Influence of Anthropogenic Development on Burrowing Owl Habitat Selection, Survival, and Reproductive Success

by

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ABSTRACT

Anthropogenic development may influence the choices animals make and their resulting reproductive success and survival. If such choices are maladaptive, the impact of changes to their habitat could be catastrophic to populations that are small or declining. The Canadian prairies have changed dramatically since European settlement. Over two thirds have been converted to cropland and the number of petroleum wells within the Burrowing Owl range has tripled over the last thirty years. It is assumed that the decline of the Burrowing Owl is linked to these changes to the prairie landscape, but so far no clear, direct links have been identified. I examined habitat selection of Burrowing Owls at several temporal and spatial scales and evaluated how habitat selection influenced survival and reproductive success. First, I identified landscape features that Burrowing Owls prefer to have surrounding their nests, and examined how these preferred features related to nest survival, fledging rate, and adult survival. Using arrival date as a measure of preference, I found Burrowing Owls prefer home ranges with more annual crop and more road surfaces. These anthropogenic landscape features had a positive influence on fledging rate, suggesting that these landscape features have not created an ecological trap for Burrowing Owls on the Canadian prairies at the home range scale. Second, I tracked adult male Burrowing Owls with GPS dataloggers and examined owl space-use during the day and night. During the day, Burrowing Owls spent more time near fences and posts, likely because they are good vantage points for detection of predators. They also avoided roads with high traffic speeds, possibly because auditory disturbance from passing vehicles interferes with their ability to communicate the presence of predators to their mates and young. At night, the infrastructure (towns, roads, petroleum facilities, and oil wells) that results from human development influenced where owls spent time much more than did sensory disturbances (artificial sound and light) emanating from these sources. However, owl selection of landscape features at night did not predict reproductive success. Instead, I found owls that spent more time near the nest burrow between sunset and sunrise had the greatest nest survival and fledging rates. The choices this endangered owl makes when hunting at night and when picking a landscape in which to settle do not seem to be maladaptive or fully explain their population decline in Canada. To better understand the Burrowing Owl decline, future studies need to focus on life history stages not examined here (e.g. post-fledging for juveniles), as well as stages that occur outside of their breeding range. My findings indicate that the Burrowing Owl has flexible habitat requirements and is able to breed successfully in a developed landscape. Such determinations will be important to make for a variety of other species to identify those that may be less likely to be able to adapt to changing landscapes.

PREFACE

A version of Chapter 3 of this dissertation has been published as C. Scobie, E. Bayne, and T. Wellicome, "Influence of Anthropogenic Features and Traffic Disturbance on Burrowing Owl Diurnal Roosting Behavior", Endangered Species Research, vol. 24, 73-83. I was responsible for data collection, analysis and manuscript composition. E. Bayne assisted with the analysis and contributed to manuscript edits. T. Wellicome assisted with data collection and manuscript edits.

Dedicated with all my love to my wife Becci and our three little miracles.

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CHAPTER 1. INTRODUCTION[1]

1.1 Scale of selection

All species make behavioural choices at several scales throughout their life. These choices affect the resources available to them and, ultimately, their resulting reproductive success and survival. Poor choices can be made at any scale, but the impact of this choice on their fitness is generally proportional to the scale at which the choice is made. For example, the negative consequences of choosing a home range with a high abundance of predators is likely greater than choosing to hunt in a particular location, on a given night, where fewer prey are captured. Four orders of selection have been defined to help describe the hierarchy of scales at which animals make choices (Johnson 1980). Patterns of use can be detected at all of these scales, but the ramifications of these patterns are greater when there are clear links to fitness.

First-order selection is the selection of the physical geographical range of a species (Wiens 1973). Typically, only a small proportion of a population venture outside their geographical range, but those that do usually have lower fitness otherwise the range would likely expand (Bloom et al. 2011, Sealy and Carter 2012). Though selection at this scale has the greatest potential impact on individual fitness, this order of selection is often unimportant when trying to understand the persistence of a population. However, studying a population at this scale helps identify range contraction and population decline within particular geographical locations. Understanding the causes of a population decline comes only when higher orders of selection are examined. Furthermore, higher orders of selection can be used to build predictive models that help identify an organism's geographical range and identify important population drivers (see Stevens et al. 2011).

Second-order selection determines the home range of an animal (Wiens 1973, Johnson 1980) and most often has the greatest realized effect on the population. Animals will settle in what they perceive to be the highest quality habitat (Clark and Shutler 1999), but the resources

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[1] Chapters 1 and 6 are my own thoughts and therefore I use the pronoun "I" throughout. The research in all other chapters was collaborative.

and risks present in the landscape ultimately dictate their fitness. Therefore, second-order selection is driven by selection at the third and fourth orders of selection. Animals will choose a home-range that has characteristics that indicate potential future food availability or predation risk (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Kristan 2003). An ecological trap occurs when the landscape characteristics do not accurately depict resources available in the home-range and animals prefer to settle in areas where they have lower reproductive success than in less-preferred areas (Kristan 2003, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007, Part et al. 2007). Once settled into a home range, the choices available to an animal are restricted, and thus the mechanisms of an ecological trap are the use of sub-optimal resources at the third or fourth orders of selection. Therefore, understanding higher orders of selection is important in understanding how ecological traps may form.

Third-order selection is most often studied by tracking individuals within their home-range. Selection at this scale refers to the use of habitat components within the home range (Johnson 1980), and could influence the fitness of an individual and potentially the population if many individuals are making the same choices (see Garabedian et al. 2014, Marchand et al. 2015). Fourth-order selection occurs at a local scale within a home-range, where an animal acquires a resource such as a den or nest (Poulin et al. 2005, Elbroch et al. 2015), roost (Blakesley et al. 1992) or food (Bond et al. 2002). A single fourth-order selection decision can affect a specific aspect of an individual animal’s life, but may have only a very slight effect on overall fitness. However, when that decision is made repeatedly it can have considerable implications for individual fitness.

There is also a temporal scale in habitat selection because the choices an animal makes in the present have repercussions in the future. Many factors determine how far into the future a choice affects an animal, but duration and degree to which they are committed to a choice defines the scale (Orians and Wittenberger 1991). Temporal and spatial scales are intertwined. For example, when choosing where to forage (third-order selection), an animal that is sessile while breeding is limited by the landscape in which it decided to breed (second-order selection). The animal’s foraging landscape is limited throughout the period of the breeding season by a choice it made at the beginning of the breeding season. Choices made at smaller temporal and spatial scales have the greatest impacts on populations, but require exploration at larger scales to understand how.

1.2 Study species

The Western Burrowing Owl (*Athene cunicularia hypugaea*) is the smallest owl found on Canada's grasslands. Typically, they nest within burrows in grazed pastures (Poulin et al. 2005). Burrowing Owls nest in holes dug by other animals, and rarely do any digging other than for the purposes of maintaining or enlarging the burrow. Throughout most of North America, Burrowing Owls rely heavily on burrows dug by prairie dogs (*Cynomys* spp.). However, in Canada, the majority of used burrows are dug by American badgers (*Taxidea taxus*), but the owls will also use holes dug by Richardson's ground squirrels (*Urocitellus richardsonii*), foxes (*Vulpes* spp.) or coyotes (*Canis latrans*; Wellicome 1997, Poulin et al. 2005). Placing the nest in a burrow allows greater concealment from predators and shelters the nest contents from adverse environmental conditions. The nest burrow and nearby burrows are also used to cache excess prey.

Burrowing Owls over-winter in the Southern United States and Mexico, and typically arrive in Canada in April, prior to breeding. They finish laying an average of nine eggs (range: five to fourteen) in May, which then hatch approximately 30 days later in early-to-mid June (Wellicome 2000). Extreme precipitation events have been found to contribute substantially to nest failures and lower owlet survival (Fisher et al. 2015). When nesting attempts are successful, typically only four chicks survive to fledging age (35 days old), with almost all of the remainder succumbing to starvation (Wellicome et al. 2013). Primary predators include American Badgers and large raptors such as Swainson's Hawks (*Buteo swainsoni*), Great-Horned Owls (*Bubo virginianus*) and Northern Harriers (*Circus cyaneus*).

Burrowing Owls are active during both day and night, but day-time movements are typically restricted to the vicinity of nest or satellite burrows (Plumpton and Lutz 1993, LaFever et al. 2008, Scobie et al. 2014) and few vertebrate prey items are delivered to the nest (Poulin and Todd 2006). Male owls travel further from the nest during dawn and dusk, primarily for the purpose of hunting for vertebrate prey (Marsh 2012). Vertebrate prey (largely mice and voles) constitute the majority of the biomass consumed by Burrowing Owls (Poulin and Todd 2006). A variety of invertebrate prey items are also eaten, including beetles, grasshoppers, moths, and occasionally earthworms and insect larvae. Males deliver mostly vertebrate prey to nestlings and females contribute mainly invertebrate prey (Poulin and Todd 2006).

The Western subspecies of the Burrowing Owl occurs within central and western North America from Canada to Mexico. They were once common in each of the four western provinces in Canada, but their breeding range has contracted southward and westward over the last 30 years (Wellicome and Holroyd 2001, Macias-Duarte and Conway 2015). Currently, they are found primarily in Alberta and Saskatchewan, with occasional individuals recorded in the southwest corner of Manitoba, and a small population in British Columbia that is maintained through a captive breeding program (Mitchell et al. 2011). The Burrowing Owl population in Canada has declined by approximately 90% since European settlement of the grasslands and was classified as endangered in 1995 (Wellicome and Haug 1995). Though not listed under the United States *Endangered Species Act*, the Burrowing Owl is listed as Endangered in Minnesota, threatened in Colorado and a Species of Concern in seven other states (Klute et al. 2003). The Burrowing Owl breeding range is contracting at the northern, eastern, and western edges (Wellicome and Holroyd 2001, Macias-Duarte and Conway 2015).

Research in my study area has found that Burrowing Owls have similar reproductive rates to owls nesting in other parts of their range. Average yearly nest success of owls nesting in the Canadian Great Plains ranges from 59% (Haug 1985) to 72% (Sissons 2003). Average nest success in other parts of their range falls within this range (Smith et al. 2005, Crowe and Longshore 2013), but was lower in Oregon (56 %; Holmes et al. 2003) and Washington (51%; Conway et al. 2006) and higher in New Mexico (86%; Berardelli et al. 2010) and North Dakota (82.5%; Restani et al. 2008). Burrowing Owl productivity is well studied in California and average yearly nest success has been observed to be as low as 48% (Ronan 2002, Trulio and Chromczak 2007) and as high as 79% (Barclay et al. 2011). On average, more than 4 juveniles fledge per successful nest each year in the Canadian Great Plains (Haug 1985, De Smet 1997, Wellicome et al. 2013). Most studies in other parts of the North American range (outside of Florida) fledge an average of no more than 4 juveniles per successful nest (Ronan 2002, Smith et al. 2005, Conway et al. 2006, Trulio and Chromczak 2007, Restani et al. 2008, Berardelli et al. 2010, Barclay et al. 2011). The greatest number of juveniles that fledged from successful nesting attempts outside of Canada was documented in Nevada (4.9; Hall and Greger 2014). Caution should be used when directly comparing the reproductive rates from these studies because they use different methods to measure nest survival, some of which (e.g. apparent nest survival) can be biased because early nest failures are often missed (Mayfield 1975, Shaffer 2004). Also, various methods were used to estimate the number of juveniles that fledged from successful nests and these methods can result in different counts (Gorman et al. 2003). However, there is value in making a rough comparison of reproductive rates in that it suggests that the productivity of Burrowing Owls in Canada is similar to the owls' productivity in the rest of their range in the United States.

1.3 Study area

This study took place in the grasslands of southern Alberta and southern Saskatchewan, Canada (Figure 1.1), mainly in the mixed-grassland ecoregion. Cattle ranching and annual crop production are the primary land-uses, but petroleum development can be found throughout the study area in Alberta and in localized areas in Saskatchewan. The native plant communities are composed of mostly needle grass (*Stipa* spp.), wheatgrasses (*Agropyron* spp.), blue grama grass (*Bouteloua gracilis*) and June grass (*Koeleria macrantha*; Natural Regions Committee 2006). Tame pasture fields are typically seeded with crested-wheat grass (*Agropyron cristatum*), tame hay fields with either crested-wheat grass or alfalfa (*Medicago sativa*), and roadside ditches are mostly smooth brome grass (*Bromus inermis*) or crested-wheat grass. The majority of crops grown in our study area are oilseed, wheat, and other types of grain. A number of primary and secondary highways intersect the study area (Figure 1.1), but the highest density of roads comes from gravel and dirt roads that are typically used for petroleum or agricultural purposes.

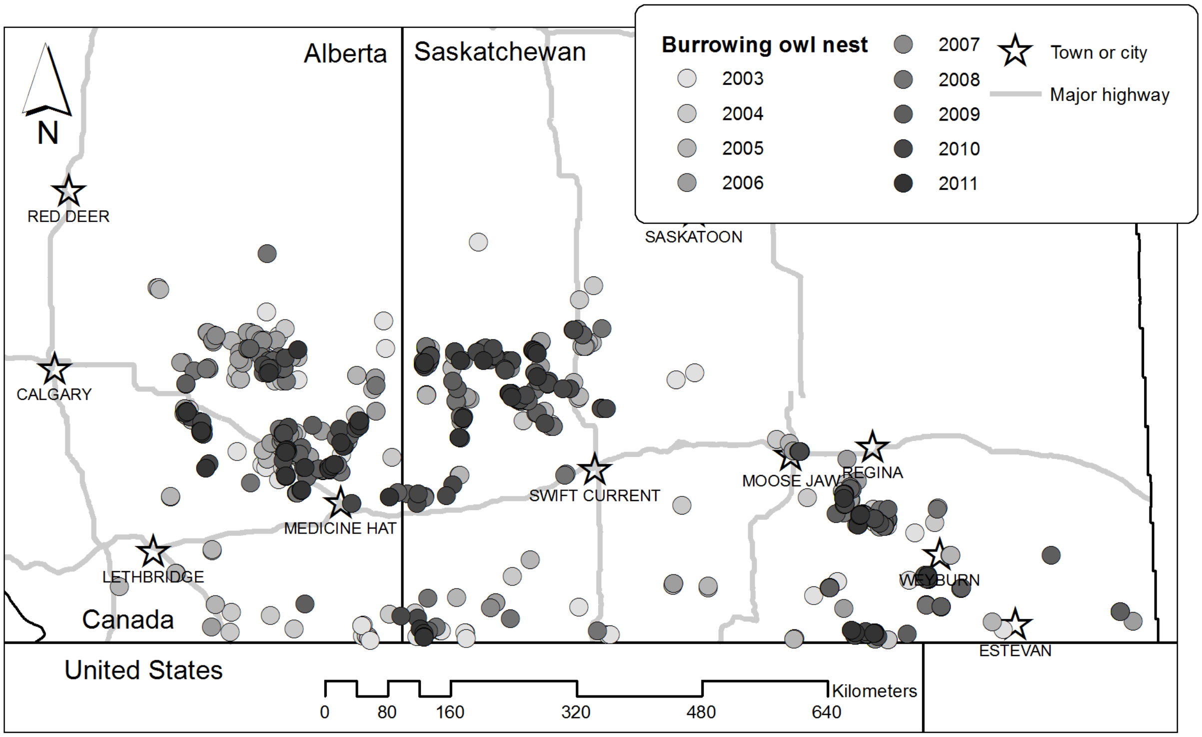

Figure 1.1. A map of my study area, in Southern Alberta and Saskatchewan, Canada, with locations of Burrowing Owl nesting attempts, major highways and cities.

1.4 Objectives and overview

My overall objective was to understand the effects of human development on Burrowing Owls in the grasslands of Alberta and Saskatchewan, Canada. Specifically, I wanted to test if changes made to Burrowing Owl breeding habitat have resulted in owls preferring to nest in low-quality habitat, causing an ecological trap. This would be one potential explanation for their population decline. Extensive changes to the prairie landscape have occurred over the last thirty years from petroleum extraction activities, concurrent to a rapid decline of the Burrowing Owl population. The number of petroleum wells and associated infrastructure on Alberta and Saskatchewan's landscape has increased by over 400% in the last thirty years (CAPP 2015). A link between anthropogenic changes to the landscape and the decline of the Burrowing Owl is often suggested. Petroleum development is one of the most recent industries to alter the grasslands, but has not changed the landscape as dramatically as has agriculture. Less than 30% of the grasslands in Alberta, Saskatchewan, and Manitoba remain uncultivated (Gauthier and

Wiken 2003). Although 80% of this conversion occurred before the 1960s (Statistics Canada 1999, 2007) , it continues to influence owls by reducing potential nest burrow availability (Hennin 2010), altering prey composition, abundance and availability (Poulin 2003), and post-fledging movements by juvenile Burrowing Owls (Todd et al. 2007). I examined the influence of changes to the landscape from agriculture and petroleum development on Burrowing Owl choices at the second and third orders of selection and on their resulting breeding success and survival.

An ecological trap occurs when habitat preference and habitat quality become uncoupled and an organism prefers to settle in areas where it performs poorly reproductively (Kristan 2003, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007, Part et al. 2007). Demonstration of an ecological trap requires simultaneous measures of habitat preference and fitness of individuals within a population, and must occur across a variety of environmental conditions (Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007). Using this definition, I evaluated if Burrowing Owls are in an ecological trap as a result of human development on the Canadian prairies.

The definition of habitat preference I used (Chapter 2) is the choice of one equally available resource over another (Johnson 1980). During their spring migration, Burrowing Owls are exposed to a diversity of landscapes and could stop and nest at any point during their route as fidelity to breeding areas is moderate and annual dispersal occurs. Habitat preference was evaluated using the date the adult male arrived at the nest burrow because the order in which animals settle in breeding habitat is a good way to assess innate species preference (Krebs 1971, Robertson and Hutto 2006). The definition of habitat selection I used when evaluating Burrowing Owl space-use patterns at the third-order of selection (Chapter 3Chapter 4Chapter 5) is the use of one landscape feature disproportionate to its availability (Johnson 1980, Hall et al. 1997, Manly et al. 2002b). Availability of landscape features was determined by plotting random locations in a biologically meaningful area around Burrowing Owl nests, and selection was evaluated by comparing data at those locations to data from owl tracking locations.

In Chapter 2, I identify the landscape features that Burrowing Owls prefer to have near their nests and the relationship between those features and their reproductive success and survival. The objective of Chapter 2 is to test the ecological trap hypothesis with the Burrowing

Owl on the Canadian prairies. I use arrival date of the adult male on the breeding ground to indicate preference and determine the types of land-cover and landscape features owls prefer to have around their nests. I then examine the association of preferred landscapes with nest survival, fledging rate and adult survival during the breeding season. If owls prefer to nest in landscapes in which their measures of reproductive success or survival are lower, that would provide support for the ecological trap hypothesis.

In Chapter 3, I assess the influence of landscape features on Burrowing Owl daytime space-use. Most foraging activities occur during the night, so owl behaviour during the day has received little attention. However, the greatest potential for disturbance from human activities occurs during the day. I tracked 18 owls during the day and evaluated their daytime locations in relation to perches and traffic.

In Chapter 4, I evaluate the influence of human infrastructure versus sensory disturbances on owl nocturnal space-use. Artificial light and sound have the potential to impact animals beyond the physical footprint of development, but it can be difficult to separate sensory disturbances from the infrastructure from which the sound or light are emanating. I tracked eighty-four adult male Burrowing Owls, and used detailed sound and light data to evaluate the influence of sensory disturbances on the night-time movement patterns of the owls.

