate populations (Hebblewhite 2005; Wilmers et al. 2007). However, although elk population growth rates have been found to decline more steeply in areas with wolf predation, winter severity can reduce elk population growth rate regardless of predation pressure (Hebblewhite et al. 2005). Although I were unable to test this, wolves as well as other unidentified factors may be influencing the response of elk to climate in 4 of the populations examined.

Increased summer temperatures were associated with decreased elk population growth rates in the Minnesota elk population. Also in Minnesota, high summer temperatures were associated with decreased moose (*Alces alces*) population growth rates, suggested to be the result of thermoregulation disruption (Murray et al. 2006). In Scotland, warmer spring temperatures resulted in the births of heavier red deer (*Cervus elaphus*) calves (Albon et al. 1987); however, elk population growth rates in Rocky Mountain National Park decreased in response to high summer temperatures (Wang et al. 2002). In the northwestern USA, neonatal elk survival declined in years following high summer temperatures, an effect that was greater than that of winter severity (Griffin et al. 2010). Warmer summers can reduce forage quality by increasing the rate of plant maturity (Finstad et al. 2000) and trends like these suggest that summer forage plays a very important role for ungulate population dynamics (McArt et al. 2009; Parker et al. 2009).

A complex and often indirect relation exists between climatic factors and wildlife population dynamics (Owen-Smith 2010). Many factors, some likely still unidentified or poorly understood may govern wildlife responses to climate (Clutton-Brock et al. 2004; Owen-Smith and Marshal 2010, Raedeke et al. 2002; Griffin et al. 2011). Although I did not find any differences in responses to climate between recently reintroduced elk versus established restored elk populations, population-specific responses were apparent. If wildlife populations are geographically separated, managers and conservationists should investigate population-specific responses to various environmental factors when assessing population growth and dynamics, as assumptions based on supported “trends” may not be accurate for every population.

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Chapter 8

Conclusions and Management Recommendations

Although the number of successful elk restoration attempts have increased over the past century, variation among success rates (population growth rates) exist. There is still a need to enhance reintroduction strategies to ensure future attempts succeed and introduced populations become self-sustaining. Major causes of elk mortality in restored populations differed between the pre- and post-acclimation phases of reintroduction. Disease, emaciation, injury and accidents were leading causes of pre-acclimation mortality for most populations; however, predation was more important in northern populations. Although meningeal worm has been suggested as a significant factor in the failure of early elk restoration attempts, it may not be as significant a factor of elk mortality as previously thought. The identified major causes of mortality and differences between pre- and post-acclimation periods of reintroduction should be considered by managers planning future reintroductions, as well as by managers of established populations where mitigation strategies can be developed accordingly.

Using an among-populations approach, I found that reintroduced elk population growth rates in eastern North America were negatively related to the percentage of coniferous forest within elk population ranges. Coniferous forests in eastern North America likely represent sub-optimal elk habitat; however, due to the small sample size of populations available for this investigation, there is potential for confounding or interacting variables that should be investigated further, once more reintroduced populations become established allowing for improvement of sample size. In the meantime, future elk reintroductions in eastern North America should consider avoiding areas dominated by coniferous forest.

Although railway ecology is underrepresented in science, railways can impact wildlife negatively in a number of ways. Vehicle and train collisions were reported as a major cause of post-acclimation mortality in several reintroduced populations, and train collisions were the most important cause of mortality of the Burwash population in Ontario. In that population, train collisions were highly site-specific and positively correlated to the proximity of bends in the railway. Although elk utilized the railway mostly in the spring and fall; behaviour likely associated with seasonal range use, most train collisions were positively related to snow depth. Railways are likely perceived by elk as easy travel corridors, and deep snow off the rails likely prohibits escape from oncoming trains. Elk managers of populations affected by train-collision mortality should identify train-collision hotspots in order to geographically focus the implementation of winter mitigation strategies, when snow depths are greatest.

I found that in a system where black bears and wolves existed as the major predators of elk, white-tailed deer, and moose, wolves preferred elk as a prey item over the other available ungulate prey species. Bears on the other hand tended to utilize all ungulate species in proportion to their availability. Wolves may be more influential to elk survival and wolf presence, abundance, and the availability of other ungulate prey species should be carefully considered when future elk reintroductions are being planned.

Elk response to climate is clearly population-specific. I found that increased snow fall was associated with declines in population growth rates for only 2 of the 7 populations that were assessed and only 1 population responded negatively to increased summer temperatures. Climate likely interacts with other environmental variables and further investigations at a broad scale are required. Because the effects of climate on elk population growth rates are not consistent among populations, managers should be cautious when incorporating climate effects into future reintroduction planning.

Overall, it is hoped that the research described in this dissertation has provided important information, useful to elk managers across eastern North America. The results should contribute to planning future reintroductions and promote continuity of established reintroduced populations through management recommendations. The information in this dissertation also highlights the importance of within- and among- populations approaches when investigating factors that influence reintroduction success.

Appendix

(Additional articles published during PhD)

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Problem behaviour of black bears (*Ursus americanus*) in central Ontario: the effects of hunting and natural food availability

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Abstract

Problem bear behaviour in residential areas often results in human anxiety and potential injury, bear mortality and demographic instability. Identifying and understanding factors related to problem bear activity and encounters is important for developing successful management strategies. Indices of natural bear forage availability and hunting pressure were related to problem bear activity in central Ontario. Data were collected 5 years before and 5 years after the cancellation of a spring bear hunt, providing a unique opportunity to study the effect of management policy on problem behaviour. Problem bear activity indices increased significantly following the closure of the spring hunt. Natural food availability from the previous year was found to be highly correlated with early season problem bear activity indices; however, natural food availability during the same year was not significantly related to early or late season problem activity rates. This demonstrates that multiple potential causal agents of problem bear behaviour need to be considered when developing management strategies.