In Chapter 5, I look for connections between Burrowing Owl resource selection at night and reproductive performance. Resource selection analyses can be misleading unless they are matched to reproductive success to ensure selection identifies high-quality habitat.

In Chapter 6, I conclude with a discussion of the implications of my findings on the conservation of this endangered prairie owl.

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CHAPTER 2. ASSESSING HOME-RANGE PREFERENCE AND BREEDING SEASON FITNESS FOR A RARE AND DECLINING PRAIRIE-HABITAT GENERALIST

2.1 Introduction

Theory suggests that individual animals should prefer to settle in what they perceive to be the highest quality habitat available to them (Clark and Shutler 1999). Resource levels that define habitat quality are typically not directly observed by individual animals (Kristan 2003). Instead, animals use environmental cues correlated with resource levels when making settlement decisions. Preference for specific environmental cues evolves when associated settlement decisions result in higher fitness (Schlaepfer et al. 2002), presumably because the preferred cues provide an accurate index of future food availability or escape cover from predators (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Kristan 2003). However, if habitat preference and habitat quality become uncoupled and an organism prefers to settle in areas where it performs poorly reproductively (Kristan 2003, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007, Part et al. 2007), an ecological trap may be present.

Ecological traps are part of the larger phenomenon of “evolutionary traps” that result when any behavioural choice of an organism becomes maladaptive because of a relatively sudden change to its environment (Schlaepfer et al. 2002). Rapid environmental change caused by human impacts are often more likely to result in ecological traps than are natural processes (Schlaepfer et al. 2002, Kristan 2003, Battin 2004) because changes that occur quickly usually do not give enough time for new behaviours to be learned or adaptive traits to be selected (Kokko and Sutherland 2001, Battin 2004). In this sense, ecological traps are a type of evolutionary lag (Rothstein 1975) between an environmental change and selection of adaptive traits (Kokko and Sutherland 2001). Demonstration of an ecological trap requires simultaneous measures of habitat preference and fitness of individuals within a population, and must occur across a variety of environmental conditions (Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007). If preference has a negative correlation with fitness, then an ecological trap is present (Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007).

Habitat preference is the choice of one equally available resource over another (Johnson 1980). Tests for habitat preference have been problematic, however, because of inconsistencies in its definition. Some studies suggest that preference is indicated by density of animals (Dwernychuk and Boag 1972, Boal and Mannan 1999, Flaspohler et al. 2001) or non-random habitat use (Misenhelter and Rotenberry 2000). These methods have been heavily criticized because alternative mechanisms may explain such patterns (Battin 2004, Robertson and Hutto 2006, Part et al. 2007). For example, in passerines with high site-fidelity, high densities of individuals in a particular area may indicate high-quality habitat in the past rather than in the present (Van Horne 1983). In addition, ideal despotic behaviour may result in low densities of dominant individuals in high-quality habitat and high densities of more submissive individuals in low-quality habitat (Fretwell 1972). Non-random habitat use (or selection) can be confounded by the area defined as available (Beyer et al. 2010) and number of random locations included (Baasch et al. 2010). In contrast, Krebs (1971) has argued that the order in which animals settle in breeding habitat is a better way to assess innate species preference (see also Robertson and Hutto 2006).

Migratory birds are exposed to many environmental conditions along their migration paths each year. When returning to their breeding habitat, birds rely on a number of environmental cues to identify high-quality habitat for nesting. It is widely believed that migratory birds make a choice where to nest based on past experience, assessment of food resources, and predation risk around the potential nest location. This assessment is critical because birds have to rely on resources around their nests, from egg-laying until their young fledge. Scientists can more easily quantify preference for specific habitat characteristics in migratory species than in resident species by observing post-migration nest-site settlement patterns (Horvath and Zeil 1996, Robertson and Hutto 2006, Part et al. 2007, Sergio et al. 2007). Earlier-arriving birds tend to have the first pick of nest sites and, given that habitat preference is adaptive and driven by natural selection, birds should choose to nest in areas they perceive to have the greatest potential for successful reproduction or survival. The resulting settlement pattern should show earliest-arriving birds nesting in the most preferred habitat and later-arriving birds settling increasingly in less-preferred habitats.

A robust test of the ecological trap hypothesis includes assessing habitat preference with respect to a complete picture of individual fitness (Battin 2004, Robertson and Hutto 2006). Most studies to date have only looked at one component of fitness, such as nest survival (Misenhelter and Rotenberry 2000, Flaspohler et al. 2001, Woodward et al. 2001). When modeling ecological traps, adult, juvenile, and nest survival, along with propensity to renest, have the greatest influences on population growth (Donovan and Thompson 2001) and thus should be evaluated when possible. A preference for areas with environmental conditions that result in lower fitness relative to non-preferred areas can have particularly severe consequences for populations at low densities (Kokko and Sutherland 2001) or for populations exposed to stochastic events (Kristan 2003).

Burrowing Owl populations have declined by over 90% in Canada over the last thirty years (Environment Canada 2012). On the Canadian prairies, most habitat modifications, especially conversion of native grassland to cropland, occurred prior to 1960 (Statistics Canada 1999, 2007). The stabilization of grassland conversion over the past few decades raises the fundamental question of why the owl population continues to decline. Nonetheless, given the relatively stable amount of grassland remaining in Canada, the decreasing density of owls over the past century should result in more high-quality grassland habitat being available per owl in the population. This, in turn, should result in higher reproductive success or survival *per capita*, leading to a stable or increasing owl population, assuming the owl population is regulated by intra-specific density dependence. One possible explanation for the continuing decline of the Burrowing Owl in Canada is that they are stuck in an ecological trap. Such a trap could result from a preference for nesting in lower-quality habitat, chosen based on an environmental cue in early spring that does not reflect habitat quality later in the season, with the result being lower fitness.

We used the spring-settlement pattern of Burrowing Owls to indicate which landscape characteristics are most preferred in the vicinity of nests. Male owls arrive in breeding habitat, select a nest site, and then attempt to attract a female mate. Because male owls arrive first and select their nesting area, male arrival date should be a good indicator of habitat preference. However, the landscape in which Burrowing Owls arrive each spring in Canada is now very different from the one in which they evolved. The grasslands of southern Alberta and

Saskatchewan have been extensively cultivated, changing the vegetation composition and structure, with a large portion of the prairies now being used to grow annual crops. Many roads and other human structures, such as fences and petroleum wells, also have been developed in this region over the past century. Thus, when selecting where to nest, it is possible that Burrowing Owls are using the same types of local (e.g. perches) or landscape cues (e.g. land-cover) that they used prior to European settlement, even though those cues may no longer provide reliable information about habitat quality.

The majority of the biomass Burrowing Owls consume comes from small mammals (Poulin 2003), so landscape characteristics that predict where such food resources are high should signal good nesting areas. The greatest Burrowing Owl prey abundance in late-summer occurs in areas with tall, dense vegetation (Poulin 2003, Sissons 2003), and this knowledge has been used to guide conservation actions to-date. Restricting cattle from riparian areas near Burrowing Owl nests has been suggested as a beneficial management practice to promote growth of tall, dense vegetation and, hence, healthy prey populations (Rangeland Conservation Service Ltd. 2004). The presence of wetlands (and therefore tall vegetation and robust small mammal populations) has even been linked to greater Burrowing Owl nest survival (Warnock and Skeel 2002).

Abundant prey is not necessarily available prey however (Marsh et al. 2014b). Though prey abundance is higher in areas with tall, dense vegetation, owls likely have difficulty catching prey there. Accordingly, Burrowing Owls capture prey where the vegetation is shorter and there is more exposed ground (Marsh et al. 2014b). Thus, in agricultural landscapes, owls may choose nests surrounded by greater proportions of cropland (Restani et al. 2008) and more fragmented landscapes (Warnock and James 1997, Ortho and Kennedy 2001) where short vegetation is adjacent to tall vegetation, as such a habitat configuration affords high overall prey availability. Owls may then use short vegetation or bare ground alone as cues for picking a landscape in which to nest each spring. Annual crop fields and road surfaces likely have high prey availability, especially in the spring before crops have begun to grow.

Approximately two-thirds of crop fields are used to grow a crop each year, meaning prey availability in the majority of these fields declines over the season as the crops grow (Poulin 2003). Owls may choose nest sites in the spring that are surrounded by optimal amounts of cropland, with short vegetation, that maximizes early prey availability, but later in the season find that prey in most of those fields are inaccessible for capture. This could be particularly important for fledging success as this time period is when Burrowing Owl reproduction is most limited by food (Wellicome et al. 2013). If owls are choosing nest sites surrounded by more bare soil and short vegetation types (such as cropland in spring) to ensure the presence of many potential prey capture sites, they may become stuck in an ecological trap once those crops grow and limit prey availability, resulting in lower fledging rates or decreased nest survival.

Many road surfaces are associated with ditches, resulting in areas with high prey abundance (ditches) adjacent to areas where prey may be more accessible (road surfaces). If the bare surfaces of roads, with high prey accessibility, and the tall dense vegetation in ditches, with high prey abundance, are used as cues for owls to choose nesting sites, then the owls may be increasing their risk of mortality from vehicle collisions, thus creating the combination of conditions required for an ecological trap.

Perches are used by Burrowing Owls during the day (Scobie et al. 2014), as well as at night when the owls are further from their nests (Sissons 2003). If owls prefer nests with more perches nearby, there could be negative consequences for their reproductive success. Increased density of perches may increase the use of those areas by other avian predators (Kay et al. 1994), resulting in lower nest and adult survival or lower fledging rates. On the Canadian prairies, livestock fences are dominant features, the majority of which lie alongside roads. Therefore, a preference to use areas near fence-line perches may also come at the cost of increased vehicle mortality on adjacent roads.

We tested for the presence of an ecological trap for Burrowing Owls by evaluating whether three measures of fitness (nest survival, fledging rate, and adult survival) were influenced by preferred landscape features. Evidence of an ecological trap would be a pattern of decreased fitness related to any preferred landscape features. We found only one other study that examined the relationship between the landscapes surrounding nests and reproductive success of Burrowing Owls at a scale similar to ours (Restani et al. 2008). That study found that owls that nested in landscapes surrounded by more crested wheatgrass and cropland fledged more juveniles on average (Restani et al. 2008). The amount of prey brought back to the nest has a large influence on number of juveniles produced and recruited in subsequent years (Wellicome et al. 2013), highlighting the importance of evaluating the relationship between landscape features in which owls tend to hunt and their resulting fitness. The importance of scale and links to fitness is highlighted by the results of one study that found that Burrowing Owl reproductive success was influenced by land-cover at a scale closer in size to their nocturnal home-range (2000 m), but not at a larger scale ((600 m; Restani et al. 2008). Most studies examining factors affecting Burrowing Owl reproductive success focus on features (e.g. burrows and perches) at a much larger scale (< 100 m), which may have more to do with nest suitability than prey availability (Green and Anthony 1989, Ronan 2002). Other studies disregard the gradient of landscape features and instead compare reproductive success of nests surrounded by land uses deemed categorically different, such as urban vs. grassland (Berardelli et al. 2010), urban vs. agricultural (Conway et al. 2006), and urban vs. parkland (Trulio and Chromczak 2007). In this study, we evaluate Burrowing Owl preference for landscape features within their entire nocturnal foraging area, and test if the ecological trap hypothesis applies to Burrowing Owls in the Canadian prairies.

2.2 Methods

Each year in early May, from 2003 and 2011, we located Burrowing Owl nests through call play-back surveys in southern Alberta and southern Saskatchewan, Canada (Figure 2.1). We observed 917 Burrowing Owl nesting attempts, visiting each nest once per week throughout the breeding season until the attempt failed or the chicks fledged (i.e., reached 35-days old). When no chicks were observed above ground, the burrow was accessed with an underground infrared camera, attached to the end of a 3–4 m hose (Garcia and Conway 2008), and contents of the nest were viewed through a portable video-viewing device.

Amount of each land-cover type and human infrastructure within the nocturnal home-range (1.4-km radius around the nest; Chapter 4) was calculated for each nesting attempt. Each year, perches (fences and power lines) and land-cover (native grassland, tame grassland, road ditches, annual crop, wetland [wetland vegetation and seasonally dry], road, water bodies [standing water all year], buildings [residential and agricultural], and shrubs and trees) were recorded on aerial photographs. These aerial photographs were digitized in a GIS environment onto SPOT5 imagery (2006 coverage). The area of each land-cover type was converted to percentage of the nocturnal home-range for each nest. The sum of percentages of land-cover types, within 1.4 km of the nest, is therefore 100%, potentially introducing problems with unit sum constraints, so percent land-cover was converted to log ratios (Aebischer et al. 1993), using native grassland as the denominator. Prior to calculating log ratios, a constant of 0.01% was added to all land-cover types to compensate for land-cover absent from some nocturnal home-ranges. The total number of gas wells within 1.4 km of each nesting attempt was also tallied. Locations of gas wells were identified from IHS Energy Inc. GIS layers (IHS Energy 2011).

Traffic was monitored on a sample of roads in our study area, enabling us to generate a metric of vehicle traffic for each road type within 1.4 km of each nest. If there is a mortality risk to Burrowing Owls from vehicles on roads, it is likely related to the number of vehicles that use those roads and the speeds at which the vehicles travel. Pneumatic tube traffic counters (MetroCount; MC5600 Series Roadside Unit) were deployed on 71 roads for three or more consecutive weeks. Traffic counters recorded the speed of each vehicle that passed, which was then used to calculate average hourly vehicle speed. Road width and road surface type (dirt, gravel, or paved) were also documented at each road. The relationship between average hourly vehicle speeds was visually inspected against road width to help identify road-width categories that best predict vehicle speed. The relationship between average hourly vehicle speed and traffic volume with road width was then used to separate all roads within 1.4 km of Burrowing Owl nests into three traffic classes. Overall traffic within the home-range was estimated by summing the weighted length of roads of each traffic class. Length of each class of road was first multiplied by the weight (1 if <= 5–m wide, 2 if > 5–m and <= 8.95–m wide, and 3 if > 8.95–m wide) and then summed. The total unweighted length of roads in each class, and total length of all roads (regardless of class), within 1.4 km of each nest, was also calculated.

Prior to analyses, all data were evaluated for outliers, homogeneity, normality, collinearity among covariates, potential interactions, and independence of the response variable (Zuur et al. 2010). Dichotomous variables were used when the variable was absent from most owl nocturnal home-ranges. When collinearity was detected, the variable with the highest variation inflation factor was removed and the variation inflation factor was then recalculated for each variable. This was repeated until all variation inflation factors were less than three (Quinn and Keough 2002). All models were validated by examining influential observations, residual homogeneity, independence of covariates, normality of residuals, and spatial independence (Zuur et al. 2007). The relationships between residuals and covariates were examined for nonlinear responses, and quadratic terms were tested where appropriate.

2.2.1 Arrival

We used 823 of the 917 nesting attempts in our analysis. We could not use the remaining 94 nesting attempts for one of the following reasons: 1) they failed before we began monitoring, 2) they were second or third nesting attempts, or 3) permission to access the property was not granted, so nest observations were from too far away to accurately ascertain reproductive stages. Nest monitoring began during egg laying (31.3%), incubation (41.3%), or between hatching and fledging (27.4%). Date that the adult male arrived at the nest burrow was calculated by subtracting 16 days from the date the first egg was laid (Wellicome 2000). There is some variation between arrival and clutch initiation date, but the relationship between the two is quite strong ($r^2 = 0.69$; Wellicome 2000). The date the first egg was laid was determined by subtracting 1.5 days for each egg observed mid-clutch or by subtracting 30 days from the hatch date (the day the first egg hatched; Wellicome 2000). Hatch date was estimated using one of the following methods, presented in order of decreasing accuracy: 1) by observing the first-hatched chick when it was one-day old; 2) capturing and measuring ninth primary and central tail feather of the oldest owlet and comparing measurements to those from owlets of known age; 3) using the underground camera to visually estimate the age of the oldest chick inside the burrow; 4) observing the oldest owlet above-ground and estimating age based on plumage and behaviour (Fisher et al. 2015). On average, the female arrives four days after the male (Wellicome 2000).

Snow cover at the burrow may affect availability of burrows and, thus, arrival date of the male owl, so the number of days the burrow was covered in snow between March 30th and arrival date was determined for each nesting attempt (National Ice Center 2008). Models containing the number of snow days as a continuous and dichotomous categorical (≥ 1 day of snow cover, ≥ 2 days of snow cover, etc.) variable were compared with AIC (Akaike's Information Criterion; Burnham and Anderson 2002). The burrow being covered in snow ≥ 1 d between March 30th and the date the male owl arrived best explained adult male Burrowing Owl arrival date (lowest AIC) and was used in all models.

All statistical analyses were performed in the statistical software Program R (R Core Team 2014). A mixed effects linear regression was used to predict arrival date as a function of land use, with burrow as the random effect. Every model contained year as a categorical variable (2003 was the reference year), snow cover and one variable from each category (Table 2.1). Variables related to roads, land-cover, and perches were first compared within each variable category (Table 2.1). These categories were chosen because they relate to one of our predictions for habitat preference (vegetation height and perch availability) or are correlated with our predictions (roads). Model comparison within the perch category was limited to the subsample of 411 nests for which we had fence and power-line data. Models containing each variable within each category were compared with AIC (Burnham and Anderson 2002). The variables in models with ΔAIC ≤ 2 within each category were then included in the global model comparison. The best fitting global model was determined by comparing models containing all possible combinations of uncorrelated variables from all categories. The top model (lowest AIC; Burnham and Anderson 2002) was then selected.

2.2.2 Nest survival, fledging rate and adult survival

Burrowing Owl daily nest survival, fledging rate, and apparent adult survival over the breeding season were examined in relation to landscape characteristics that owls preferred within their home-ranges (Table 2.2). Variables correlated ($r \geq 0.5$) with preferred landscape characteristics were also examined (Appendix 2.2).

For all three analyses, each model contained year as a categorical variable and date (Ordinal) the first egg was laid within each clutch (clutch initiation date). This controls for the greater survival of nests and adults, and the greater number of juveniles that fledge, from nests that began earlier in the season. The date the nest was first visited (first-visit date) was a covariate in the adult survival analyses, which helped compensate for the greater survival of adults found in later nesting stages and any adults that died early in the season that we did not find. These covariates (year, clutch initiation date, first-visit date) were included in each model, along with one landscape variable. We considered only those landscape features that resulted in statistically significant effects on daily nest survival, fledging rate, or breeding season apparent adult survival.

Daily nest survival was modeled using a logistic exposure model (Shaffer 2004) in Program R (R Core Team 2014) with a generalized linear mixed model, a custom logistic exposure link function (Herzog 2013, Bolker 2014), and burrow as the random effect. Nests were categorized as successful if at least one juvenile fledged (i.e., reached 35 days-of-age). Thirty four nests that failed because the nest burrow was flooded by rain were excluded from this analysis because extreme precipitation events are stochastic and occur independent of the landscape in which the nest is imbedded. Factors that may influence the flooding of a nest occur at a much larger scale than the nocturnal home-range or are independent of land-cover and other landscape features up to 1.4 km from the nest (Fisher et al. 2015).

The number of juveniles that fledged from successful nests was analysed using zero-truncated Poisson regression. The number of offspring at approximately 30 days post-hatch was determined for each nesting attempt. Above-ground camera systems were used to record fledglings approximately 30 days post-hatch for 18–24 hrs. These videos were later transcribed and the maximum number of owlets observed above ground at any one time was tallied. In a small number of cases, the nest was visited and the number of fledgling owls was tallied by observing the nest area with binoculars or a spotting scope for ≥ 30 min.