Keywords

Black bear; natural food availability; Ontario; problem behavior; spring hunt cancellation; *Ursus americanus*

Introduction

Understanding factors that contribute to nuisance behaviour of wildlife species is very important. With public pressure on wildlife managers to act, inappropriate strategies may be developed with inadequate information. Problem bear behaviour

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in residential areas can result in human anxiety, human injury, bear mortality and demographic shifts. Analyses of human-bear interactions, as well as bear population and habitat quality fluctuations are central to understanding the causes of problem bear activity and for the development of effective management strategies.

In 1961, the black bear (*Ursus americanus*) was classified as a big game species in Ontario, Canada, while prior to that, hunting of black bears was unrestricted. Bears were harvested under combined deer-bear hunting and trapper's licenses until 1980, when bear-only licenses were introduced. A new black bear management program was initiated in 1987 which included a Bear Management Area (BMA) system, with two hunting seasons: spring (April 15th to June 15th) and fall (September 1st to October 15th) (Poulin et al., 2003).

In Ontario, bears have been traditionally hunted over bait (Lompart, 1996). Most hunters pre-bait their sites 1-2 months prior to the hunting season in an attempt to ensure habituation of foraging bears to these locations. Hunting over bait is considered unethical by many people and it has been blamed for creating problem bears by association of humans with food. However, some Ontario bear hunters claim that it reduces problem bear activity by providing supplementary food sources in the natural environment (Poulin et al., 2003).

At central Ontario latitudes, common natural foods of black bears include; young ferns (*Osmundaceae*), grasses and sedges (*Graminae*), clovers (*Leguminosae*) and other forbs, aspen (*Populus spp.*) leaves, catkins and buds, a variety of northern berries, especially blueberries (*Vaccinium spp.*), and hard mast, such as acorns (*Quercus spp.*), beaked hazelnuts (*Corylus cornuta*) and American beechnuts (*Fagus grandifolia*). As opportunistic omnivores, bears also consume carrion and live prey such as bird eggs and nestlings, spawning fish, newborn ungulates, rodents, and insects such as grasshoppers and crickets, but mainly members of the Order *Hymenoptera* (ants, wasps and bees) (Jonkel & Cowan, 1971; Rogers, 1976; Boileau et al., 1994; Romain, 1996; DeBruyn, 1999; Pelton, 2000).

In Ontario, bears emerge from dens in April and their physical condition continues to decline until mid-summer, as energy-rich food is scarce during this period (Obbard, 2003). Thus, bears are most likely to access anthropogenic food sources during spring. Natural food varies in availability and abundance from year to year (Usui et al., 2005; Romain et al., 2013), and in central Ontario, blueberry production can vary from less than 10 kg to more than 100 kg per hectare (Landriault et al., 2000). Berry crop failures may occur as a result of late spring frost or summer drought, causing short growing seasons and inducing bears to seek alternate food sources (Banfield, 1974; Howe et al., 2010). Cub survival is often low following berry crop failures and few females produce offspring in the following winter (Rogers, 1976, 1987).

In January 1999, the Ontario Ministry of Natural Resources (OMNR) officially ended the spring bear hunt. The reason given for ending the hunt was the purported orphaning of cubs by hunters mistakenly killing lactating females. Ultimately, the end of the spring bear hunt was brought about through effective political lobbying by animal rights organizations, rather than sound scientific evidence (Poulin et al., 2003).

The spring bear hunt cancellation was expected to have an effect on black bear demography and problem activity. Prior to 1999, about 6000 bears were shot annually by hunters in Ontario, with the estimated spring cull ranging between 3000 and 5000 (OMNR unpublished data) and it is widely believed that the lack of spring hunting caused a substantial increase in the provincial bear population. Traditionally, the spring harvest targeted the male segment of the population, especially dispersing juveniles (OMNR unpublished data), and it was believed that higher numbers of males would increase competition for food and incidents of problem behaviour. As the standard OMNR management measure for dealing with problem bears in residential areas for 40 years (late 1970s to late 2000s) was trapping and relocation (Landriault et al., 2009), it was expected that the need for this OMNR management strategy would increase after the cancellation of the spring bear hunt.

In an effort to appease public concerns about anticipated increases in human-bear conflicts after the cancellation, the fall bear hunt period was expanded, starting in August 15th rather than September 1st. Subsequently in November 2013, the Minister of Natural Resources and Forestry announced the return of a two-year "pilot spring bear hunt", limited to 8 Wildlife Management Units (WMUs), which had previously reported high levels of "nuisance bear activity". The main impetus for reinstating the modified spring bear hunt according to the Ministry of Natural Resources and Forestry was the concern for safety of northern Ontario residents (OMNR, 2013). The reinstatement of the spring bear hunt has caused a considerable regional rift in public opinion. In this context, it is therefore important to examine and bring forward scientific information on the factors influencing the dynamics of problem bear behaviour.

Natural food availability and bear numbers are presumed to be the main determining factors affecting problem bear activity (Rogers, 1987, Obbard et al., 2003) and in northern Ontario, there is a general public perception that the 1999 cancellation of the spring bear hunt has resulted in increased problem bear behavior (Poulin et al., 2003). The primary objective of this investigation was to test the relationship between annual natural forage availability and problem bear activity. It was expected that problem bear activity would be inversely related to natural forage availability. The data for this study were collected prior to and after the 1999 cancellation of the Ontario spring black bear hunt, allowing for a direct comparison of the effects brought about by the policy change.

Materials and methods

Study area

Sudbury, Ontario is located at latitude 46°37′N and longitude 80°48′W and has a regional population of approximately 160 274 people (Statistics Canada, 2011). Mining and smelting operations had caused soil acidification, providing good conditions for blueberry production and extensive disturbances from logging, fire, and smelter operations have resulted in tree cover dominated by early succession species such as trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and white birch (*Betula papyrifera*). Hardwoods, such as sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are limited, while jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and eastern white cedar (*Thuja occidentialis*), occur where suitable soils remain (Rowe, 1972; Landriault, 1998). The topography consists of numerous rock outcrops and ridge systems that promote the growth of red oak (*Quercus rubra*) and attract wildlife dependent on mast food to the proximity of residential areas. There are numerous lakes and various wetlands and soils are primarily composed of shallow surface deposits containing silts and sands (Rowe, 1972). Mean daily temperatures range from −13.6°C in January to 19°C in July, with a mean annual rainfall of 656.5 mm and a mean annual snowfall of 274.4 cm (Anonymous, 2006). The mean number of days with measurable snowfall is 78.4 (Environment Canada Sudbury Weather Station data).

Bear and natural forage statistics

Problem bear capture statistics between 1994 and 2004 were obtained from the Ontario Ministry of Natural Resources (OMNR). Captures occurred annually from May to November and followed a standard Ministry of Natural Resources problem bear handling protocol (Landriault et al., 2009). Since bear captures were implemented only if property damage occurred and/or a threat to residents, pets or livestock was perceived, they were considered a more accurate representation of problem bear activity than telephone complaint calls, which were also collected.

Bear Population Index surveys were initiated in 1997 by OMNR and continued until 2004. The surveys were based on the annual 'hit rate' (visits) by bears to 50 km transects with sardine can stations set out in a standardized manner 1 km apart along secondary roads (McLaren, 1999). Bait stations consisted of three cans of partially opened sardines packed in oil and suspended from a horizontal branch 2.5 meters from ground. Smooth, soft-barked tree species, such as balsam fir and poplar were selected to detect bear claw marks. Bait station transects were initiated during the 3rd week of June and checked one week after installation. Evidence of a bear "hit" included claw marks on the tree, tooth marks on cans, hair, scat, tracks, sardine cans pulled down, consumed sardines, and missing cans. The annual number of bear "hits" was compared to the annual number of problem bear captures, with the goal to provide a rough index of annual population changes in local bear numbers and activity.

Howe and Obbard (2014) calculated black bear natural food indices using data from Wildlife Food Availability surveys implemented by the Ontario Ministry of Natural Resources and Forestry. The prevalence and productivity (in terms of seed and fruit production) were recorded in given areas for 20-30 plant species, or groups of plant species, used as food by black bears (Obbard et al., 2014). The black bear natural food index for the Sudbury region was subsequently analyzed with respect to problem bear captures from 1998 to 2002 for correlations. In order to substantiate a cause and effect relationship between forage quality and problem black bear behaviour an experimental study design would be ideal, however; due to the lack of availability of a control site in our study, we were restricted to an observational study.

The spring bear hunt was closed in 1999 and using 4 years prior to the hunt cancellation (1995-1998) and 4 years after its cancellation (2001-2004), the effect of the cancellation on problem bear activity, as measured by the total number of bear captures per annum, was analyzed by Chi-squared test.

Monthly profiles of bear problem behaviour rates (measured by captures) were created to examine the time of year when problems were most prevalent. Based on this profile, capture rates were compiled into early (May to July) and late (August to October) seasons. As time series data can be auto-correlated, Durban-Watson tests were used to determine whether there was significant auto-correlation in the data. Regression analyses were then used to determine if early and late season capture rates were correlated to the bear natural food index (Howe & Obbard, 2014) in the same year, as well as 1-year later. All data were analyzed using the statistical package “R”.

Results

Annual numbers of problem bear captures were significantly higher during 4 years after the cancellation of the spring bear hunt as compared to 4 years before ($X^2 = 172.53$, df $= 1$, $P < 0.001$). The bear capture rate was highest in 2001; two years after the closure of the spring hunt (fig. 1), which was an unusually poor year in natural food availability (Howe & Obbard, 2014). Additionally, problem bear captures in Sudbury followed a bimodal pattern with an early season peak in June and another in September-October (fig. 2) and the number of bait transect hits by bears were highly correlated with the number of captures ($R^2 = 0.77$, fig. 3).

Neither early nor late season capture rates were strongly correlated with bear food availability during the same year (Early: $R^2 = 0.001$, $P = 0.96$; Late: $R^2 = 0.62$, $P = 0.11$); however, early season bear capture rates were highly correlated with the previous year’s bear food quality ($R^2 = 0.94$, $P = 0.007$; fig. 4). Late season bear captures were not significantly related to previous year’s bear food quality ($R^2 = 0.10$, $P = 0.60$).