We used the Cormack-Jolly-Seber (CJS) model in program MARK to examine adult Burrowing Owl apparent survival (Φ) and recapture rate (p), during the breeding season, in relation to landscape variables to which owls show a preference. A weekly encounter history was created for the adult male and adult female, starting with the week in which the first egg was laid within the owl's clutch and ending 10 weeks later, when the juveniles fledged. Each model contained constant survival over the nesting period, but with different slopes for male and female owls. Re-sightings were held constant over the nesting period, with sex and all years combined. Each model contained one landscape variable. Encounter histories for adults from failed nests were excluded, except for failures resulting from adult mortality. When an adult was found dead, the encounter history of the other adult was excluded because the surviving adult typically leaves the nesting area soon after the death of its mate. Only those nesting attempts with at least two visits were included.

2.3 Results

We monitored 823 nesting attempts. Both the average and median arrival dates were April 25 (range = March 30 to May 27), but the modal arrival date was April 22. Average arrival dates were later in 2008, 2009, and 2010 than in any year from 2003–2007 (Figure 2.2). Owls arrived 4.5 days later when their nest burrow was covered by snow for at least one day between March 30 and their arrival (Appendix 2.1).

Within each variable category, the top variables from our settlement pattern analysis were as follows: 1) percent bare ground (annual crop + road surfaces) and percent annual crop, 2) number of gas wells and length of power lines, and 3) lengths of traffic class 1 roads, class 2 roads, and class 3 roads (Table 2.1). The top global model contained year and percent bare ground (Table 2.2), indicating that earlier-arriving owls chose nest burrows surrounded by a greater amount of land bare of vegetation in spring than did later-arriving owls (Table 2.3 and Figure 2.3). There was no spatial pattern in the residuals (Moran's I = -0.0015, $p = 0.98$) across the study area.

A total of 823 nesting attempts were used for the apparent nest survival analysis, 644 nests for the fledging rate analysis and 1065 adults (529 male and 536 female) for the apparent adult survival analyses. Apparent nest survival was 78%, average number of juveniles fledged from all nesting attempts was 3.5 (SE = 0.1, range = 0–10), and the average number of juveniles fledged from successful nests was 4.5 (SE = 0.1, range = 1–10). Landscape variables used in the nest survival, fledging rate, and adult survival analyses included the most preferred landscape variable (bare ground land-cover) and the variables with which it was correlated (Appendix 2.2). Fledging rate was significantly affected by amount of home-range covered by bare ground ($\beta = 0.011$, SE = 0.005, $p = 0.05$; Figure 2.4), road surface ($\beta = 0.016$, SE = 0.008, $p = 0.05$; Appendix 2.2), and annual crop ($\beta = 0.008$, SE = 0.008, $p = 0.04$; Appendix 2.2). Re-sighting probability of an adult was 63% (SE = 0.007, $p = < 0.01$) for each weekly visit, but there were no significant relationships between adult survival of either sex and preferred landscape features (Appendix 2.2).

2.4 Discussion

Burrowing Owls do not prefer to nest in areas with landscape features that result in lower reproductive success and, therefore, these features do not seem to have created an ecological trap for owls in the grasslands of Canada. Our results suggest the opposite of an ecological trap, as owls prefer to nest in areas where they have a greater fledging rate.

Early-arriving owls chose burrows surrounded by land-cover that was comprised of mostly bare ground in the spring (road surfaces and annual crop). When the owls arrive in late April, fields used to grow annual crops typically have very short vegetation with a high proportion of bare soil. Almost all road surfaces had no vegetation. It is plausible that the characteristics of these land-cover types are used as cues of habitat quality by arriving Burrowing Owls. Burrowing Owls evolved in a landscape dominated by relatively homogeneous grasslands where areas of high prey availability (short sparse vegetation and/or bare ground) were limited by disturbances such as grazing and fire. This choice, however, was not associated with reduced survival or reproductive success for the owls.

Before European settlement of the grasslands, vegetative structure was most affected by fire and the plains bison (*Bison bison bison*). Large herds of bison created shifting vegetation patchiness as they travelled across the grasslands eating grass, trampling vegetation, and wallowing in dust hollows (Knapp et al. 1999, Fuhlendorf and Engle 2001). Bison were effectively removed from the grassland ecosystem by the late 19th century, coinciding with the decline of another regular prairie disturbance, fire. Large, free-roaming bison herds and regular fires would have been responsible for creating areas with short vegetation and bare soil in otherwise relatively homogenous grassland. Areas recently disturbed by fire or large bison herds may have had greater prey availability for Burrowing Owls. Burrowing Owls evolved with the grazing of large herbivores and fire and, before the loss of these disturbances, would likely have relied on the resulting vegetation structure as cues when choosing nesting sites.

Studies examining the landscapes in which Burrowing Owls choose to nest have used habitat selection models that compare occupied nest locations to available or unoccupied locations (Ortho and Kennedy 2001, Ronan 2002, Lantz et al. 2007, Stevens et al. 2011). As in our study, Ortho and Kennedy (2001) found that owls selected nest sites surrounded by more cropland than native vegetation, though their land use data was coarser than ours. Stevens et al. (2011) found that Burrowing Owls select for nest sites with 10-70% grassland within 1.6 km of their nests. However, they combined tame and native grass into their grassland land-cover type. Thus, it is difficult to compare our results to these studies because of the coarse nature of the land-cover data that they used. More importantly, habitat suitability models that compare active nest sites with available nest sites instead of measuring preference based on arrival dates makes direct comparison problematic.

The Burrowing Owl population has been reduced by at least 90% and their range in Canada has contracted to 36% of its former area during the last thirty years (Environment Canada 2012). A greater proportion of the owls nesting in Canada have access to higher quality habitat and the sample of nesting attempts we studied may be surrounded by a narrower range of landscape conditions than if the population was at a higher density. Although this would have made the signals of an ecological trap stronger, because there would also be an abundance of low quality habitat which would have resulted in overall low reproductive success and survival. The nesting success and fledging rates of owl pairs in our study is similar or higher than in comparable studies in the United States (Conway et al. 2006, Restani et al. 2008, Berardelli et al. 2010), indicating that the owls in our study do not nest in generally low-quality habitat. Also, we found preference for specific landscape features, indicating our sample of nesting attempts occurred across a broad range of environmental conditions.

More juveniles were fledged by owl pairs that had larger areas of annual crop and road surfaces within their nocturnal home-range. Amount of prey brought back to the nest greatly affects fledging rate (Wellicome et al. 2013), and the relationship between fledging rate and amount of land covered by bare ground likely relates to the greater availability of prey where there is little vegetative cover. Approximately two thirds of crop fields actively grow crops each year, which then support larger populations of small mammals later in the breeding season (Poulin 2003). This juxtaposition of crop fields, with high prey abundance, alongside idle crop fields, with short vegetation, results in high prey availability in these idle fields (Marsh et al. 2014b). There also may be higher prey availability on road surfaces that are typically adjacent to roadside ditches, which have high prey abundance (Poulin 2003). Owls are probably capturing those small mammals that reside in roadside ditches or in active crop fields when those prey venture out onto adjacent roads or into idle crop fields where prey are more accessible. Owls foraging in areas with these habitat configurations likely bring more prey back to the nest and, hence, fledge more offspring.

Burrowing Owls are a generalist predator that adapt their foraging patterns to opportunistic events such as prey outbreaks (Sissons et al. 2001) which can then translate into more juveniles fledging (Poulin et al. 2001). They can forage effectively in many natural and human-modified land-cover types (Marsh et al. 2014a), adapting their diet to the prey that is available (Cavalli et al. 2014). Because burrowing owls are a generalist predator and have evolved in a landscape with a high degree of stochasticity (prey outbreaks, large herds of herbivores, and fires), it is unlikely that burrowing owls are in an ecological trap. If present, the evidence of ecological trap would be quite obvious, because the landscape cue to which they show preference would need to be novel (on an evolutionary time-scale) and related inversely to at least one measure of fitness to affect this adaptable generalist grassland raptor. We did not detect any evidence for this.

Ecological traps can be detrimental to small or declining populations (Kristan 2003), highlighting the importance of studies such as the current one. Fortunately, the decline of the Burrowing Owl population in Canada does not likely result from an ecological trap, and there is in fact evidence that human changes to the breeding landscape have neutral or even improved effects on reproductive success and survival in this endangered owl. Our study suggests generalist predators, such as Burrowing Owls, may be less susceptible to ecological traps than specialist species, even when found on an extensively-developed landscape. Ecological traps are an interesting theoretical phenomenon that does not apply to all species, but the process of identifying habitat preference and exploring links between fitness and habitat characteristics is important and, regardless of whether an ecological trap is identified or not, will help inform the conservation of any species.

Table 2.1. Home-range landscape variables and categories used in determining which variables best predicted adult male owl arrival at the nest burrow. Traffic volume and average vehicle speed is greatest in class 3 roads and lowest in class 1 roads. * Log ratio (native grassland as denominator) of each land-cover variable was used.

Category	**Variables**	**Variables in top models**
Land-cover*	percent area covered by annual crop, wetland, road ditches, road, tame pasture, tame hay, tame grass (tame pasture + tame hay), hay (tame hay + road ditches), bare ground (annual crop + road), tall vegetation (tame hay + wetland + road ditches)	annual crop, bare ground
Perches	number of oil wells, number of gas wells, length of fences, length of power lines, number of all perches	number of gas wells, length of power lines
Roads	lengths of: class 1 roads, class 2 roads, class 3 roads, and all roads	class 1 road length, class 2 road length, class 3 road length

Table 2.2. All models with ΔAIC ≤5 in global model comparison of variables that explain adult male owl arrival date at the nest burrow. Models were developed using mixed effect linear regression with the nest burrow identifier as the random effect. Traffic volume and average vehicle speed is higher in class 3 roads and lowest in class 2 roads.

Model	***k***	**AIC**	**ΔAIC**	***wi***
Year + Snow + Bare ground	13	5798.8	0.00	0.62
Year + Snow + Bare ground + Class 3 road	14	5801.7	2.95	0.14
Year + Snow	12	5802.0	3.22	0.12
Year + Snow + Bare ground + Class 2 road	14	5802.2	3.45	0.11

Table 2.3. Model averaged coefficients from models with ΔAIC ≤5 in global model comparison predicting adult male owl arrival at nest burrow. Models were developed using mixed effect linear regression with the nest burrow identifier as the random effect.

Variables	**β**	**SE**	**Lower 95% Confidence Interval**	**Upper 95% Confidence Interval**	**Relative Importance**
Intercept	106.82	1.65	103.60	110.05	–
2004	3.35	1.79	-0.16	6.86	1.00
2005	4.10	1.73	0.71	7.49	
2006	5.98	1.73	2.59	9.37	
2007	1.36	1.80	-2.17	4.89	
2008	8.53	1.64	5.32	11.74	
2009	9.54	1.62	6.37	12.71	
2010	8.88	1.62	5.70	12.06	
2011	5.93	2.33	1.38	10.49	
Snow	4.50	0.81	2.92	6.08	1.00
Bare ground	-0.25	0.09	-0.42	-0.08	0.88
Class 3 road	-0.12	0.21	-0.53	0.29	0.14
Class 2 road	-0.10	0.16	-0.41	0.20	0.11

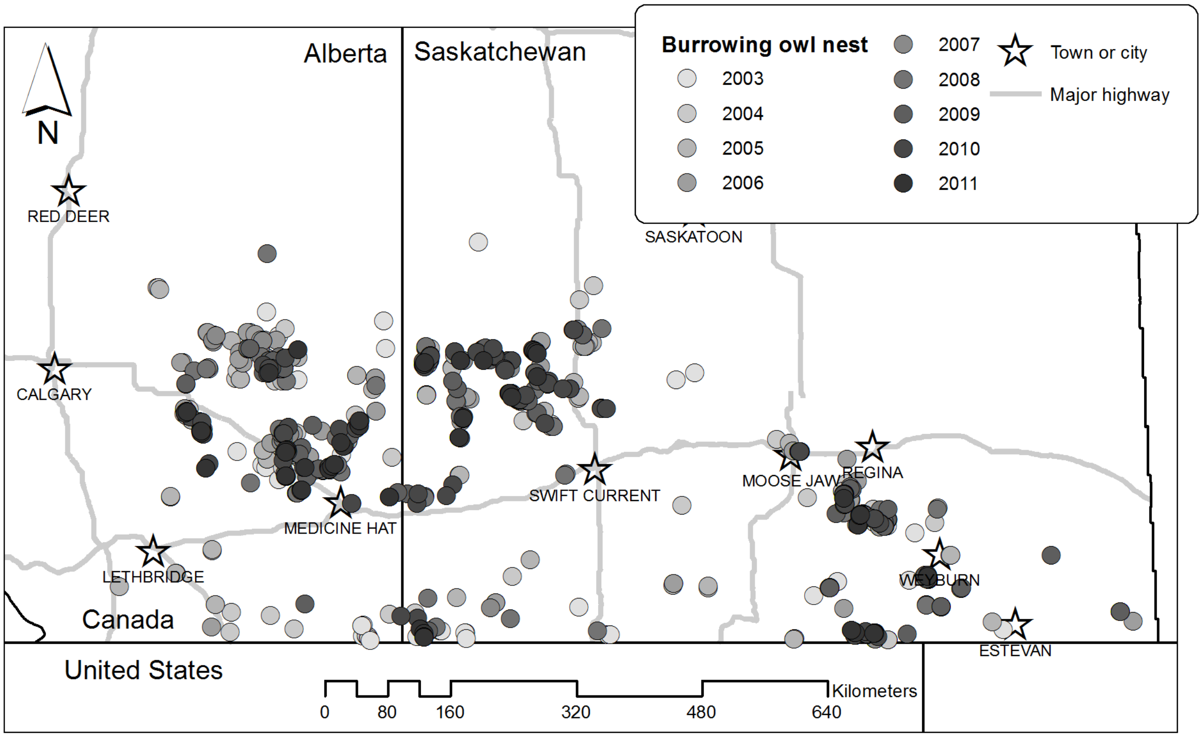

Figure 2.1. A map of our study area in Southern Alberta and Saskatchewan, Canada, with locations of Burrowing Owl study nests, major highways and cities.

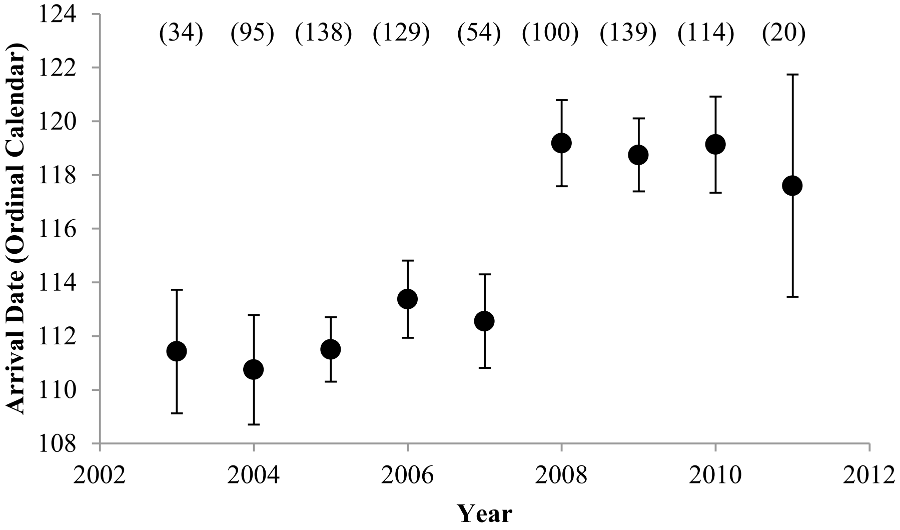

Figure 2.2. Average date of adult male owl arrival at nest burrow for each year. Error bars are 95% confidence intervals. Numbers at the top are the number of Burrowing Owl nests monitored each year.

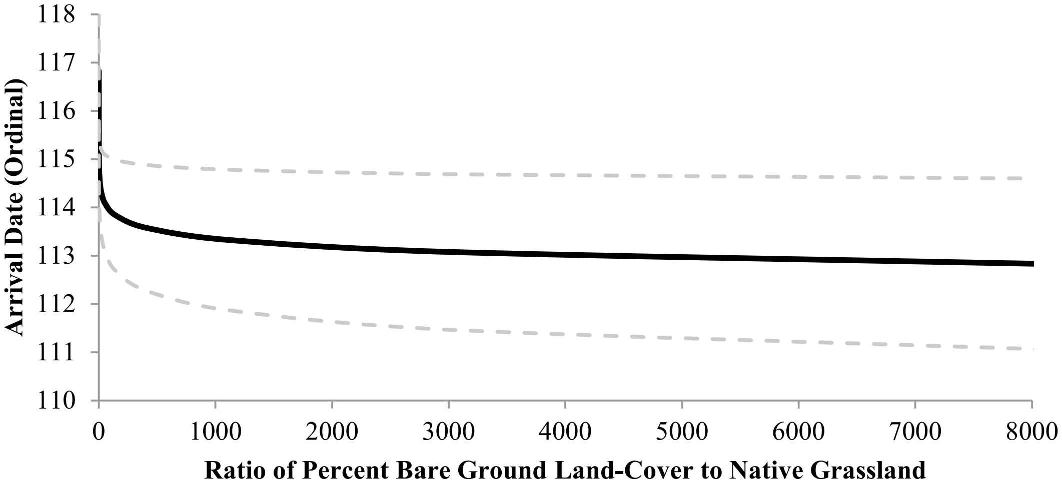

Figure 2.3. Predicted date of adult male owl arrival at nest burrows with various quantities of home-range covered by bare ground land-cover (annual crop + road). Snow and year held constant at the average values. Grey dash lines are 95% confidence intervals.

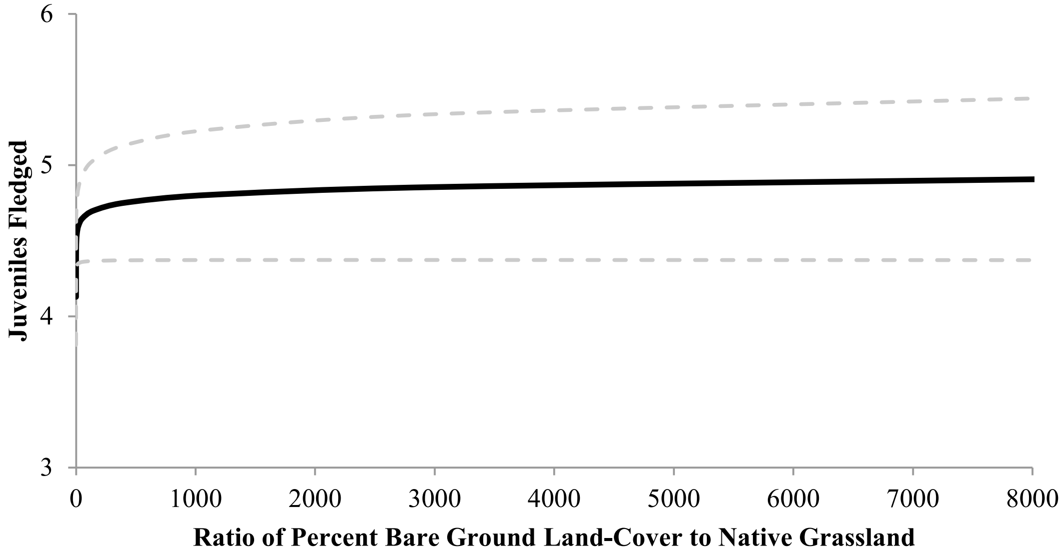

Figure 2.4. Predicted number of juvenile Burrowing Owls that fledge from successful nests as a function of the ratio of percent bare ground land-cover (annual crop + road) to percent native grassland within the nocturnal home-range. Clutch initiation date and year held constant at the average values. Grey dash lines are 95% confidence intervals.