Discussion

Adequate natural food availability is essential for successful bear reproduction and thus a primary determinant factor influencing bear numbers (Herrero, 1985). The availability and quality of preferred bear foods normally fluctuate from year to year (Craighead et al., 1995). In our study, current year’s bear food availability in the

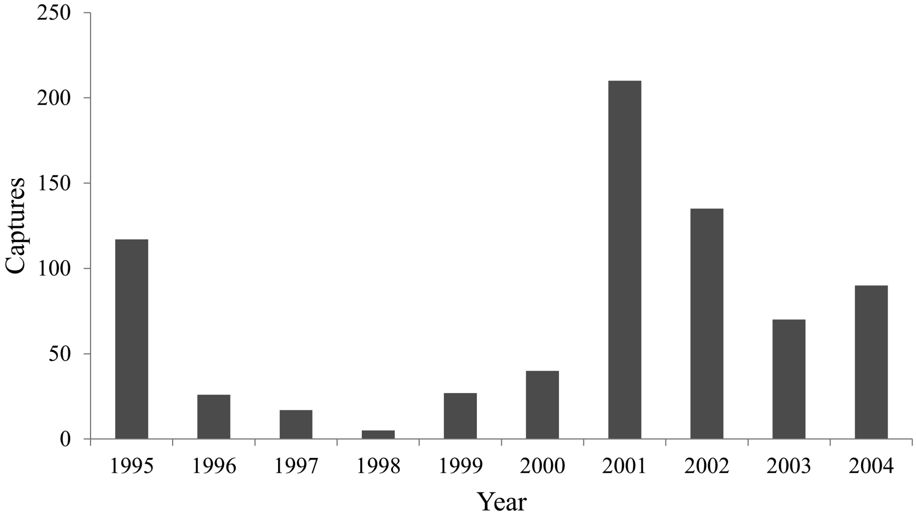

Figure 1. Annual number of black bear (*Ursus americanus*) captures in the Sudbury area of central Ontario.

Sudbury area of central Ontario was not correlated with either early or late seasonal bear problem behavior; however, previous year's bear food quality correlated strongly with bear problem behaviour early in the following season. This supports the conclusion that low natural food availability in one year makes bears more prone to seeking alternate food sources, causing an increase in problem activity in the following spring. Although the validity of the bait transect surveys has been questioned (Obbard, pers. comm.), the annual number of bear hits on bait stations showed a close relationship to the annual number of problem bear captures during 8 summers.

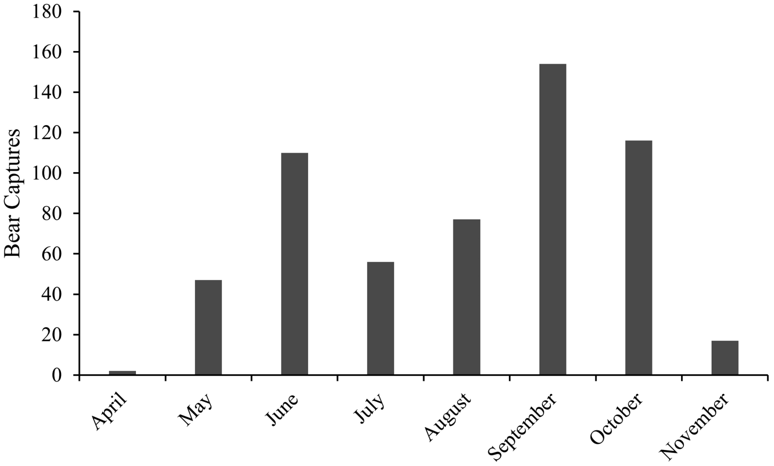

Figure 2. Total number of monthly problem black bear (*Ursus americanus*) captures in the Sudbury area for data collected between 1995 and 2004.

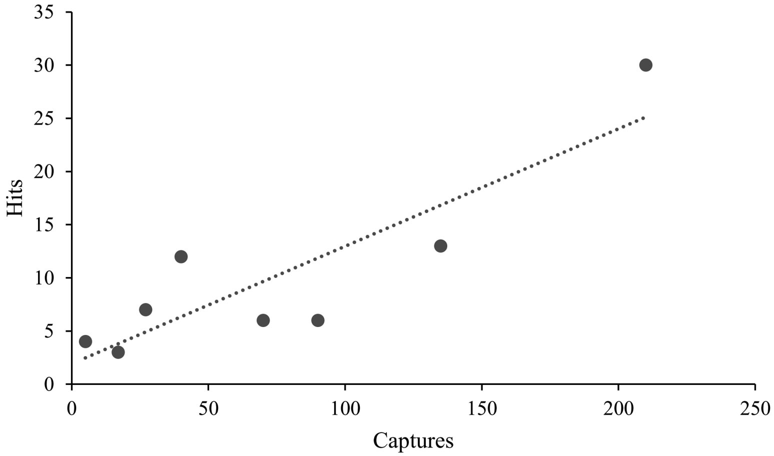

Figure 3. Correlation of the annual number of black bear (*Ursus americanus*) "hits" per bait transect survey and the number of problem bear captures in the Sudbury area between 1997 and 2004.

This finding supports the conclusion that bait station hits are a reasonable indicator of natural food availability rather than bear population density. Noyce & Garshelis (1997) observed that the annual number of harvested black bears in Minnesota depended more on natural food availability than bear density, as most hunters used bait to attract bears. Garshelis (1989) also found a relationship between summer natural food availability and problem bear activity levels in Minnesota.