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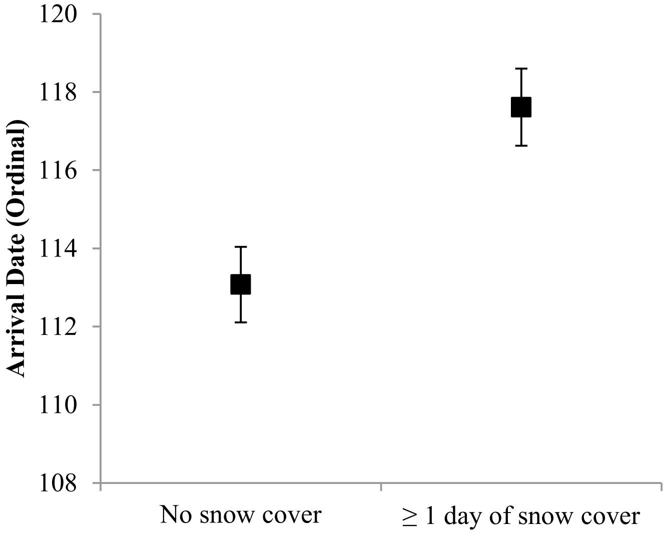
Appendix 2.1. Predicted date of adult male Burrowing Owl arrival at the nest burrow with at least one day of snow between March 30th and arrival. Error bars are 95% confidence intervals.



Appendix 2.2. Regression coefficients and (in parentheses) standard error from fledging rate, nest survival, and adult survival models that contained bare ground land-cover or correlated variables (r ≥ 0.5). * p-value < 0.05.

				Adult Survival	
Variable	**r**	**Fledging β (SE)**	**Nest Survival β (SE)**	**Female β (SE)**	**Male β (SE)**
Bare ground	–	0.011 (0.005)*	-0.004 (0.021)	-0.018 (0.070)	0.005 (0.059)
Road	0.82	0.016 (0.008)*	0.014 (0.037)	0.157 (0.185)	0.262 (0.266)
Annual crop	0.97	0.008 (0.004)*	-0.006 (0.015)	-0.031 (0.050)	-0.014 (0.040)
Tame hay	0.70	0.009 (0.006)	-0.008 (0.025)	-0.0919 (0.075)	-0.065 (0.062)
Tame pasture	0.64	0.009 (0.008)	-0.010 (0.030)	-0.057 (0.115)	0.003 (0.092)
Tame pasture & road ditches	0.65	0.010 (0 .008)	-0.009 (0.030)	-0.109 (0.106)	-0.069 (0.093)
Road ditches	0.54	0.015 (0.008)	0.013 (0.033)	0.057 (0.124)	0.0811 (0.123)
Tall vegetation	0.67	0.010 (0.009)	-0.023 (0.035)	-0.036 (0.109)	-0.036 (0.109)

CHAPTER 3. INFLUENCE OF ANTHROPOGENIC FEATURES AND TRAFFIC DISTURBANCE ON BURROWING OWL DIURNAL ROOSTING BEHAVIOUR[2]

3.1 Introduction

Nocturnal birds must select daytime roosts that minimize predation risk and negative effects of adverse weather (Hayward and Garton 1984, Belthoff and Ritchison 1990, Churchill et al. 2000). Individuals balance these factors to maximize their own fitness (Kerth et al. 2001), but during the breeding season they may risk increased exposure to these elements to facilitate guarding mates and offspring (Sunde et al. 2003). The success of a reproductive event may rely on the ability of a parent to efficiently detect and react to threats (Gotmark et al. 1995, Magana et al. 2010), highlighting the significance of daytime roost characteristics for nocturnal species. The daytime activities of nocturnal animals is an understudied subject despite the higher predation risk that occurs during the day (Sunde et al. 2003) and a greater potential for disturbance from human activities.

The western Burrowing Owl (*Athene cunicularia hypugaea*) in Canada is an endangered species (Wellicome and Haug 1995) that lives in the relatively flat, treeless grasslands. Lack of cover and an increasing human presence in these grasslands leaves this nocturnal species potentially susceptible to disturbance during the day. Almost all foraging activities occur at night (Poulin and Todd 2006) and thus past research has focused on minimizing human impacts during the night (Sissons 2003, Grzywaczewski 2009, Williams et al. 2011). Little is known about owl behaviour during the day when most human activities occur and predation risk is assumed to be high, so understanding diurnal space use patterns of owls may be crucial in mitigating disturbance effects.

Burrowing Owls nest in underground burrows where the female spends most of her time incubating eggs and brooding chicks (Plumpton and Lutz 1993). The concealed nature of their nests minimizes predation risk (Martin and Li 1992), but escape is almost impossible if owls are in the burrow when a predator enters. Mammalian predators are the most common nest predators

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[2] A version of this chapter has been published. Scobie, C., E. Bayne, and T. Wellicome. 2014. Endangered Species Research 24: 73–83.

(Wellicome 2000), but after brooding, the female and young spend more time above ground near the burrow entrance (Plumpton and Lutz 1993), where they are susceptible to avian predators (Shyry 2005). Throughout the nesting period, the male remains above ground (Plumpton and Lutz 1993), though during the day the male spends little time capturing prey (Poulin and Todd 2006). Observations suggest male Burrowing Owls spend most of the day on elevated perches, engaging in vigilance behaviour (Plumpton and Lutz 1993, Chipman et al. 2008). Prior to European settlement of the prairies, Burrowing Owls likely relied on burrow mounds, rocks and hilltops as elevated perches, but may now rely on anthropogenic perches such as fence posts which are prolific on the landscape. From these perches, the male actively defends its nest and uses auditory signals to communicate risks to its mate and young (Martin 1973a, Martin 1973b). Anthropogenic noise may hinder the ability to give or receive such acoustic signals (Brumm 2004, Bee and Swanson 2007, Parris and Schneider 2009, Lampe et al. 2012), so owls may avoid roosting where noise levels are high. However, anthropogenic perches in the western prairies tend to be close to roads, so the value of roosts may vary as a function of whether they are adjacent to quiet versus noisy roads. Therefore, landscape features and anthropogenic activities near the nest that influences the ability of male owls to detect predators and communicate predation risk to the female or young need to be determined.

To evaluate this, we examined diurnal space use of adult male Burrowing Owls wearing GPS dataloggers to identify landscape features used by Burrowing Owls during the day. We then determined if disturbance from traffic altered the patterns of daytime space use by male Burrowing Owls. We predicted that males would select elevated perches to maximize detection of predators when close to the nest and avoid noisier areas to facilitate acoustic communication with the female and young.

3.2 Materials and Methods

Between 2007 and 2009, 387 Burrowing Owl nesting attempts within the dry mixed-grass ecoregion of Southern Alberta and Saskatchewan, Canada, were found and monitored and the adult male was tracked with a GPS datalogger at 18 of these nests (Figure 3.1). Nests were located in early May using call play-back surveys, and were visited once per week throughout the breeding season. After the chicks hatched, each adult male owl was captured with either a one way walk in (Winchell 1999) or a bow-net trap, baited with a dead mouse, a speaker playing a Burrowing Owl primary call, a decoy Burrowing Owl, or a combination thereof. A seven gram GPS datalogger (TechnoSmArt, Guidonia Montecelio, Italy) was attached to each owl, using Teflon ribbon in a backpack style configuration. The dataloggers we used were upgraded by the manufacturer each year, resulting in varying program schedules. Dataloggers were programmed to turn on and take two fixes every 15 minutes (2007), turn on for five minutes and take one location every second, then turn off for 55 minutes (2008), or to take one location every second continuously (2009). The following data were stored on internal memory within the GPS datalogger: latitude, longitude, speed, altitude, dilution of precision, Greenwich Mean Time, and date. To retrieve the data, owls were re-trapped after three days once the GPS micro-datalogger battery was depleted. Owl locations were filtered by dilution of precision (≤ 1.5), speed (≤ 64 km/h), and altitude (> 20 m below and < 80 m above the elevation of the owl's nest). Dilution of precision is a measure of the accuracy of a GPS location calculated using the number and location of satellites relative to the GPS datalogger. A dilution of precision close to one is the most precise. One location every 15 minutes (2007 and 2009), or else one location every hour (2008), was selected for these analyses. To avoid inclusion of locations from crepuscular foraging activities, we included in our analyses only those locations taken between one hour after sunrise to one hour before sunset (Poulin and Todd 2006). The accuracy of the GPS dataloggers was tested by measuring the distance between locations from a stationary GPS datalogger placed on a fence post in the field for three days and the stationary datalogger's location as determined with a hand-held GPS unit. All data were collected by trained field staff in possession of valid animal care approval, federal and provincial research permits and bird banding licenses.

GPS datalogger locations were used to calculate fixed kernel density for each owl with the least squared cross validation method for calculating bandwidth in the adehabitat package (Calenge 2006) in R. The fixed kernel was determined for a five meter by five meter pixel, a resolution that matches the accuracy of the GPS datalogger. Kernel density bandwidth was calculated using least squared cross validation because it is the best method for a central place forager with over 20 locations per animal when mapping areas of highest concentration of use (Gitzen et al. 2006). Kernel density for each owl was transformed to utilization distributions by dividing the kernel value for each pixel by the sum of the kernel values for all pixels combined.

Each year, land-cover and perches surrounding the nest of each tracked owl were recorded on aerial photographs (Figure 3.2). These aerial photographs were digitized in a GIS environment onto SPOT5 imagery (2006 coverage). Locations of the nest burrow and secondary burrows (any burrow where five or more pellets were observed over the nesting period) were recorded with handheld GPS units. Land-cover types (native grassland, tame grassland, crop, idle field, wetland [sparse vegetation and seasonally dry, including during our study], road ditch, dirt road, gravel road, and paved road) were all included in statistical models with native grassland being the reference category.

Prior to analyses, all data were evaluated for outliers, homogeneity, normality, collinearity among covariates, potential interactions, and independence of the response variable (Zuur et al. 2010). When collinearity was detected, the variable with the highest variation inflation factor was removed and the variation inflation factor was then recalculated for each variable. This was repeated until all variation inflation factors were less than three (Quinn and Keough 2002). All models were validated by looking for influential observations, residual homogeneity, independence of covariates, normality of residuals, and spatial independence (Zuur et al. 2007).

Land-cover, and distance to nearest perches, burrows and roads were extracted, for each pixel of the utilization distribution (Figure 3.3), and examined using a resource utilization function (RUF). Initial data exploration revealed outliers and lack of normality for the utilization distribution for each owl so they were log-transformed prior to analysis. There was also strong evidence for spatial dependence among the utilization distribution values for each owl, so spatial regression using spatial simultaneous autoregressive error model estimation was used (Bivand 2013). Land cover and distance to nearest perch, nest burrow, secondary burrow, and each class of road type (dirt, gravel, paved) was determined for each utilization distribution pixel. Collinearity between these covariates was examined for each owl using the aforementioned method, and the model for each owl contained all variables that were used by that owl (overlapped the 100% kernel) and had variation inflation factors less than three (Quinn and Keough 2002). The coefficients and standard errors from the model for each owl were then used to calculate the inverse variance weighted mean, standard error, z value and p value for each covariate for the entire sample of owls. The negative coefficients are presented for distance variables so that the response of the owl (attracted versus avoided) matches the signs (positive versus negative) of the coefficients for the other variables. Use of roads as a land-cover variable was further examined by comparing the relative concentration of use. This was done by calculating the average utilization distribution value for each land-cover type for each owl (excluding all utilization distribution values for each owl for the land-cover in which the nest was embedded), then calculating the inverse variance weighted mean and standard error. Removal of the utilization distribution values for the land-cover in which the nest was embedded helps adjust for the inflated values that result near the nest from the clustering of owl locations at the nest burrow.

A resource selection function (RSF) was also used to examine owl space use in relation to land-cover, burrows, perches, and roads. Five random locations were generated for each datalogger location, within a radius around each nest equal to the furthest distance the adult male owl travelled from the nest during the tracking period (Glenn et al. 2004). Land-cover and distance to nearest perch, nest burrow, secondary burrow, and each class of road type (dirt, gravel, paved) was determined for each owl datalogger location and each random location. Distance to the nearest perches and roads was limited to features that were within a radius equal to the furthest distance the owl travelled plus 100 m and 500 m respectively. This distance was selected for perches because owls may choose to be in areas with readily accessible perches nearby (within ~100 m) and factors that may result in avoidance such as predator use of these perches are likely of little concern when they are further than 100 m. We included roads up to this distance because owls are able to hear vehicles driving on roads 500 m away, but beyond this distance the visual disturbance is not likely perceived as a threat because there is plenty of time for an owl to react if a threat was present. The model for each owl contained all covariates with variation inflation factors less than three. A generalized linear model with a binomial error and logit link was used to analyse the data for each owl. Random locations were given one fifth the weight of the datalogger locations of used points when computing statistical significance (see Aldridge and Boyce 2007). Again, a two-step approach was used whereby the coefficients and standard errors from the model for each owl were used to calculate the inverse variance weighted mean, standard error, z value and p value for each covariate. As was done for the RUF, the negative coefficients are presented for distance variables. Selection ratios for each land-cover type were also calculated (Manly et al. 2002b) for each owl, while excluding all of the owl and random locations that occurred in the land-cover type in which the nest was embedded. This was done to reduce a bias toward the land-cover type in which the nest was embedded, which can result from clustering of locations near the nest. The selection ratio for each owl was then used to calculate the inverse variance weighted mean and standard error for each land-cover type.

We also looked at percentages of locations on roads and perches. The number of GPS datalogger locations on each type of road and the number of locations within five meters (equal to GPS datalogger error) of a perch were each divided by the total number of locations for that owl. The resulting values were then averaged across all owls to estimate percentage of time adult male owls spend on these features.

We subsampled one location per hour from the datalogger locations from 2007 and 2009 and re-ran the RSF models for these 14 owls to confirm that different sampling frequency between years did not influence our results. Although the standard errors changed for some estimates, the direction of the response of the owls (attracted versus avoided) did not change for variables with samples from more than one owl (Appendix 3.3). Differences in sampling frequency would not significantly affect the utilization distribution for each owl because the number of locations would have a negligible effect on the kernel density estimation for each owl. One owl did not have the reference land-cover available (native grass), so the land-cover coefficients and standard errors from that one owl was excluded from the inverse variance weighted mean for both the RUF and RSF. All statistical analyses were performed in R (R Core Team 2013).

3.2.1 Traffic

Traffic and road characteristic data were collected from roads that ran near Burrowing Owl nests in our study. Pneumatic tube traffic counters (MetroCount; MC5600 Series Roadside Unit) were deployed on 11 roads, one of which ran near two nests. Traffic counters recorded each vehicle that passed, vehicle speed and vehicle class. Traffic counter data from two roads were collected simultaneous to the deployment of dataloggers, and data from the remaining roads were collected the following summer. All roads were within a distance from the nest equal to the maximum distance that that owl travelled from the nest plus 500 m. Two of those roads were paved, one was dirt, and the rest were gravel. Each traffic counter collected data for at least 21 consecutive days to enable us to calculate average traffic volume, speed, and percent heavy vehicles with minimal bias from single traffic events (e.g. holidays, ranching events, etc.). Data collected from the traffic counters were used to calculate average hourly daytime traffic volume, average speed, and percent heavy vehicles during the same period of the day (one hour after sunrise to one hour before sunset) and period of the week (weekday vs. weekend) that the owls were tracked. Vehicles were identified as belonging to one of 14 classes using the method developed by the United States Federal Highway Administration (Federal Highway Administration 1999). Vehicle classes F8 to F13 were aggregated into a heavy vehicle category that was used to calculate the average percent of heavy vehicles that travelled on each road. Road width, ditch width, distance from road to nest, presence of fences, and road surface type were documented at each of these roads as well. Traffic and road characteristics for each monitored road are presented in Appendix 3.2.

We examined the response of the owls nesting near these roads to the traffic and road characteristics using weighted linear regression. The negative coefficient from the RSF was used as the response of each owl and the weighting was the inverse of the variance of that coefficient. Data exploration identified that traffic volume and road width had the greatest variation inflation factors, so both were run in separate models with no other covariates. One observation had a very large influence (weighted Cooks distance = 38.8), so it was removed from the final models. Models containing all possible combinations of uncorrelated variables were compared with AICc (Burnham and Anderson 2002) to determine which variables most influenced the owls' responses to roads.

3.2.2 Sound

To explore the relationship between vehicle speed, road surface type and sound, we measured sound from a single vehicle driving past a stationary sound meter. These sound measurements were taken on roads at least 50 km away from any owl nest sites. A handheld Brüel & Kjær Type 2250 sound level meter was used to measure the sound made by a passing two axle passenger vehicle driving on a dirt road at 20, 40 and 60 km/h, a gravel road at 60, 80, 100, and 110 km/h, and a paved road at 80, 100, and 120 km/h. The sound meter microphone was held six to seven meters horizontally from the passing vehicle and one meter off the ground. The L_{Smax} sound power level was calculated for each one-third octave band between 500 Hz and

10,000 Hz for each road surface type and speed. The formulae from International Standard 3746:2010 (ISO 2010) were adapted for these calculations. A Burrowing Owl audiogram was not available, so the lower hearing threshold was determined from the behavioural audiogram of an Eastern screech owl (*Megascops asio*) (Brittan-Powell et al. 2005) and converted to a weighting. This weighting was applied to the vehicle sound power levels, giving owl-weighted sound power levels (dBO), which more accurately depict the Burrowing Owls' perception of the sounds (Pater et al. 2009). Linear regression was used to examine the relationship between vehicle speed and owl weighted sound power levels.

3.3 Results

We tracked 17 owls for an average of 1.7 days (SD = 0.55) each and gathered a total of 1,428 independent GPS micro-datalogger locations (mean = 79, range = 24–150). The GPS dataloggers were successful in obtaining fixes 91% of the time (range = 62%–100%). Locations from the stationary test datatalogger with a dilution of precision <= 1.5 were an average of 4.26 m (SD = 2.94) from the test location. One owl was tracked in 2007 and again in 2008, for a total of 18 tracking events (13 in 2007, four in 2008 and one in 2009). All owls were tracked after the eggs hatched, but before the juveniles were able to fly (range: 7 to 22 days after hatch). The average 95% minimum convex polygon (MCP) was 2.59 ha, the average 95% kernel was 0.49 ha and the average maximum distance travelled from the nest during the day was 250 m (Table 3.1). Details about the number of locations, tracking duration and home range characteristics for each individual owl can be found in Appendix 3.1.

The least squared cross validation would not converge for one owl when calculating the bandwidth for the fixed kernel, so it was excluded from the RUF analysis. Owls were significantly attracted to nest burrows with all 18 owls showing a positive response in the RSF and all but two owls showing a positive response in the RUF. Our sample of owls was significantly attracted to fences and posts, but selection of posts differed somewhat between individuals (Table 3.2). On average, owls spent 17.4% (range= 0%–55.0%) of their time on fences (Figure 3.5). Three owls had tall perches (two with tall shrubs and one with a power line) near their nests, but none used these tall features as perches (Figure 3.5). Collinearity with other covariates resulted in the removal of these features from the RSFs for two owls, but the model for the remaining owl showed avoidance of tall shrubs (Table 3.2). The RSF shows that the number of owls attracted to dirt roads was less than the number that avoided them, but the inverse weighted mean indicates significant attraction, a result driven by a few owls that were greatly attracted to dirt roads (Table 3.2). The RSF and RUF results both show that owls are almost equally divided between attraction and avoidance of gravel roads (Table 3.2). Our analysis of road types as land-cover show significant attraction to gravel road surfaces compared to available (selection ratios; Figure 3.4) and significantly higher use of gravel road surfaces than other land-cover types (concentration of use; Figure 3.4). On average, owls spent 13.5% of their time on roads of any type, but the majority (9.7%) was spent on gravel roads (Figure 3.5). Only a few owls had paved roads near their nests and their responses to this road type varied between individuals and the two analyses (Table 3.2).

3.3.1 Traffic

We further explored the responses of owls to roads as a function of traffic and road characteristics. These roads were on average 146.9 m (0 – 679 m) from the nest, the average ditch width was 11.9 m (0 – 30 m), five roads had at least one fence present, average vehicle speed was 79.1 km/h (50.9 – 103.9 km/h), average traffic volume was 2.7 vehicles per hour (0.12 – 16.25), and average proportion of heavy vehicles was 0.10 (0 – 0.25). The top model (Table 3.3) contained average hourly vehicle speed ($\beta = -1.21$, SE = 0.28, $p = <0.01$). This significant negative relationship between owl response to roads and average daytime vehicle speed was consistent across all models containing this variable. Owls were attracted to roads with lower average daytime traffic speeds, but began avoiding roads (negative RSF coefficient switched from positive to negative) when average daytime traffic speeds were over 80 km/h (Figure 3.6).

3.3.2 Sound

At least nine trials per surface type and speed (except 40km/h on the dirt road and 110km/h on the gravel road which had five and two trials respectively) were used to calculate sound power levels. Owl weighted sound power levels increased significantly as vehicle speed increased ($\beta = 0.259$, $t = 8.71$, $p = <0.01$) (Figure 3.7). The overall model fit was $R^2 = 0.90$. The owl weighted sound pressure level when traffic is moving at 80 km/h was 86.2 dB (SE = 0.90). The A-weighted sound pressure level (weighted to human hearing) at that speed was 96.1 dB (SE = 1.02).

3.4 Discussion

Owls avoided roads with higher traffic speeds, which are highly correlated with sound levels, giving support to our hypothesis that owls are avoiding noisy areas during the day. Other studies have found that passerine density in areas near roads was not related to the visual disturbance caused by high volumes of traffic (Reijnen et al. 1995), but that vehicle speed better predicted reduced abundance (Reijnen et al. 1995, Reijnen et al. 1996). Sound from traffic increases with vehicle speed (Stephen 2005), and greater sound levels could hinder the ability of owls to communicate with their mate and young (Rheindt 2003). Traffic volume and proportion of heavy vehicles are also important variables that affect sound emissions from traffic (Besnard et al. 2009), but the effect they had on sound levels from the roads we monitored was negligible. Irrespective of why they avoid roads with greater vehicle speeds, the data we present here indicates it would be beneficial to owl habitat if vehicle speed is below 80 km/h near Burrowing Owl nests.

Owls selected and showed increased use of both fence lines and posts, indicating predator vigilance is a priority for male owls during the day. Fences and posts in this study were a similar height (~1.25 m tall) and likely used by the owls as perches to increase their field of vision (Andersson et al. 2009) and maximize detection of predators. Increased visual detection should shorten response time (Devereux et al. 2006) and therefore increase the probability of successfully reacting to a threat (Kenward 1978, Fitzgibbon 1990, Krause and Godin 1996). If male owls were only concerned with detecting predator threats to themselves they would not need to remain near the nest burrow during the day. Owls are presumably staying near the nest because they are not only avoiding predators, but also communicating threats to the young and female.

Paved, gravel and some dirt roads in our study area are raised above the surrounding prairie and most owls in our study had at least one road of this type near their nest. Owls may be attracted to roads with low traffic speeds because there is increased visibility when used as perches, but these types of roads could also be visual barriers. If owls are choosing to nest near roads that are visual barriers, they need a raised perch, such as a fence or the road surface itself, to see avian predators approaching from the direction of the road. This is particularly important because not only is visibility reduced when nesting near a road, but diurnal raptors also follow roads while hunting (Meunier et al. 2000).

Owls were attracted to shorter perches, but may be avoiding taller perches. Though only available to a small portion of our sample of owls, perches over two meters tall (power lines and tall shrubs) were not used by any owls. Larger raptors like hawks prefer taller perches (Bohall and Collopy 1984, Berkelman et al. 2002, Leyhe and Ritchison 2004) because of increased prey visibility (Andersson et al. 2009). Increased risk from other raptors is the most likely reason Burrowing Owls are not using these taller perches.

Results from this study provide evidence that perches are valuable features for adult male Burrowing Owls while roosting during the day. Whether perches increase survival of eggs, nestlings, fledglings, or adults is not known, but owls are likely considering the presence of vantage points when selecting nest sites. Thus, removal of perches around the nest may hinder their ability to be effectively vigilant and detect predators during the day. Though we found perches to be important to owls during the day, we are hesitant to recommend installation of additional perches near Burrowing Owl nests because this could also increase the presence of other avian predators (Kay et al. 1994) and potentially increase owl mortality. If perches are installed near active owl nests, we recommend they be added as part of a research program that would monitor owl response and nesting attempt success. Such an experiment could be used to identify quantity and configuration of perches that result in the greatest benefit to the owls. Overall, further work is required to determine the net benefit of perches to Burrowing Owl demography. Burrows (both nest and secondary) are important for owls during the day, and we know owls choose nest burrows surrounded by more burrows (Poulin et al. 2005). The features that owls are using and selecting (perches and burrows) within 250 m of the nest (average maximum distance travelled from the nest) should be left undisturbed to avoid potentially affecting nesting attempts.

Traffic and most other human disturbances will always be highest during the day, concurrent with the resting period for nocturnal birds. More effort needs to go into understanding the needs of these nocturnal species during the day to avoid disturbing them when they are vulnerable to predation and disturbance from humans.

Table 3.1. Spatial characteristics of adult male Burrowing Owl diurnal home ranges. * this method of home range size estimation uses distance owl travelled from the nest and the area is estimated assuming a circular daytime home range. All other methods use area and calculate the radius of a circle around the nest with an equivalent area.

Method	**Radius (m)**	**Area (ha)**	**Min.**	**Max.**	**SE**	**Number of owls**
100% kernel	67.73	1.44	0.14	8.41	0.5	17
95% kernel	39.35	0.49	0.03	2.98	0.2	17
100% MCP	108.43	3.69	0.33	31.64	1.7	18
95% MCP	90.74	2.59	0.13	30.11	1.6	18
Max. dist. from nest*	250.29	19.68	60.53	838.64	43.3	18

Table 3.2. Resource selection function and resource utilization function for 18 Burrowing Owl tracking events during the summers of 2007, 2008 and 2009. Results for land cover selection and use were omitted for one owl that did not have native grass near its nest. There are different numbers of owls for some covariates between the RSF and RUF because different covariates were removed due to collinearity. * -β is shown for these distance variables.

Covariate	**Resource Selection Function**						**Resource Utilization Function**					
				Owl Response						**Owl Response**		
	β	**SE**	**p**	+	**-**	**n**	**β**	**SE**	**p**	+	**-**	**n**
Intercept	3.18	0.27	<0.01	3	15	18	-1.9	0.05	<0.01	1	16	17
Burrow*												
Nest	11.12	1.19	<0.01	18	0	18	0.32	0.05	<0.01	14	2	16
Secondary burrow	9.18	6.85	0.09	1	1	2	3.67	1.22	<0.01	4	0	4
Land Cover												
Crop	-0.39	0.55	0.24	0	4	4	0.03	0.09	0.39	2	0	2
Dirt road	0.33	0.48	0.25	5	8	13	-0.08	0.05	0.04	2	6	8
Gravel road	0.2	0.51	0.35	3	4	7	-0.01	0.05	0.54	1	3	4
Idle field	6.68	1.36	<0.01	1	3	4	-0.08	0.18	0.33	1	1	2
Paved road	-2.4	2.4	0.16	0	1	1	-0.19	0.06	<0.01	0	1	1
Road ditch	-0.65	0.82	0.21	0	4	4	-0.14	0.03	<0.01	0	3	3
Tame grass	-0.7	0.5	0.08	1	4	5	-0.07	0.04	0.02	0	4	4
Wetland	1.16	0.55	0.02	4	8	12	0.05	0.05	0.15	4	4	8
Perch*												
Dugout spoil pile	1.71	5.44	0.38	1	0	1	–	–	–	–	–	–
Fence	12.37	3.53	<0.01	7	3	10	3.69	1.25	<0.01	8	3	11
Gas well head	10.71	2.19	<0.01	1	3	4	2.08	1.81	0.13	2	1	3
Post	23.17	10.81	0.02	1	1	2	2.69	1.54	0.04	2	1	3
Tall shrubs	-16.63	11.8	0.08	0	1	1	–	–	–	–	–	–
Road*												
Dirt	5.06	2.84	0.04	3	5	8	0.53	0.15	<0.01	1	0	1
Gravel	-0.17	3.17	0.48	4	5	9	-0.38	1.01	0.35	2	2	4
Paved	6.52	2.17	<0.01	1	1	2	0.26	0.22	0.12	1	0	1

Table 3.3. The top ten models explaining owl selection of roads with varying characteristics. Models were developed using weighted least squares regression.

Model	***k***	**AICc**	**ΔAICc**	***w***
speed	2	100.3	0.0	0.622
speed + ditch width	3	102.1	1.8	0.256
speed + fence	3	105.0	4.7	0.060
distance to nest	2	107.5	7.2	0.017
speed + ditch width + fence	4	108.3	8.0	0.011
speed + ditch width + distance to nest	4	108.4	8.1	0.011
null	1	108.6	8.3	0.010
speed + ditch width + percent heavy	4	109.2	8.9	0.007
fence	2	110.9	10.6	0.003
ditch width	2	112.5	12.2	0.001
percent heavy	2	112.5	12.2	0.001
speed + ditch width + fence + percent heavy	5	116.6	16.3	0.000

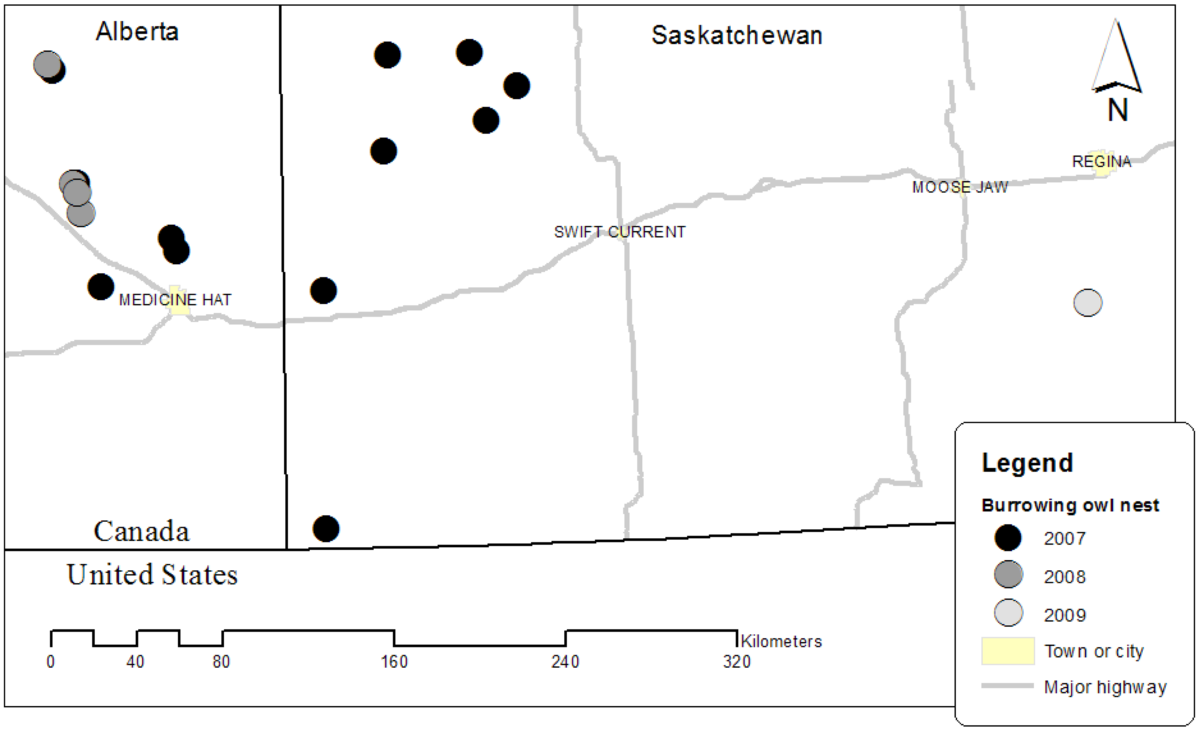

Figure 3.1. Distribution of Burrowing Owl nests from which the adult male was tracked with a GPS datalogger during the day.

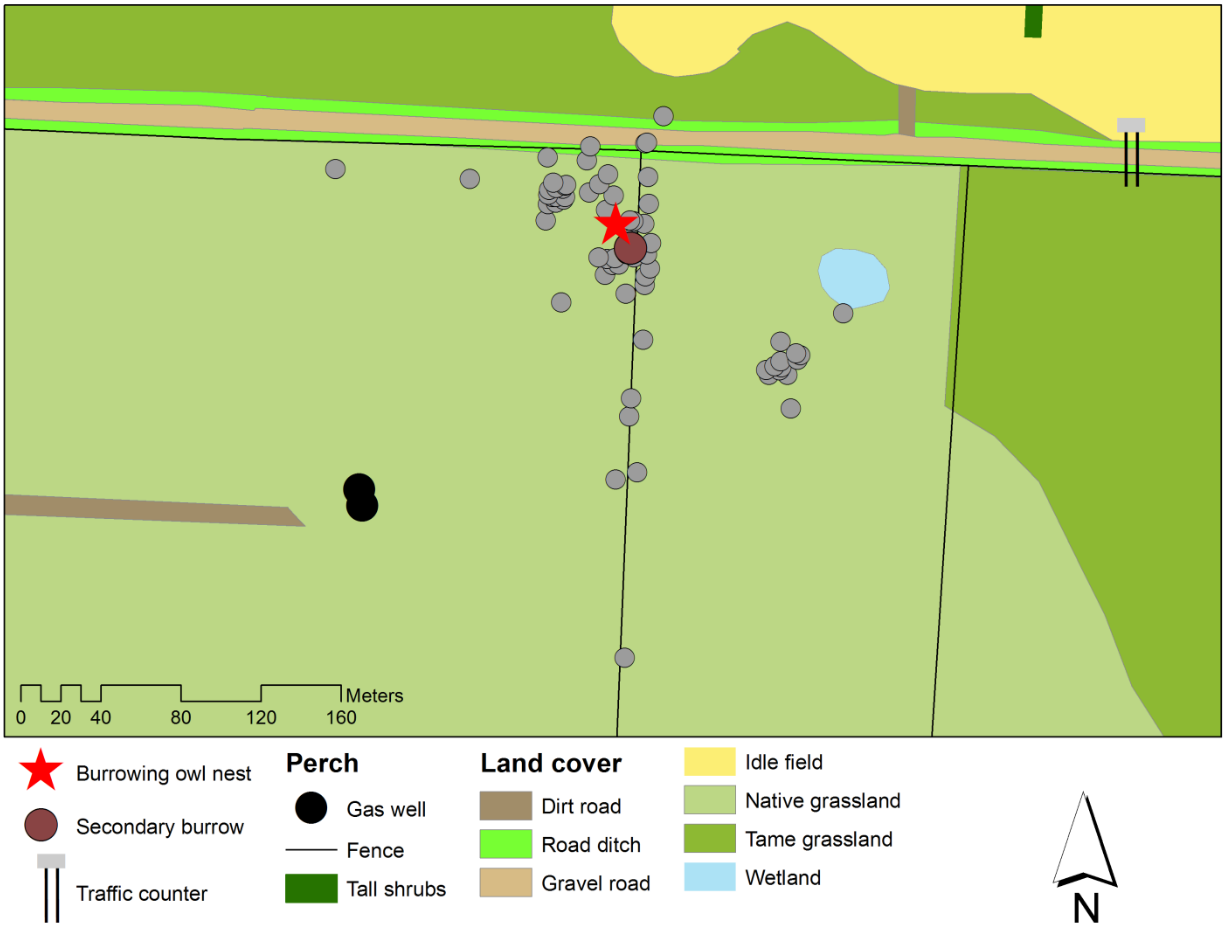

Figure 3.2. Burrowing owl locations and landscape around one nest.

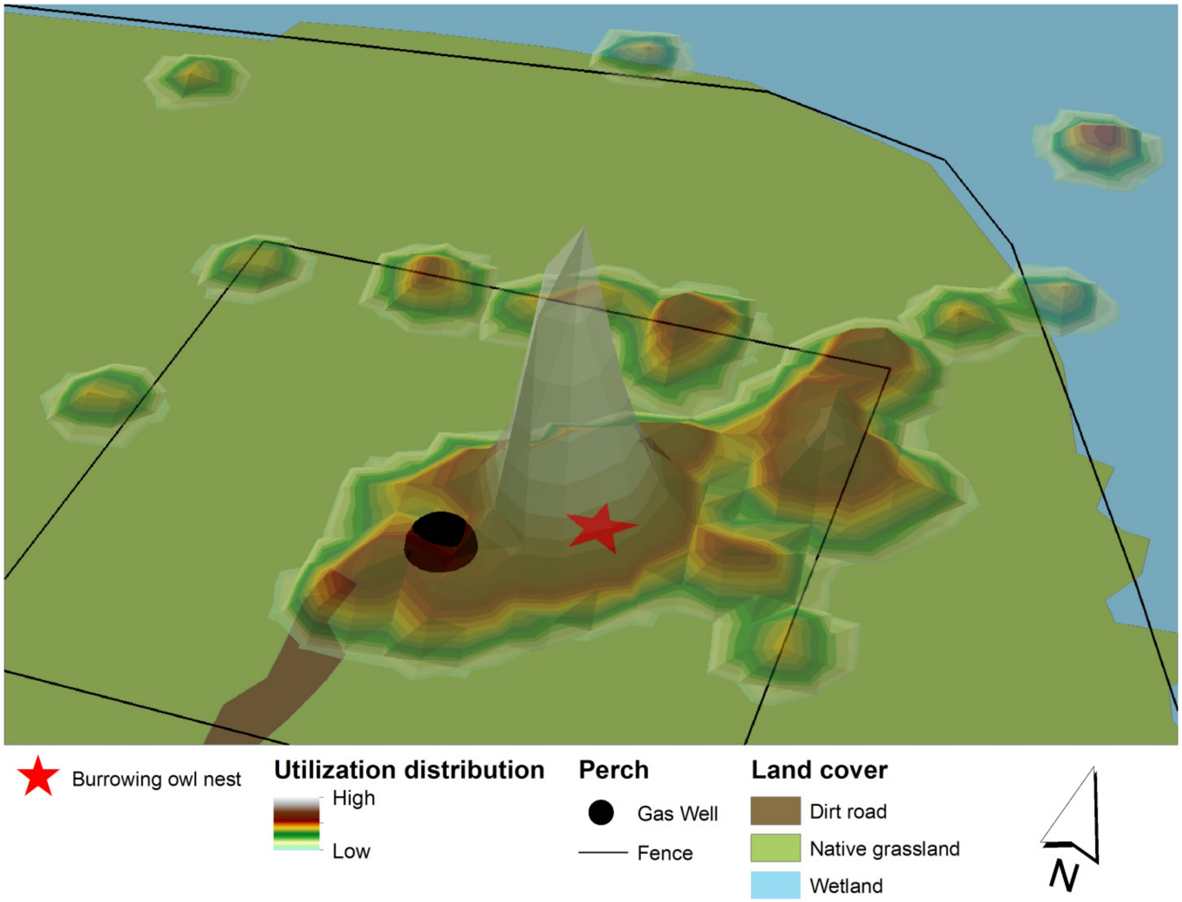

Figure 3.3. An example of a utilization distribution, showing one adult male Burrowing Owl, in relation to land-cover, perches, and its nest burrow. Utilization distributions were calculated for 17 owls in this study.