Effects of food availability on problem bear activity have been observed by others during and following years of natural crop failures (Rogers, 1976; Shull, 1994; Obbard et al., 2003). When natural food is scarce, bears forage more widely and are more likely to come into contact with humans and human-based food sources

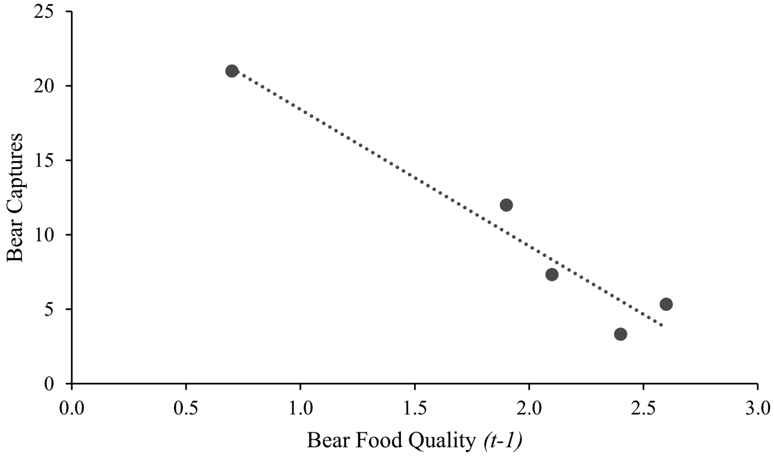

Figure 4. Early season (May, June, July) black bear (*Ursus americanus*) captures in relation to bear food quality of the previous year.

(Garshelis & Pelton, 1981; Garner & Vaughan, 1989; Garshelis, 1989; Gunther et al., 2004). Garshelis (1989) suggested that increases in problem bear activity following poor food years may be related to poor body condition at emergence from dens. It has also been noted that seasonal fruit and nut production can influence reproductive success and body mass the following spring (Rogers, 1976, 1987).

Significant increases in public complaint calls and problem bear captures occurred in central Ontario after the 1999 cancellation of the spring bear hunt in both rich and poor food years (Brown, 2007). Thus, either problem bear activity, or public sensitivity to bears, or both, likely increased after the cancellation of the spring bear hunt, independently of changes in food availability. Intense publicity increases public sensitivity to the presence of bears. Ordinary animal sightings often lead to complaint calls to the authorities requesting problem bear control (Ontario Provincial Police, OMNR, pers. comm.). The apparent 1999 increase in problem bear complaints by the public in some central Ontario jurisdictions should be viewed in this light. Obbard et al. (2003) also suggested that heightened public awareness of black bear issues may have led to an increase in reporting rates after the 1999 spring hunt cancellation. However, the present study suggests that natural food availability, in the previous year, is likely the chief determinant factor of problem bear activity in any given year.

Since the cancellation of the spring hunt, the annual bear harvest in Ontario has been reduced by approximately 1550 animals, representing about 1.5-2.1% of the estimated provincial population (Poulin et al., 2003). Obbard (2003) noted that black bears are long-lived mammals with low reproductive rates, whose females do not begin to breed until 4-5 years of age. He therefore speculated that any immediate increase in problem bear activity could not be attributed solely to changes in bear numbers, since bear numbers change slowly. Garshelis (1989) also reported that increases in complaint calls were poorly correlated with increases in bear numbers in Minnesota. A recent study by Obbard et al. (2014) on the relationships between food availability, human-bear conflicts and bear harvest in Ontario showed that human-bear conflicts were negatively correlated with food availability across the province. The authors also found no evidence that larger prior bear harvests reduced subsequent human-bear conflicts (Obbard et al., 2014).

Poor food years result in reproductive synchronization of female black bears, which results in the appearance of a large cohort of cubs two years after the crop failure (McLaughlin et al., 1994). As these animals later become dispersing juveniles and attempt to establish home ranges of their own, the chances of encountering humans and causing conflicts can increase. Obbard et al. (2003) reported large cohorts of cubs born in Ontario in 1997, 1999 and 2001, which were attributed to synchronization of the female breeding cycle after the 1995 crop failure. Along with increased public sensitivity to bears following the spring hunt cancellation, a large class of dispersing juveniles may have accounted for the 5-fold increase in captured problem bears in Sudbury from 1998 to 1999.

In conclusion, results of this study lend support to the notion that natural food availability and problem bear activity are linked. Effects of annual and regional fluctuations in natural food production on problem bear behaviour appear to overshadow changes in bear harvesting practices, such as the cancellation of the spring bear hunt. Therefore, it follows that the recently introduced pilot spring bear hunt will not likely induce significant changes in problem bear activity across central Ontario. Importantly, the one year time lag in the effects of natural food production on problem bear activity allows for the design of predictive models of problem bear activity as a function of annual natural food yields. If widely adopted, this approach could facilitate management and conservation of this important species.

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Fine-scale tertiary-road features influence wildlife use: a case study of two major North American predators

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Abstract

Roads have become a major concern for wildlife managers. Determining if fine-scale features influence wildlife road use is crucial information when developing management strategies to protect species at risk or to assist in preventing negative trophic interactions. We investigated the effects of fine-scale habitat and road-related features on the tertiary-road use of two major predator groups, the American black bear (*Ursus americanus*) and wolves (*Canis lupus*, *C. lycaon*, and hybrids). Scat occurrence, used as a measure of a species' intensity of use, along with several road-related features and surrounding fine-scale habitat variables, were recorded within tertiary-road segments near Sudbury, Ontario, Canada. An information theoretic approach was used to determine which of several different candidate models best predicted tertiary-road use by our major predator groups. Road width and distance to primary roads were found to be the strongest predictors of occurrence on tertiary roads for both predators, with smaller road width and greater distances to primary roads leading to higher levels of occurrence. Habitat cover and cover type, expected to influence foraging opportunities, were not found to be strong predictors of tertiary-road use. Our findings highlight the importance of fine-scale studies for understanding road use.

Keywords

Anthropogenic disturbance; black bear; *Canis lupus*; road; *Ursus americanus*; wolf

Introduction

Wildlife habitat studies are a major aspect of ecological research and are often examined over multiple spatial scales. Broad-scale habitat selection studies based on landscape level classifications are common, as larger scales will inherently constrain decisions made at finer scales (Johnson, 1980); however, research also

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highlights the importance of understanding the fine-scale aspects of specific habitat patches or features, especially when considering anthropogenic disturbance. For instance, animals can select for or avoid habitat patches based on fine-scale features such as the level of cover or the abundance of a particular type of forage (Briand et al., 2009; Godbout & Ouellet, 2010). Changes in fine-scale features caused by anthropogenic disturbance can result in the lowered use or abandonment of previously utilised areas (Hodson et al., 2010; Pike et al., 2010). Understanding fine-scale relationships between wildlife and their respective habitats can assist managers in mitigating the impacts of anthropogenic disturbance.

Roads have become a common feature in many managed wildlife landscapes and have been linked both directly, and indirectly, to wildlife mortality, reproductive depressions, and population persistence (Hu et al., 2005; Whittington et al., 2011; Heinrichsa et al., 2015; Souza et al., 2015). Multiple broad-scale habitat selection studies have underlined the tendencies of animals to avoid roads, thus becoming barriers to movement (Dyer et al., 2001; Meisingset et al., 2013; Litvaitis et al., 2015). Decisions to avoid roads by wildlife have been shown to be related to the level of traffic, with heavier traffic generally leading to greater levels of disturbance for wildlife (Montgomery et al., 2012; Northrup et al., 2012). Although some wildlife has been documented avoiding higher level traffic areas, many predators have been observed utilising low traffic roads which enable easier movement through habitats (Dickson et al., 2005; Northrup et al., 2012; Van Manen et al., 2012; Zimmermann et al., 2014). However, roads can facilitate movement for some species but can act as barriers to movement for others (Laurance et al., 2004; Hu et al., 2005; Bartzke et al., 2015). The presence of roads can therefore lead to dramatic shifts in trophic interactions (Whittington et al., 2011; Courbin et al., 2014; Graeme et al., 2014), and altered predation pressures on prey species (Kunkel & Pletscher, 2000; Whittington et al., 2011). Understanding the fine-scale habitat and road-related features influencing predator use of low-traffic, tertiary roads, can thus not only help managers understand predator-road relationships, but can also potentially assist in mitigating the impacts of roads on prey species. However, few studies have identified fine-scale features associated with road use beyond traffic level, such as road width or road-side vegetation.

We selected two common major large predators with extensive ranges across North America to determine if fine-scale features are associated with predator road use. The American black bear (*Ursus americanus*) and the grey wolf (*Canis lupus*) have been shown to avoid high activity roads (Gurarie et al., 2011; Van Manen et al., 2012); however, they have been found to strongly select for tertiary or low-use roads (Gurarie et al., 2011; Latham et al., 2011; Lesmerises et al., 2012). By using scat location as a measure of a species' occurrence, a method that has been introduced as a non-invasive way to identify space use (Wasser et al., 2011), we evaluated whether surrounding fine-scale habitat and road-related features influenced the use of tertiary roads by each species.

Materials and methods

Study area

Our study area was located approximately 30 km south of the City of Greater Sudbury in Ontario, Canada in the Great Lakes – St. Lawrence Ecotonal Forest Region (Rowe, 1972). It consisted of an area approximately 300 km^2 mainly comprised of mixed conifer-hardwood forests (Chambers et al., 1996) with many valleys and water bodies (lakes, rivers, wetlands), and approximately 4000 ha of open abandoned fields. There were two primary roads, one adjacent to (Hwy 69) and one through our study area (Hwy 637; fig. 1). Tertiary roads within our study area were defined as unpaved roads used primarily for logging and recreational purposes.

The two major large predator groups in the region are black bears and wolves (*Canis lupus*, *Canis lycaon*, and hybrids between the two). Because of the "Canis soup" in the upper Great Lakes region (Wilson et al., 2009), we use the term "wolves" to describe wolves and their hybrids as they are difficult to distinguish. Our study area had an estimated 0.24 black bears per km^2 (OMNR, 2014). Wolf density in the area was estimated to be between 0.02 to 0.03 wolves per km^2 (Kittle et al., 2008). Common prey species to these predators within our study area include white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), moose