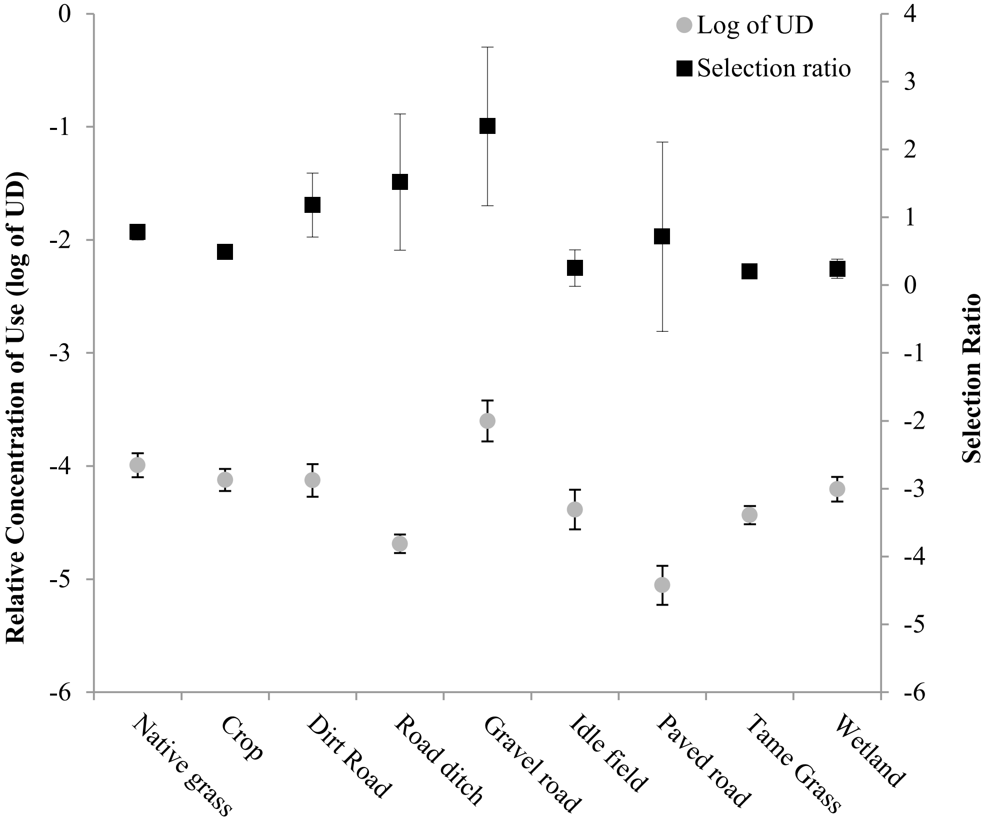

Figure 3.4. Weighted average relative concentration of use and weighted average selection ratios of different land-cover types by adult male Burrowing Owls during the day. For each owl, all utilization distribution values and owl and random locations for the land-cover in which the nest was embedded were excluded. Utilization distribution is log transformed. Error bars are 95% confidence intervals.

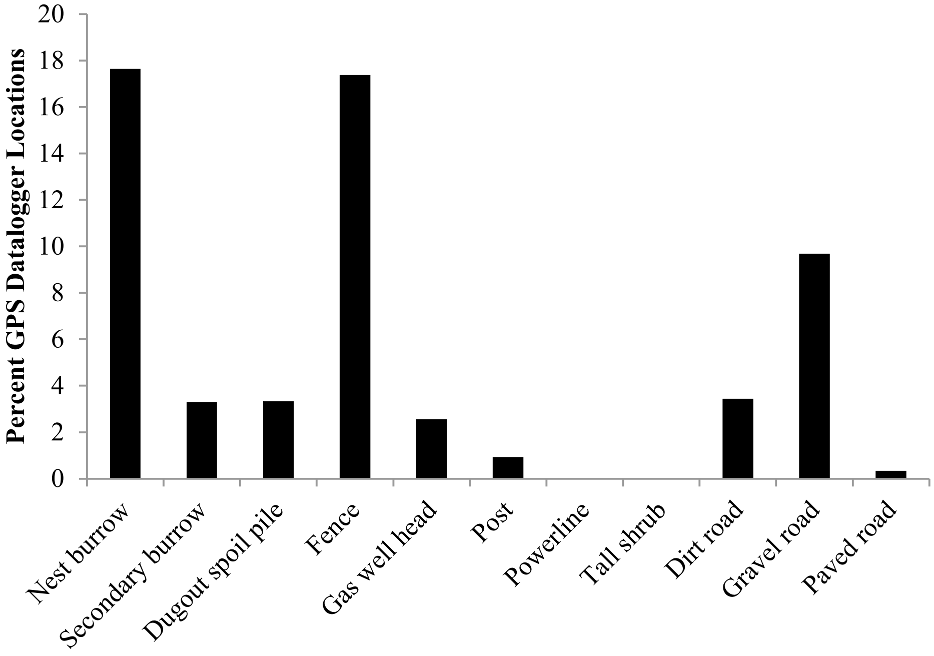

Figure 3.5. Average percent owl locations within 5 m of burrows and perches and on roads.

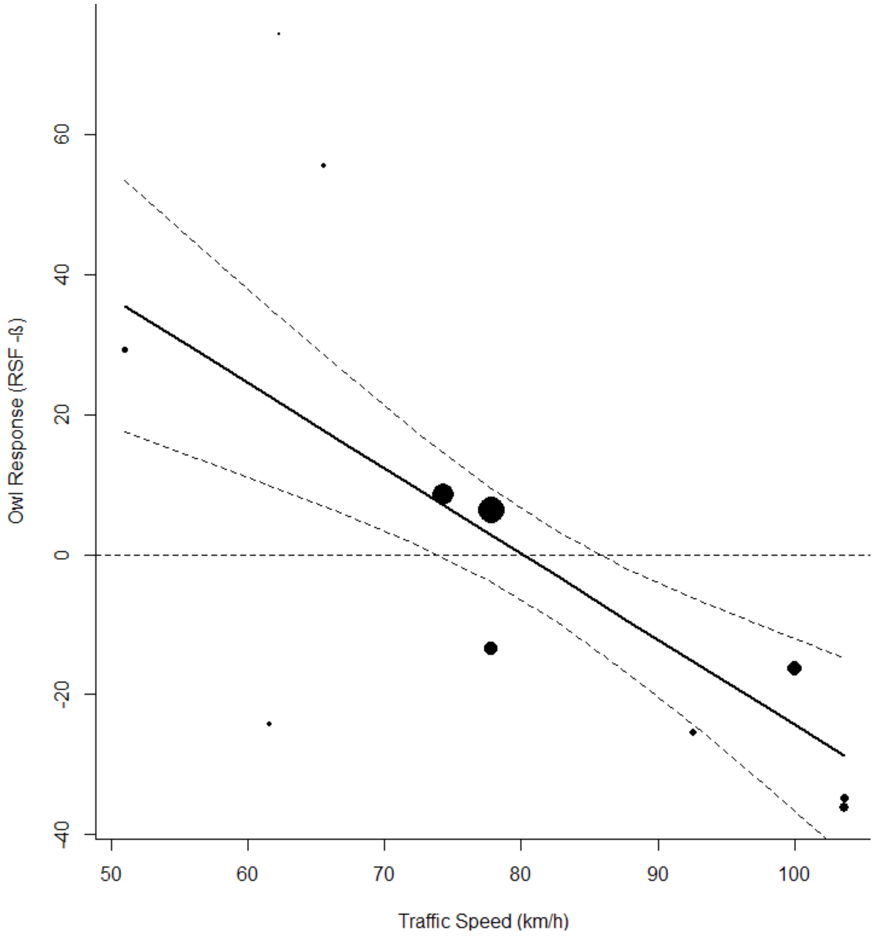

Figure 3.6. Predicted response of owls to roads as a function of vehicle speed, derived from weighted regression. Sizes of dots on figure are proportional to their weightings. Dashed line is 95% confidence interval.

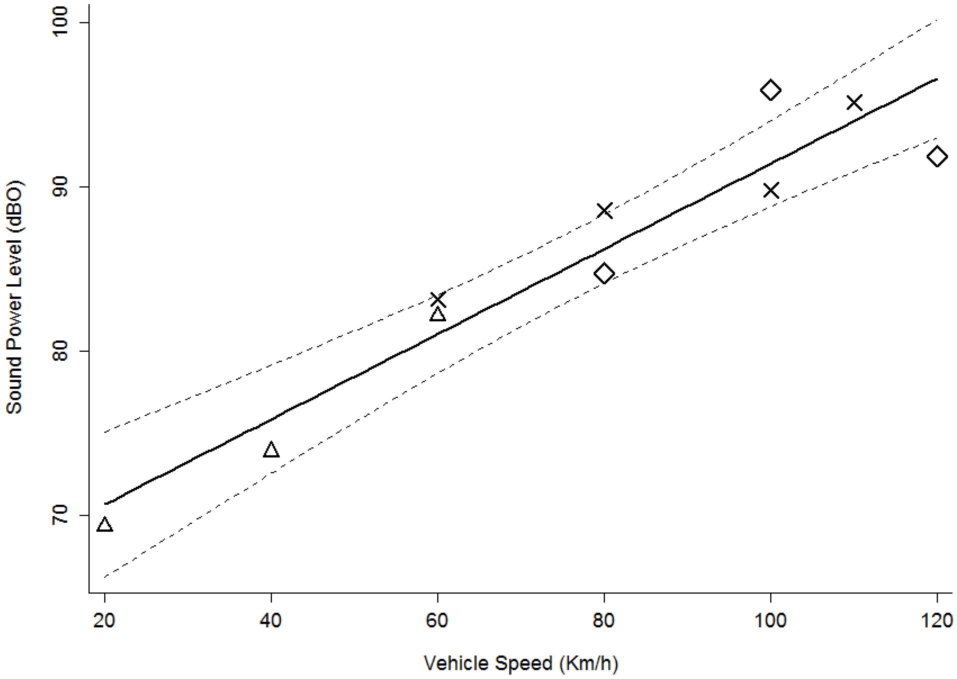

Figure 3.7. Average owl weighted broadband sound power level of a half-tonne pick-up truck driving on dirt (triangle), gravel (x) and paved (diamonds) roads. Dashed lines represent 95% confidence intervals.

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Appendix 3.1. Tracking effort and home range characteristics for each adult male owl tracked. * Fixed kernel density estimation would not converge for this owl.

Year	Owl ID	Days tracked	Numb. of Locations	100% MCP (ha)	95% MCP (ha)	100% Kernel (ha)	95% Kernel (ha)	Max. dist. from nest (km)
2007	49	2.38	150	31.64	30.11	8.41	2.98	0.84
	50	1.86	93	2.09	0.69	0.28	0.21	0.18
	104	1.17	72	0.35	0.17	0.91	0.30	0.06
	105	1.36	53	2.41	2.09	1.77	0.53	0.36
	108	2.25	122	1.14	0.22	0.83	0.29	0.15
	115	0.55	54	0.63	0.54	0.57	0.19	0.12
	131	2.15	123	4.97	1.38	1.38	0.41	0.35
	215	1.55	70	3.54	1.85	2.26	0.80	0.22
	743	2.79	150	3.24	0.55	1.36	0.44	0.27
	747	2.04	100	1.66	0.72	1.44	0.50	0.13
	749	1.76	71	0.99	0.56	0.68	0.24	0.11
	751	1.49	58	2.00	1.88	1.70	0.53	0.37
	756	2.38	142	1.47	1.13	1.73	0.55	0.14
2008	108	1.53	28	0.33	0.98	0.15	0.04	0.09
	608	2.07	32	1.98	0.44	N/A*	N/A*	0.31
	837	1.57	29	3.42	0.62	0.14	0.03	0.43
	838	1.49	24	4.09	2.52	0.66	0.19	0.23
2009	862	1.00	57	0.51	0.13	0.25	0.04	0.13
Mean	–	1.74	79.33	3.69	2.59	1.44	0.49	0.25
SE	–	0.13	10.10	1.67	1.63	0.46	0.16	0.04
SD	–	0.55	42.86	7.10	6.90	1.91	0.68	0.18

Appendix 3.2. Traffic and road characteristics for each road monitored with a traffic counter. * This observation was removed from the final model because of its disproportional influence (weighted Cooks distance = 38.8).

Traffic Counter ID	**Distance to Nest (m)**	**Road Surface**	**Road Width (m)**	**Ditch Width (m)**	**Fence Present**	**Average Vehicle Speed (km/h)**	**Average Vehicles per Hour**	**Proportion Heavy Vehicles**
34	55	Paved	18.0	42.0	Y	111.3	30.76	0.09
99	142	Paved	10.0	30.0	N	100.0	16.25	0.10
33	679	Gravel	8.0	20.0	Y	77.9	5.28	0.13
31	39	Gravel	8.0	8.0	N	77.7	2.50	0.04
44	595	Gravel	10.0	7.5	Y	74.2	1.75	0.06
39	40	Gravel	8.0	10.0	N	62.2	1.77	0.13
22	5	Gravel	9.5	10.0	Y	103.7	1.50	0.10
22	50	Gravel	9.5	10.0	Y	103.7	1.50	0.10
43	47	Gravel	10.0	9.0	N	92.6	1.24	0.08
38	0	Dirt	4.0	0.0	Y	50.9	0.29	0.25
82	18	Gravel	4.4	14.0	N	65.5	0.12	0.00
81	0	Gravel	7.2	12	N	61.52	0.36	0.06

Appendix 3.3. Results from resource selection analysis using one location per hour versus four locations per hour. Results of land-cover use were omitted for one owl that did not use native grass. * -β is shown for these distance variables.

	One Location Per Hour					Four Locations Per Hour					
				Owl Response					Owl Response		
Covariate	**β**	**SE**	**p**	+	-	**β**	**SE**	**p**	+	-	**n**
Intercept	3.23	0.65	0	7	7	2.86	0.31	0	12	2	14
Burrow*											
Nest	6.17	2.16	0	14	0	7.15	1	0	14	0	14
Secondary Burrow	9.95	13.28	0.23	1	1	9.18	6.85	0.09	1	1	2
Land-cover											
Crop	-0.49	1.28	0.35	2	2	-0.39	0.55	0.24	0	4	4
Dirt Road	0.82	1.16	0.24	4	6	0.24	0.49	0.31	4	6	10
Gravel Road	0.72	1.06	0.25	3	1	0.11	0.56	0.42	2	2	4
Idle Field	8.59	3.37	0.01	2	2	6.68	1.36	0	1	3	4
Paved Road	-18.05	3124.44	0.5	0	1	-3.15	1.52	0.02	0	1	1
Road Ditch	-0.4	1.54	0.6	1	3	-0.06	0.67	0.53	1	3	4
Tame Grass	-0.71	0.96	0.23	1	3	-0.69	0.45	0.06	0	4	4
Wetland	0.85	1.2	0.24	1	8	0.95	0.56	0.04	3	6	9
Perch*											
Dugout Spoil Pile	6.68	10.99	0.27	1	0	1.71	5.44	0.38	1	0	1
Fence	24.78	10.25	0.01	7	2	13.5	3.85	0	6	3	9
Gas Well Head	-8.61	4.48	0.03	0	4	-8.02	2.23	0	0	4	4
Post	35.78	34.63	0.15	1	1	23.17	10.81	0.02	1	1	2
Tall Shrubs	12.68	24.13	0.3	1	0	-16.63	11.8	0.08	0	1	1
Road*											
Dirt	8.02	4.78	0.05	2	3	8.13	2.38	0	2	3	5
Gravel	-23.55	10.4	0.01	1	6	-2.1	3.62	0.28	3	4	7
Paved	7.74	3.84	0.02	1	1	-16.24	9.07	0.04	1	1	2

CHAPTER 4. INFLUENCE OF HUMAN FOOTPRINT AND SENSORY DISTURBANCES ON NIGHT-TIME SPACE-USE OF A NOCTURNAL RAPTOR.

4.1 Introduction

The greatest threat to native species from human development is habitat loss (Brooks et al. 2002, Fischer and Lindenmayer 2007). However, an increasing body of evidence suggests that habitat degradation caused by anthropogenic sensory disturbances (e.g. noise and light) often exacerbates the direct effects of habitat loss by degrading quality of the remaining habitat (Francis and Barber 2013). Sensory disturbances affect a wide range of taxa (Longcore and Rich 2004, Francis and Barber 2013), and can alter a variety of breeding and foraging behaviours (Brumm 2004, Titulaer et al. 2012). In extreme cases, sensory disturbance has resulted in animals completely avoiding otherwise suitable habitat (Rotics et al. 2011, Blickley et al. 2012). Thus, if the impacts of sensory disturbances are not quantified, the cumulative area impacted by human developments may be underestimated.

It is challenging to separate the behavioural effects caused by the physical changes in vegetation structure and composition resulting from human development (hereafter, ‘footprint’) from those caused by sensory disturbances (hereafter, ‘disturbance’). Studies evaluating the effects of noise on terrestrial wildlife typically have compared animal abundance or behaviour in the vicinity of quiet versus noisy roads, or close to versus far from noisy roads. With such study designs, it is difficult to separate the effects of footprint from disturbance (Delgado et al. 2008, Summers et al. 2011); especially for wide-ranging species whose home ranges are influenced by multiple sensory disturbances. In these situations, it is difficult to use a noisy versus quiet or bright versus dark dichotomy when conducting analyses. Nonetheless, understanding how wide-ranging species, such as predators, react to disturbance is essential because they rely heavily on visual and auditory cues to detect and capture prey.

Sound emanating from anthropogenic sources has the potential to affect both predators and their prey. While travelling, prey may disturb vegetation causing it to rustle, and rustling vegetation typically creates sound in frequencies above 1.6 kHz (Miller 1978, Schomer and Beck 2010). Predators rely on sound in these high frequencies to detect, locate, and capture small mammals (Payne 1971, Knudsen and Konishi 1979, Singheiser et al. 2010). Mice select routes to minimize visibility and production of sound in these frequencies (Barnum et al. 1992), and in some situations travel on quieter substrates (Roche et al. 1999). Consequently, predators that use acoustic cues may avoid hunting in noisy areas if such noise affects their ability to detect the specific sounds made by moving prey (Hübner and Wiegrebe 2003, Goerlitz et al. 2008, Siemers and Schaub 2011). When noisier areas are not avoided, predators that rely on acoustic cues for hunting are less successful in capturing prey than when hunting in quieter areas (Schaub et al. 2008). Importantly though, high frequency sounds travel shorter distances from the source than low frequency sounds (see ISO 1993), so the impact of anthropogenic sound on hunting may depend on which frequencies of sound are emitted.

Artificial light can affect circadian rhythms of animals at all times of day, but the greatest impacts are typically on species active at night (Longcore and Rich 2006, Gaston et al. 2013). However, the impact of artificial light on predators in particular is unclear. Nocturnal predators, such as owls, rely on both sight and sound when hunting (Dice 1945, Kaufman 1974). They therefore require a minimum light level and acoustic cues to detect prey. Accordingly, most owls are more active (Penteriani et al. 2011, Frye and Jageman 2012), and bring more prey back to their young (Poulin and Todd 2006, Zarybnicka et al. 2012), during crepuscular periods. Artificial light could benefit owls if it extends the period of time that they can see prey at night. Conversely, though light increases the detectability of prey, it could be detrimental if prey availability decreases because prey remain closer to cover when it is brighter (Lockard and Owings 1974, Kaufman and Kaufman 1982, Clarke 1983, Wolfe and Tan Summerlin 1989, Kotler et al. 1991, Daly et al. 1992). With increased illumination, prey move and forage less (Abramsky et al. 2004, Bird et al. 2004, Rotics et al. 2011), likely in response to increased predation risk (Clarke 1983, Kotler et al. 1991), so predators may need to search larger areas to find the same amount of prey (Rockhill et al. 2013).

The effects of anthropogenic activities on hunting predators are commonly studied by tracking individuals as they travel through a landscape. However, few studies have attempted to separate the relative importance of footprint versus disturbance on predatory behaviour. Those studies that have attempted to determine the relative importance of footprint versus disturbance (Chubbs et al. 1993, Jiang et al. 2010, Neumann et al. 2013) have typically been confounded because they rely on coarse proxies of sensory disturbances (high versus low) rather than directly measuring the magnitude of sensory disturbances. Given the strong overlap in space and time of multiple disturbances in the ‘disturbance landscape’ for a wide-ranging predator, more precise measurement is needed to evaluate how disturbance levels alter predator behaviour.

Crucial to understanding how the behaviour of individual animals is influenced by sensory disturbance and physical footprint is how the analyst defines availability. Animals that repeatedly return to a stationary landscape feature (e.g. a den or nest) during part of their life history are typically viewed as central place foragers. Central place foragers are constrained in their movement patterns by the fact they repeatedly return to the den or nest. Central place foragers tend to have circular home ranges and quite often a fixed radius buffer around the central place is used to define what is available. However, factors such as conspecifics, predators, or differential resource availability can affect the shape of the home range that is actually used (Covich 1976, Andersson 1981). Thus, an analyst that uses the home range to define what is available may reveal a very different pattern of selection than when a fixed circular buffer around the central place is applied. Thus, it is critical when evaluating sensory disturbance or physical footprint to evaluate if the placement of the home range is influenced by these features as well as evaluating if such features are selected or avoided in the actual home range.

Detailed measures of sensory disturbances are needed to evaluate the response of predator space-use to artificial light and sound. Both light and sound are types of energy that move as waves through the air and decay as a function of distance. However, modelling only the distance to the nearest sound or light source will not accurately reflect sound and light levels because of their differing physical properties and attenuations. Also, when sound or light from two sources spatially and temporally overlap, there is an increase in magnitude because of an additive effect, which is not captured by distance to source alone. Light waves are much smaller than sound waves, making them less susceptible to attenuation. Environmental conditions (wind, humidity, temperature, atmospheric pressure) and ground surface have a large effect on the propagation of sound waves, but those factors do not affect light as it travels from a source. The intensity of sound and light emanating from human structures can be quite diverse, resulting in a landscape with spatially and temporally varying sound and light levels. This is the first study to consider these factors and develop detailed measures of light and sound in an effort to examine space-use of a nocturnal predator in relation to artificial sensory disturbances.

To study the influence of both light and sound on the space-use of a predator that relies on both auditory and ocular cues while hunting, nocturnal movement patterns must be quantified. Burrowing Owls (*Athene cunicularia*) live in a landscape with varying levels of anthropogenic light and sound. Burrowing Owls capture the majority of their prey during twilight (Poulin and Todd 2006); however, Burrowing Owls do not have asymmetrical ears (Volman and Konishi 1990) to help them effectively locate prey, so they cannot capture prey in very low light conditions like owls that do have asymmetrical ears (Dice 1945). Thus, Burrowing Owls rely on both hearing and sight to detect prey. If owl movement patterns are influenced by artificial light and sound, that influence will be most pronounced during twilight hours when owls are moving most and the largest number of prey are brought back to the nest (Poulin and Todd 2006).

To examine the night-time movement patterns of a predator in relation to human infrastructure and associated artificial light and sound, we tracked the nocturnal foraging of adult male Burrowing Owls, wearing GPS dataloggers, under two definitions of availability (maximum distance and minimum convex polygon) and two temporal periods (twilight and night). If owl nocturnal space-use is influenced most by sensory disturbance associated with human development, then models containing only those variables will fit best. If the best models contain variables relating to the footprint, then owls are affected more by the physical landscape changes that result from human development. We predict that male owls will be most influenced by sensory disturbances during twilight hours under either definitions of availability and will select areas with lower sound levels in high sound frequencies and lower levels of artificial light to enable effective detection of prey in areas where prey availability is greatest.

4.2 Methods

Between 2007 and 2010, we monitored 521 Burrowing Owl nesting attempts within the dry mixed-grass ecoregion of Southern Alberta and Saskatchewan, Canada. At a subset of these, 84 adult males were tracked with a GPS datalogger (Figure 4.1). Nests were located in early-May using call play-back surveys, and were visited once per week throughout the breeding season. After the female finished laying, and before juveniles fledged, each adult male owl was captured with either a one way walk in (Winchell 1999) or bow-net trap (Bloom 1987). Each trap had one of the following lures: 1) a dead mouse, 2) a speaker playing a Burrowing Owl primary call, 3) a decoy Burrowing Owl, or 4) some combination of these three lures. A 7-gram GPS datalogger (TechnoSmArt, Guidonia Montecelio, Italy) was attached to each owl, using Teflon ribbon in a backpack style configuration. Teflon was secured to the datalogger with light-weight packing tape containing a tear-proof fiberglass cross-weave. Males were returned to their nest burrows for release after dataloggers were attached. The dataloggers were upgraded by the manufacturer each year, resulting in varying options and program schedules over time. Dataloggers were programmed to turn on and take locations every two seconds (2009 and 2010), every 15 minutes (2007, 2009, and 2010), or every hour (2008). The following data were stored on internal memory within the GPS datalogger: latitude, longitude, speed, altitude, dilution of precision, Greenwich Mean Time, and date. To retrieve the data, each owl was re-trapped after approximately 12 days, by which time its GPS datalogger battery had been depleted. Owl locations with dilution of precision > 1.5, speed > 64 km/h, and altitude ≤ 20 m below and ≥ 80 m above the elevation of the owl's nest were excluded. One location every 15 minutes (2007, 2009, and 2010), or else one location every hour (2008), was selected for these analyses. The accuracy of the GPS dataloggers was tested by measuring the distance between locations from a stationary GPS datalogger placed on a fence post for three days and the stationary datalogger's location as determined with the averaging function in a hand-held GPS unit. All data were collected by trained field staff in possession of valid animal care approval, federal and provincial research permits and bird banding licenses (permit number 10796).

Burrowing Owl GPS datalogger locations were used to examine owl foraging areas and movement patterns. For each owl, we delineated the area of the 100% minimum convex polygon (MCP) and step length (distance between successive owl locations) for each night tracked using ArcMap 10.1 (ESRI 2012) and Geospatial Modelling Environment (Beyer 2012). Average step length and distance to nest were calculated for each owl for each hour of the night. Each year, land-cover surrounding the nest of each tracked owl was documented by driving the roads around the nest and recording the land-cover types on aerial photographs. These aerial photographs were digitized in a GIS environment onto SPOT5 imagery (2006 coverage). Land-cover types (permanent cover [native and tame grassland], annual crop, riparian area [sparse vegetation and seasonally dry], road, water bodies [standing water all year], buildings [residential and agricultural buildings], shrubs and trees) were all included in statistical models, with permanent cover being the reference category.

We included in our analyses owl locations taken between nautical twilight start and end, to ensure we used only locations from nocturnal foraging activities (Poulin and Todd 2006). Owl prey delivery rates vary considerably between the twilight and night period (Poulin and Todd 2006), so locations in these two periods were analysed separately. All locations between sunset and sunrise were categorized as night locations and all remaining locations that occurred between night and nautical twilight start and night and nautical twilight end were categorized as twilight locations. Sun position times were determined from the National Research Council of Canada website (http://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html) using the coordinates of the nest.

Two methods were used to define the area that was available. Each area had a separate set of random locations plotted within its boundary. The first defined available as a radius around the nest equal to the maximum distance that owl travelled during the period tracked (Glenn et al. 2004) (Figure 4.2) herein referred to as MD (Maximum Distance) and the second method defined available as the 100 percent minimum convex polygon (Figure 4.2), herein referred to as MCP (Minimum Convex Polygon). Using MD as the available area allows an examination of the factors that influenced where owls placed their foraging areas in relation to their nest burrows. The use of the MCP helps to understand the selection of features within their foraging areas.

Prior to analyses, all data were evaluated for co-linearity among covariates. When co-linearity was detected, the variable with the highest variation inflation factor was removed and the variation inflation factor was then recalculated for each variable. This was repeated until all variation inflation factors were less than three (Quinn and Keough 2002).

We used resource selection functions (RSFs) to examine owl space-use in relation to human infrastructure and in relation to the light and sound emanating from this infrastructure. To understand if the sensory disturbance or the footprint of human development most strongly influenced Burrowing Owl night-time movements, three models (baseline, disturbance, and footprint) were compared for each nocturnal period (twilight and night) and each available area

(MD and MCP). The baseline model contained land-cover and distance to the nest burrow. The disturbance model contained land-cover, distance to nest burrow, light, and sound. The footprint model contained land-cover, distance to nest burrow, and the nearest distance to each feature from which either sound or light emanates (compressor station, oil well, paved road, town and human building). Distance to each of these landscape features was used because sound emanates from compressor stations, oil wells and high traffic-volume roads and light emanates from compressor stations, cars driving on paved roads, and towns and human buildings (e.g. farm yards, agricultural buildings, etc.). Sound and light levels are not perfectly correlated with distance to sound and light sources because each source has different levels of light and sound that are subject to differing sources of attenuation as well as the fact that sound and light can combine to produce areas with higher disturbance levels.

Five random locations were generated for each owl location within each available area; one set of random locations was generated for each MD RSF and one for each MCP RSF. Land-cover, sound, light (2009 DMSP average light images [Data collected by the US Air Force Weather Agency and processed by NOAA's National Geophysical Data Center]), and distance to nest burrow, nearest compressor station, oil well, paved road, human building, and town were determined for each owl datalogger location and each random location. Distance to the nearest compressor station, paved road, and oil well was limited to features that were within a radius equal to the available area plus five km. Features within these spatial limits were used because that area includes all the sound sources used to calculate the sound pressure level at each datalogger and random location. Also, it is possible that light from features outside the available area, extend into the available area, so we wanted to ensure that these light sources were included in the footprint models. The model for each owl contained all covariates with variation inflation factors less than 3.

The three models (baseline, disturbance, and footprint) were compared only for owls with exposure to artificial light or sound in the disturbance model and if all three models converged. A generalized linear model with a binomial error and logit link was used to analyse the data for each owl. Random locations were given one-fifth the weight of the datalogger locations of used points when computing statistical significance (see Aldridge and Boyce 2007). A two-step approach was employed, whereby the coefficients and standard errors from the model for each owl were used to calculate the inverse variance weighted mean (Nielsen et al. 2009), standard error, z-value and p-value for each covariate. A mixed effect logistic regression (with each owl as the random variable) was also used to determine owl selection within each available area. Models with the lowest AIC (Burnham and Anderson 2002) were identified as the best fitting models. The negative regression coefficients are presented for distance variables so that the response of the owl (selected versus avoided) matches the signs (positive versus negative) of the coefficients for the other variables.

4.2.1 Sound

The number of decibels above what can be detected by an owl was determined for each one-third octave band for each owl and random location. Following the protocol outlined in ISO 8297 (ISO 1994), sound was measured with a handheld Brüel & Kjær Type 2250 sound level meter at all compressor stations within the MD available area plus five km. Sound from individual oil wells does not vary significantly, so following ISO 3746 (ISO 2010), sound was measured at a subset of each type of sound producing oil well (pump jacks and screw pumps). The LZ_{eq} sound power level was then calculated for each one-third octave band between 0.5 kHz and 10 kHz for each sound source, using the calculations provided in each corresponding standard. The average sound power level of all oil wells for each one-third octave band was used when modeling sound propagation from each oil well. During each day of sound data collection in the field, ambient sound (L_{eq} (1min)) was measured at locations at least five km away from sound producing structures. All of our ambient sound measurements were taken during the day, so the lowest sound pressure level of all ambient sound measurements for each one-third octave band was used as the night-time ambient sound pressure level (Appendix 4.2). The sound level meter was calibrated with a Brüel & Kjær sound level calibrator type 4231 at the beginning of each day prior to the collection of sound measurements.

Traffic data were collected from fifteen roads that ran near Burrowing Owl nests in our study. Pneumatic tube traffic counters (MetroCount; MC5600 Series Roadside Unit) were deployed on nine roads, traffic data for four roads were provided by the Saskatchewan Ministry of Highways and Infrastructure, and data for two roads were provided by Alberta Ministry of Transportation. The pneumatic tube traffic counters recorded the date, time, speed, and class of each vehicle that passed. Data provided by the provinces contained average hourly traffic volume, speed, and proportion of heavy vehicles for each day. All data were collected for dates during the summer within one year of the owl being tracked. Individual vehicle hits recorded on the traffic counters were used to calculate average traffic volume, speed, and percent heavy vehicles for each hour the owls were tracked (sunset to sunrise).

Average hourly continuous energy equivalent sound power level of traffic (herein average traffic sound) was calculated for roads within the available area plus five km. Hourly traffic volume, speed, and proportion of heavy vehicles were used to calculate energy equivalent sound level for each hour (L_{eq} (1hr)) for each road (using (Besnard et al. 2009). Only roads with at least 20 vehicles per hour, for at least one hour during the nocturnal period were included. Traffic volumes less than 20 vehicles per hour produce infrequent sensory disturbance and would not likely affect owl movement patterns at a scale detectable by the frequency of our owl locations. For the same reason, average traffic sound was used instead of the instantaneous sound from the loudest vehicle (L_{eq} (max)) that passed each hour.

Sound propagation and attenuation, from sound sources within the MD or MCP available area, to each owl and random location, were calculated using international standards ISO 9613-1 (ISO 1993) and 9613-2 (ISO 1996). Sound was modelled from each compressor station and each road with ≥ 20 vehicles per hour, and from the nearest ten oil wells, to each owl location and each MD and MCP random location. For calculating the attenuation of sound due to atmospheric interference, five random locations were randomly matched with one owl location by assigning the same above-ground height, date, and time as for the corresponding owl location. Characteristics of the tallest hill (Natural Resources Canada 2000) blocking the line-of-sight between the sound source and receiver (owl or random location) were used to calculate attenuation from screening. Hourly temperature, humidity, and atmospheric pressure from the nearest Environment Canada weather station (http://climate.weather.gc.ca/index_e.html#access) were used to calculate the atmospheric attenuation coefficient for each owl and random location. ArcMap 10.1 (ESRI 2012) was used to extract all other cartographical variables needed for attenuation calculations. The sound-pressure levels from all sources were then added together for each owl and random location.

4.2.2 Owl detection of sound

In most studies of noise impacts, researchers report noise levels either qualitatively (quiet versus loud; Habib et al. 2007, Goodwin and Shriver 2011) or quantitatively using a human-based criterion (e.g. A-weighting; Conomy et al. 1998, Maier et al. 1998). However, it has been well established that different species have different hearing sensitivities which may strongly influence how they respond to artificial sound. To adjust for these differences in hearing sensitivities, the minimum sound level that an animal can detect in each frequency can be extracted from lower hearing threshold audiograms and used in sound detection calculations to better reflect how a species perceives sound (Pater et al. 2009). The audiogram of a closely-related animal can be used if an audiogram is not available for a particular species, but caution should be used because there still can be large differences in hearing between closely related species. For example, Barn Owls (*Tyto alba*) rely heavily on auditory detection of prey, have asymmetrical ears (Norberg 1977, Knudsen and Konishi 1979) and can detect sounds above -18.6 dB in the 4 kHz frequency band (Dyson et al. 1998), but Eastern Screech Owls (*Megascops asio*) have symmetrical ears, rely less on hearing prey while hunting and cannot detect sounds below -7.5 dB in the frequency of 4 kHz (Brittan-Powell et al. 2005). By comparison, humans have more-similar hearing to Eastern Screech owls than do Barn Owls, as humans can hear sounds above -5.4 dB in the 4 kHz frequency band (ISO 2003). A Burrowing Owl audiogram was not available, but they have symmetrical ears and hunt similar prey to that of Eastern Screech Owls, so the auditory brainstem response for the latter species (Brittan-Powell et al. 2005) was converted to a behavioural lower hearing threshold by subtracting 30 dB from the sound pressure level in each one-third octave band (Brittan-Powell et al. 2002).

Sound from the source(s) was detectable at the receiver location (owl or random location) if the sound pressure level was above ambient sound levels when ambient sound was above the lower hearing threshold (Appendix 4.2). If ambient sound was below the lower hearing threshold, then sound was detectable if the sound pressure level from the source(s) was greater than the lower hearing threshold. These criteria were then used to calculate the number of decibels that could be detected at the receiver location for each one-third octave band. A value of zero was assigned if no sound could be detected.

Eastern Screech Owls hear best in the 4 kHz one-third octave band (Brittan-Powell et al. 2005), but have similar abilities to detect sounds between 1.6 kHz and 6.3 kHz when masking from ambient sounds is also considered (Appendix 4.2). The sound levels were highly correlated for all frequencies for both the MD and MCP data sets, so the frequency with the highest variation inflation factor was selected. The one-third octave band with the highest variation inflation factor for both the MD RSF and MCP RSF models was 2.5 kHz.

The distance from which Burrowing Owls can still detect sound from each source (i.e., the listening area; see Barber et al. 2010) in each one-third octave band from 0.5 kHz to 10 kHz was calculated. The average sound power level of each sound source (Figure 4.5) and the formulae from international standards 9613-1 (ISO 1993) and 9613-2 (ISO 1996) were used to calculate sound propagation and attenuation under the average night-time environmental conditions experienced by owls while they were being tracked. The calculations assumed no barriers, that there was grassland between sound source and receiver, and that wind speed was negligible. Owl detection of sound was determined using the same criteria outlined above.

4.2.3 Oil wells

To better understand where owls spent time in relation to the most common sound source (oil wells), we looked at percentages of owl locations on oil well sites. The numbers of GPS datalogger locations within ten meters (equal to radius of the footprint of oil wells plus the GPS datalogger error) of an oil well were each divided by the total number of locations for that owl. The resulting values were then averaged across all owls to estimate the percentage of time adult male owls spent on oil wells.