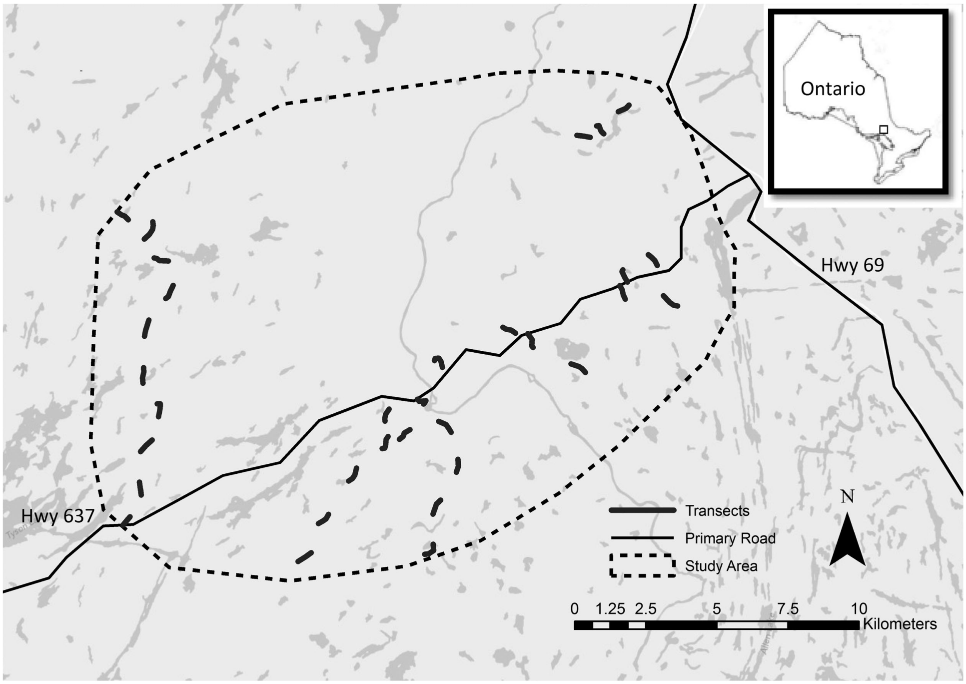

Figure 1. Location of study area and transects with respect to primary roads in Ontario, Canada. The upper right inset shows the location of the area within the contour of Ontario. The darker grey areas represent water bodies; the transects were on tertiary roads. Abbreviation: Hwy, highway.

(*Alces alces*), beaver (*Castor canadensis*), and muskrat (*Ondatra zibethicus*) (Popp, *unpublished data*).

Data collection

We used tertiary-road transects (of 500 m stretches) as our primary sampling unit ($N = 32$), as this allowed us to relate surrounding habitat and road-related features to intensity of use. Wolf and bear scat locations along tertiary roads were recorded over a three-year period from the beginning of May to the end of August from 2013 to 2015. We selected the summer season because of the high sightability of scat. Scats were identified and recorded by the same observer to remove bias (Spaulding et al., 2000). An ATV was used to search for scat; we maintained driving speeds of 10-15 km/hour to ensure consistent sightability. Roads were sampled every 2 weeks at each location and once scat locations were recorded, scats were removed from the road to eliminate resampling. To ensure thorough coverage of the study area, every tertiary road with adequate ATV access was sampled.

Tertiary roads were subdivided into 500 m segments that were $\geqslant$1 km from each other if on a continuous stretch. We calculated Moran's I using the R package 'ape' (Paradis et al., 2004) for wolf and bear scat contained within each road segment to determine their spatial independence. To characterise fine-scale habitat within each 500 m road segment, several habitat features were recorded every 100 m of each road segment at the end of our study period in our last study year. Road-related features measured included road width, as well as road cover type in a 1-meter span across the entire road width (% herbaceous cover, % gravel and dirt cover). The percentage of different habitat types within a 10×10 m area starting from the roadside were recorded (% herbaceous, shrub, wetland, forest) with the road side examined (left or right) chosen randomly. The percentage of canopy cover was measured using a densitometer held at waist height 5 m from road edge. Because both wolves and bears have been shown to avoid high traffic areas (Gurarie et al., 2011; Van Manen et al., 2012), we used ArcGIS v10 to measure the straight-line distance of the center of each road segment to the nearest primary road within our study area.

Data analysis

Values for each habitat variable from all sites measured within each transect were averaged to create one value per transect (Elzinga et al., 2001). Where strong correlation between independent variables was found (Pearson Correlation value > 0.5), only one variable was kept within the analysis.

We created 6 different candidate regression models expected to reflect different habitat features that may have been influencing animal road-use based on their relation to anthropogenic disturbance and foraging opportunities. Forage availability was assumed to be related to the percentage of vegetation cover. Black bears forage on green vegetation, such as grasses and sedges, as well as fruit during the summer

(Raine & Kansas, 1990; Costello, 1992; Romain et al., 2013), and have been found to select areas with higher abundances of food items, including wetlands and open canopy areas (Costello & Sage, 1994; Fecske et al., 2002). Wolves have been shown to select for areas where there is a higher abundance of their prey items (Lesmerises et al., 2012). Wetlands, grasslands and shrub-rich areas are likely to contain moose, white-tailed deer or elk during the summer season (Cairns & Telfer, 1980; Ricca et al., 2003; Nikula et al., 2004; Anderson et al., 2005; Masse & Cote, 2012; Street et al., 2015). Smaller prey species like beaver and muskrat are generally found in wetland areas. Therefore, the percentage of wetland, shrub, and herbaceous area was predicted to represent potential foraging opportunity.

All statistical analyses were conducted using the 'R' statistical software v.3.0.1 (R Core Team, 2013). Interaction terms were only maintained within candidate models if found to be significant (Zuur et al., 2009). Akaike's Information Criterion corrected for small sample sizes (AICc) was used to determine model fit among candidate models using the package 'MuMIn' (Barton, 2014). If the top ranking model had a model weight below 0.90, then model averaging was applied to all models which had a weight above 0.10.

Results

In total, 73 wolf and 97 bear scats fell within transects. Moran's I was non-significant for both wolves and bears ($P > 0.05$), and road segments were therefore treated as independent. Strong correlations were found between the percentage of forest on road sides and the amount of canopy cover (Pearson Correlation value = 0.90), as well as between our two road-cover variables (Pearson Correlation value = −0.58). As such, only canopy cover and the percentage of herbaceous road-cover were included within our statistical analysis.

The information theoretic approach identified the importance of the same two features in determining bear and wolf occurrence on a tertiary-road transect: the distance of a road transect to highway primary-road, and the width of the road they were utilising (table 1). Models containing vegetation features, as well as road-surface features were found to be among the lowest ranking models for both species (table 1). The model which did not contain distance to a primary road or road width was our lowest-ranking model for both species (table 1).

Both bears and wolves tended to utilise road transects with decreased width (table 2). There was also a higher level of bear occurrence on road transects farther away from primary roads within our study area (table 2). Wolf occurrence was influenced by an interaction between road width and distance to a primary road, which suggests that as wolves become farther from primary roads, the effects of road width on wolf occurrence decreased (table 2). Similarly, as wolves become closer to primary roads, road width became more important in predicting their occurrence on tertiary roads.

Table 1.
Relative support for candidate models explaining variation in wolf and bear scat occurrence in relation to road and habitat features.

No.	Model	df	LogLik	ΔAICc	W
Bear					
1	road width + distance to primary road	4	−31.41	0.00	0.79
2	distance to primary road	3	−34.21	2.97	0.18
3	road width + canopy cover	4	−35.00	7.18	0.02
4	distance to primary road + % herbaceous + % shrub + % wetlands	6	−33.35	9.75	0.01
5	road width + % herbaceous + % shrub + % wetlands	6	−34.81	12.67	0.00
6	% herbaceous road cover + % herbaceous + % shrub + % wetlands	6	−35.77	14.59	0.00
Wolf					
1	road width × distance to primary road	5	−32.35	0.00	0.83
2	distance to primary road	3	−37.11	4.07	0.11
3	road width + canopy cover	4	−36.99	6.45	0.03
5	road width + % herbaceous + % shrub + % wetlands	6	−34.93	8.21	0.01
4	distance to primary road + % herbaceous + % shrub + % wetlands	6	−35.71	9.78	0.01
6	% herbaceous road cover + % herbaceous + % shrub + % wetlands	6	−35.74	9.84	0.01

Abbreviations: df, degrees of freedom of each model; LogLik, the natural logarithm of maximum likelihood for each model; AICc, the Akaike's information criterion adjusted for small sample size bias; ΔAICc, the change in AICc; W, the Akaike weight for each model.

Table 2.
Model-averaged summary statistics for top ranking candidate models predicting the probability of predator scat occurrence on a road.

Covariate	β	SE	95% CI		i
			Lower	Upper	
Bear					
Distance to primary road	1.33	0.54	0.23	2.42	1.00
Road width	−0.20	0.08	−0.36	−0.02	0.80
Wolf					
Road width × distance to primary road	−1.35	0.51	−2.38	−0.31	0.88
Distance to primary road	1.04	0.58	−0.14	2.22	1.00
Road width	−0.23	0.09	−0.42	−0.04	0.88

Each of the models co-variables are presented with its coefficient (β), standard error (SE), 95% confidence interval (95% CI), and relative variable importance (i).

Discussion

We found that bears and wolves are sensitive to road features that are measurable on a fine scale. For both of our study species, road width and distance to a primary road were the most important features influencing species occurrence. Although predator road-use has been found to be related to increased forage availability (Roever et al., 2008), our results indicate that wolf and black bear occurrence on roads was not strongly driven by vegetation features. Wolves are active predators that select for areas with a high abundance of prey items (Lesmerises et al., 2012), whereas black bears tend to be more opportunistic, drawn to habitats with abundant vegetation (Bastille-Rousseau et al., 2011). We found strong similarities in the variables predicting the occurrence of wolves and bears on tertiary roads, despite their different foraging strategies. This suggests food does not motivate fine-scale selection of roads. Future studies should directly measure prey-species abundance near roads and species-specific forage occurrence to further investigate food motivations underlying road selection. Regardless, anthropogenic disturbance appeared to be the major driver of tertiary-road use for each species. Our results therefore suggest that black bears may be utilising tertiary roads to facilitate movement during the summer, just as other research has found for wolves (Gurarie et al., 2011; Zimmermann et al., 2014); however, GPS collaring of black bears to monitor movement should be used to test this hypothesis.

Habitats with increased exposure to anthropogenic features have been previously linked to increased levels of stress in multiple large mammal species including wolves and black bears (Creel et al., 2002; Wasser et al., 2011; Ditmer et al., 2015). Decreased road width may increase the level of security that a predator feels when utilising a road, which may therefore increase road use. This idea is supported by the interaction we observed between road width and the distance to a primary road on wolf occurrence. Higher levels of traffic are perceived as a greater risk for most wildlife species (Gavin & Komers, 2006; Wasser et al., 2011); therefore wolves may feel more secure on roads with smaller widths when closer to high disturbance areas (such as a highway). It is also possible that tertiary roads with greater width are utilised more for human recreation than those with smaller widths. Similarly, there may have been easier access to tertiary roads near the major highways for recreational road users, which may have increased road use. Future investigations which distinguish distance from primary roads and road width from human traffic will be of great value to managers, as they could suggest the effectiveness of seasonal road closures to increase predator tertiary-road use. It is also important to note that because our data was restricted to the summer season, seasonal interactions associated with road use could not be deduced; however, they likely are present for both species. As such, further investigation into seasonal interactions related to predator road use should be conducted.

The results of this study could be used by managers to mitigate the effects of tertiary roads on predators at risk. Decreasing tertiary-road width will likely help decrease the impacts of roads on predators within a managed area, decreasing the level of predator habitat fragmentation. On the other hand, creating roads with larger widths and maintaining tertiary roads near higher level traffic areas may decrease predator road use as travel corridors. This could potentially help to reduce the predator-prey imbalance created by tertiary roads which can lead to higher levels of predation threat to prey species (Kunkel & Pletscher, 2000; Whittington et al., 2011). In addition, these results should be considered by researchers seeking high probability of occurrence of these large predators (i.e., camera trap or scat collection locations), as it is likely that sightings will be greater on tertiary roads with smaller width and farther from major human disturbances.

We found that predator use of tertiary roads is influenced by both the distance to primary roads and road width, suggesting that these attributes should be considered in wildlife habitat assessments. We suggest that fine-scale road features can provide crucial baseline information to both managers and researchers for mitigating the impacts of roads on ecosystem function.

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