4.2.4 Home range size

We also used linear regression to examine the relationship between the total area within each owl's nocturnal home range (MD and MCP) and the area within the home range that was exposed to artificial light and sound in the 2.5 kHz one-third octave band. Prior to analysis, light and sound were log-transformed because they each contained outliers, and we also modelled these variables as categorical variables (present in home-range = 1, absent = 0). All models contained the number of nights tracked as a covariate, and we used AIC to select the form of the sensory disturbance variable that best fit the data.

4.3 Results

We tracked 84 male owls for an average of 3.7 nights (SE = 0.33; 1 – 10) per owl. From these owls, we acquired a total of 8760 locations, with an average of 104 locations (SE = 9.67; 7 – 332) per owl. The GPS dataloggers were successful in obtaining fixes 96% of the time (74 – 100%). Locations from the stationary test-datalogger were an average of 4.26 m (SD = 2.94) from the test location, with a dilution of precision <= 1.5. Average owl foraging area stabilized at 623 ha (Appendix 4.1), an area equivalent to a circular home range with a radius of 1.4 km. Eighty-five percent of all owl locations were within 1.4 km of the owl's respective nest (Figure 4.3). Average distance to the nest and step length both differed between twilight and night hours (Figure 4.4). Average hourly humidity was 76.5% (SE = 5.11), temperature was 11.7°C (SE = 1.31), atmospheric pressure was 93.1 kPa (SE = 0.32), and wind speed was 3.3 km/h (SE = 0.64) while owls were being tracked.

Owl step length and foraging area (100% MCP) were lower in the first full night after datalogger attachment than in the remaining tracking nights (Appendix 4.1), so owl locations from the first full night were excluded from the analysis for each owl. This left 6196 locations from 63 owls, over an average of 4.7 nights (SE = 0.38), with an average of 98 locations per owl (SE = 10.92).

We measured sound at 38 compressor stations, 44 oil wells (35 pump jacks and 9 screw pumps), and took 21 ambient sound measurements. Sound power levels for all sound sources were greatest in the lower frequencies (Figure 4.5). On average, there were two compressor stations (0 – 11) and 31 oil wells (0 – 346) within the Burrowing Owl MD available area.

Average traffic sound was calculated for 14 paved roads that passed near the nest burrows of 29 owls tracked with dataloggers. The average hourly vehicle speed was 96.9 km/h (91.0 – 100.1 km/h), average hourly proportion of heavy vehicles was 0.21 (0.15 – 0.38), and average hourly traffic volume was 58 vehicles per hour (19.0 – 146.8; Figure 4.6). These roads were, on average, 4.58 km (0.04 – 10.12 km) from the nest. The average sound power level on these roads in the 2.5 kHz one-third octave band was 64.2 dB (55.6 – 72.9 dB). Compared to the sound power levels of oil wells and compressor stations, average traffic sound was low, especially in the high sound frequencies, primarily because of low traffic volumes (< 100 vehicles/hour for all hours except 21:00 and 22:00 (Figure 4.6). The average speed of vehicles travelling at night was 97 km/h. The maximum sound power level (L_{eq} (max)) of a pickup truck travelling at 97 km/h is 79.3 dB in the 2.5 kHz one-third octave band.

Owls are likely able to detect sound in the 2.5 kHz third octave band up to 1020 m, 187 m, 156 m, and 504 m from compressor stations, oil wells, traffic, and a passing pickup truck driving at 97 km/h, respectively, but they can hear sound in the 1.25 kHz or 1.6 kHz one-third octave band from all these sources the furthest (Figure 4.7). This is because owls hear best in higher frequencies (i.e. 4 kHz), but sound in high frequencies are affected more by atmospheric attenuation, and therefore do not travel far from the source. The sound levels produced by these sources are also higher in the low frequencies (Figure 4.5) and owl hearing ability declines dramatically in frequencies lower than 1.25 kHz (Appendix 4.2).

On average, 8.8% (SE = 0.19; 0 – 85.6%) and 3.2% (SE = 0.01; 0 – 26.7%) of the MCP and MD home-ranges respectively contained sound audible to Burrowing Owls in the 2.5 kHz one-third octave band. We found no significant relationship between owl MD and MCP home-range sizes and amount of artificial light or sound in the 2.5 kHz one-third octave band.

During both night-time and twilight, the MCP and MD footprint RSF models were better predictors of selection than the disturbance or baseline models (Figure 4.8). The footprint model was also better for all GLMM models (Table 4.1). Models containing sensory disturbance variables were the best models during the twilight hours for 33% and 39% of the owls in the MCP and MD analyses respectively (Figure 4.8).

The IVW mean and GLMM RSF coefficients indicate that owls were weakly attracted to areas with higher sound levels in the 2.5 kHz one-third octave band, in both the MD and MCP models, but only about half of the owls had a positive RSF coefficient (Figure 4.9 & Figure 4.10). Although there is only about a 15% difference between the number of owls avoiding sound during night versus twilight, more owls were avoiding higher audible sound during twilight hours for both the MD and MCP models (Figure 4.9 & Figure 4.10).

Significance between RSF coefficients in the IVW mean and GLMM models for light were very different from each other, but followed a similar trend where there were smaller values (increased avoidance) during twilight hours and larger values (increased selection) during night-time hours in both the MD and MCP models (Figure 4.9 & Figure 4.10).

There were less agreement between the IVW means and GLMM RSF coefficients for distance to nearest facility and oil well, although most owls are attracted to these features during both twilight and night-time, in both the MD and MCP models (Figure 4.11 & Figure 4.12). Also, a greater proportion of owl locations were within 100 m of oil wells than both MD and MCP random locations (Figure 4.13). Though not always significant, the IVW mean RSF coefficients for both MD and MCP available areas showed more attraction to these features during the night than during twilight hours (Figure 4.11 & Figure 4.12). All RSF coefficients in both scales of availability showed owls were significantly attracted to paved roads in both time periods, with the exception of the night period MCP RSF model. Only about half the owls were attracted to paved roads (Figure 4.11 & Figure 4.12).

4.4 Discussion

Owl night-time space-use was better predicted by distance to infrastructure on the landscape than by degree of sensory disturbance. The best model for the majority of owls, and mixed effect models, contained distance to nearest human structures, and not variables related to the sound and light that these human structures emit. This differed from our predictions that owl nocturnal space-use would be most influenced by anthropogenic sound and light levels. Owls rely on auditory and visual cues when hunting at night, but our analysis indicates their night-time owl movement patterns were better predicted by changes to the physical landscape than by sensory disturbances. The construction of buildings, roads, compressor stations, and oil wells on the landscape changes land-cover type, vegetation height and density, presence of perches, and amount of edge habitat. These alterations to the landscape could affect prey abundance, prey availability, predation risk, and perch availability. It is likely a combination of these landscape changes that is influencing owl nocturnal space-use.

We suggest that the greatest influence on owl nocturnal space-use from alterations to land-cover resulted from changes to prey habitats and populations. Small mammals depend on vegetation for cover and food, without which their populations cannot persist. Although artificial sound and light can influence prey abundance and availability (Francis et al. 2011, Gaston et al. 2013), changes to the vegetation from construction of human features on the landscape probably has a much larger impact on prey populations than noise or light (Andren 1994, Sauvajot et al.

1998, Mortelliti et al. 2009). Most roads in the Canadian grasslands follow the one-mile section lines originally laid out by the Dominion Land Survey of Canada. Agricultural and industrial access roads reach deep inside those square mile sections, leaving little of the landscape < 400 m from the nearest road and, therefore, almost all land is influenced by proximity to this human footprint. Construction of any road removes vegetation and typically changes adjacent vegetation type and height, resulting in widespread changes to grassland vegetation alongside roads and across the landscape (e.g. Wellicome et al. 2014b). Ditches are associated with many roads, and vegetation grows more tall and dense in ditches, because of greater local moisture levels, thus supporting greater small mammal populations (Poulin 2003). Direct removal and alteration of vegetation has a greater effect on small mammals, and thus space-use of the Burrowing Owl while hunting, than does indirect effects from sensory disturbance.

If Burrowing Owl nocturnal space-use was influenced by artificial sound, it would most likely be high frequency sounds, because they have the greatest potential to mask sounds made by prey (Miller 1978, Schomer and Beck 2010). Burrowing Owls do not show a pronounced avoidance of high frequency sounds because these sounds do not travel very far from the sources and therefore impact a very small area on the landscape. Sound in the 2.5 kHz one-third octave band could only be potentially detected by owls within 8.8% of the MCP home-range area, and sound in higher frequencies could be heard in smaller percentages of their home-range. During dawn and dusk, the majority (slightly more than half) of the owls avoided areas with greater sound levels in high frequencies, but selection coefficients indicated some individuals were attracted to these areas. Even if owls had showed strong avoidance of sounds in high frequencies, the impact to their foraging areas would have been negligible because the amount of area where owls can hear high frequency sounds was small.

Our results suggest owls are attracted to areas with greater sound levels, but it seems more likely that they are attracted to other characteristics of the developments that are producing these sounds. Owls spend more time within 100 m of oil wells, but sound in frequencies above 2.5 kHz cannot be detected by owls at that distance from oil wells. There are a number of features other than sound associated with these wells that are more likely to be attracting owls. Though the pump at an active well is moving and producing sound, there are typically other structures within this area (e.g. fences) that do not move or produce sound that could be used as perches, which are important features for Burrowing Owls (Sissons 2003, Scobie et al. 2014). In addition, gravel roads are constructed to access oil wells, many of which have ditches that likely have high abundances of small mammals (Adams and Geis 1983, Sabino-Marques and Mira 2011, Ruiz-Capillas et al. 2013).

Owl movement patterns and selection differ between twilight and night hours. Owls are actively hunting and bringing prey to the nest during twilight hours (Poulin and Todd 2006), but we are unsure what they are doing during the darkest part of the night. They are moving less, but are still remaining within approximately 0.5 km of the nest. They may be passively hunting from perches and that is why there is increased selection for roads (and the fence lines often associated with roads) and oil wells during this time.

Owl selection was similar regardless of which measure of availability we were using, indicating that sensory disturbances and landscape features are unlikely to be influencing the configuration of the foraging area around the nest. If owls were choosing to avoid or include specific features or sensory disturbances within their foraging area (100% MCP) then selection would have differed between the models that used different areas of availability. The lack of relationship between MD and MCP home-range size and amount of artificial light and sound supports the idea that owl nocturnal space-use is not influenced by these sensory disturbances.

Sound in the middle frequencies (1.25 kHz and 1.6 kHz) can be heard by Burrowing Owls furthest from the source, compared to either higher or lower frequencies. Anthropogenic sound in mid-to-low frequencies may not significantly affect the owl's ability to detect prey, but could affect their ability to attract a mate or effectively communicate warnings to mates or young. The primary song of the male Burrowing Owl that is used in pair formation and territory defense is comprised mostly of sound in low frequencies, ≤ 1.3 kHz (Martin 1973b). Warning calls given by adult Burrowing Owls also consist mostly of low frequency sounds, not exceeding 2.5 kHz except when the highest degree of threat is being communicated (Martin 1973b).

There are many challenges when trying to evaluate the influence of artificial sound on the movement patterns of a rare and endangered species such as the Burrowing Owl. Burrowing Owl nests in Canada occur at a very low density across their range, which makes them difficult to find, especially when there is a desire to find some nests with artificial sound sources nearby.

When nests are found near sound sources and the male owls are tracked, it can be difficult to detect a pattern of avoidance from the widespread pattern of locations from this generalist predator, which travels up to 6 km from its nest while foraging at night. Also, the owls cannot hunt in their entire home range over one night, so they need to be tracked over a long period of time to be able to determine if the observed pattern is due to their choice of where to hunt on the night tracked, or if they are influenced by features in their home range over a longer period of time. The technology has become available only recently to track such a small foraging raptor over a long period with high accuracy. A high level of accuracy is needed because avoidance of the small areas impacted by high frequency anthropogenic sound would not be possible with locations with high spatial error. This study was able to overcome these challenges and utilize this new technology to track owls nesting in a diversity of landscapes surrounded by varying degrees and combinations of artificial light and sound.

There is weak evidence that owls are influenced by artificial sound and light while foraging at night, but those effects are small when compared to the influence of physical changes to the landscape. Changes to prey abundance and/or availability and corresponding owl nocturnal space-use likely explain why owls were most influenced by landscape changes from human development rather than by the sensory disturbances associated with human developments. Although owl nocturnal space-use was least influenced by sensory disturbances, these effects should be considered, together with the effects from physical landscape changes, when determining effective habitat loss or degradation from development. While habitat loss is the greatest threat to terrestrial species (Wilcove et al. 1998, Sala et al. 2000), the extent to which ecosystems are impacted by artificial sound and light is becoming more clear (Francis and Barber 2013, Gaston et al. 2013) and needs to be considered when assessing the total effect of human development on species.

Table 4.1. Comparison of generalized linear mixed models (GLMM) using AIC.

Maximum Distance				**100% Minimum Convex Polygon**			
Model Description	***k***	**AIC**	**ΔAIC**	**Model Description**	***k***	**AIC**	**ΔAIC**
Twilight				**Twilight**			
Footprint	14	29386	0	Footprint	14	30916	0
Foot	12	29818	433	Foot	12	38014	7099
Baseline	9	30052	667	Baseline	9	38140	7224
Night				**Night**			
Footprint	14	27945	0	Footprint	14	31418	0
Foot	12	28964	1018	Foot	12	39417	7999
Baseline	9	29529	1584	Baseline	9	39567	8149

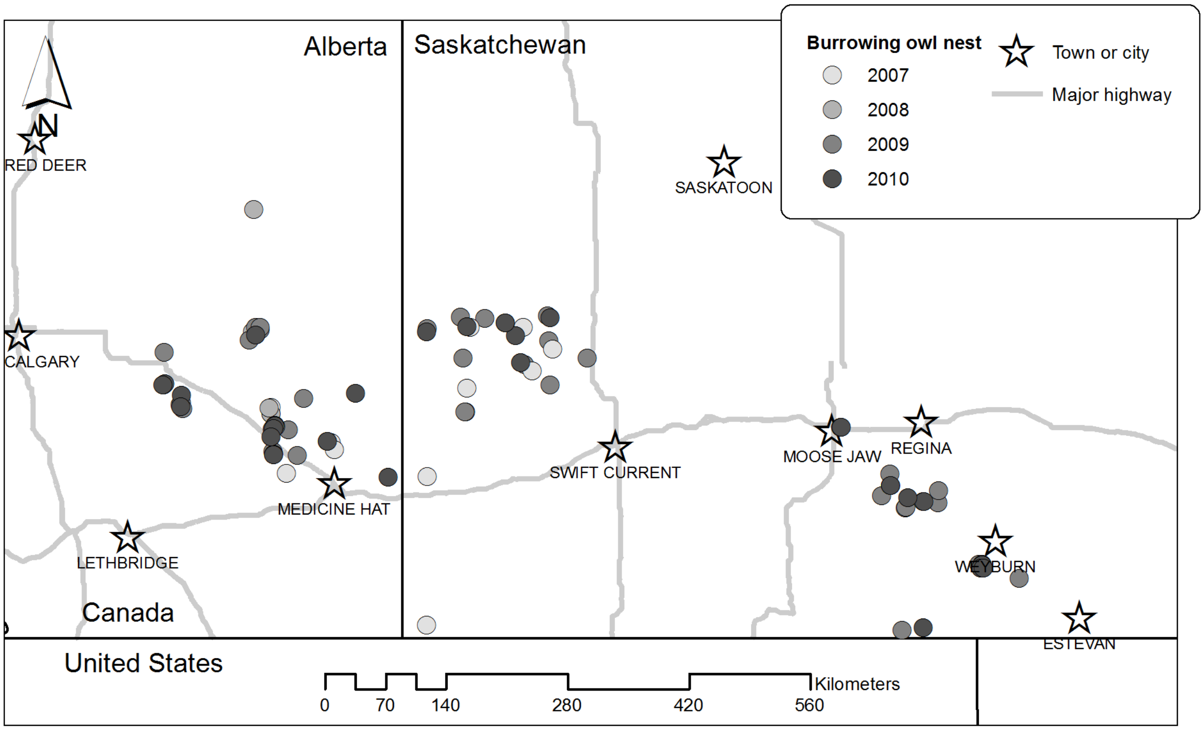

Figure 4.1. Locations of Burrowing Owl nests from which each adult male was tracked with a GPS datalogger.

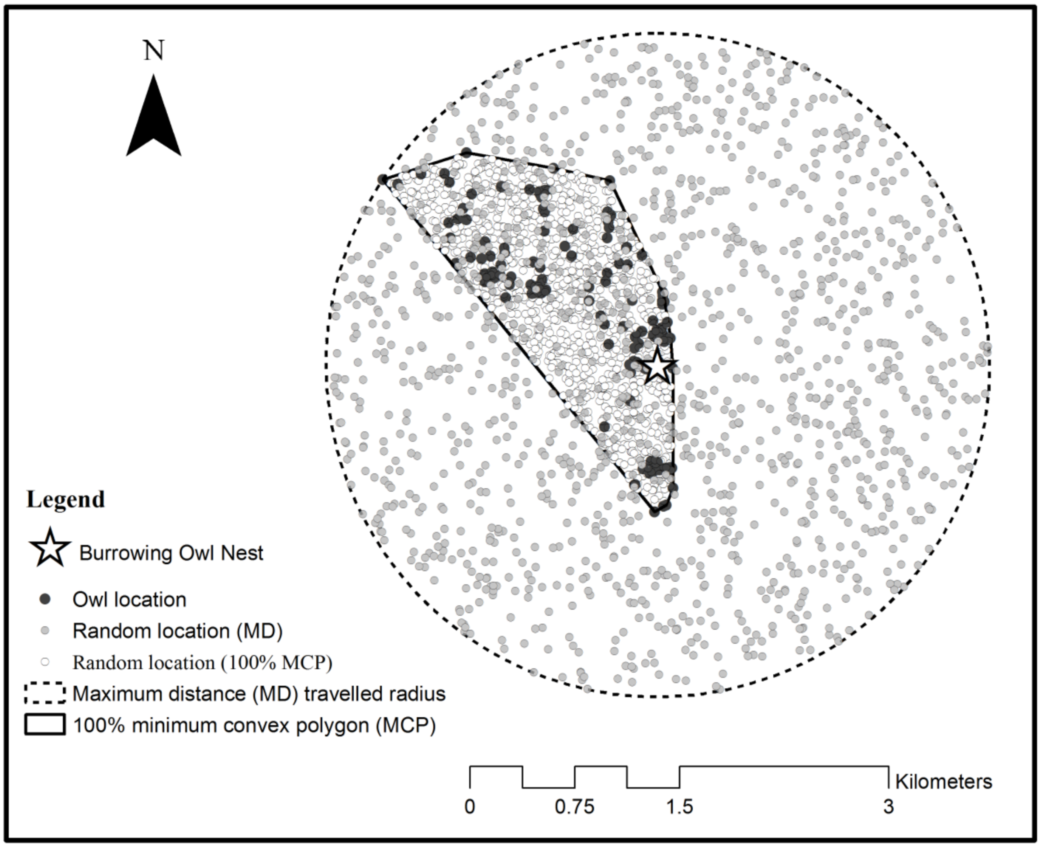

Figure 4.2. Examples of Burrowing Owl and random locations using maximum distance travelled from the nest as available and using 100% minimum convex polygon as available.

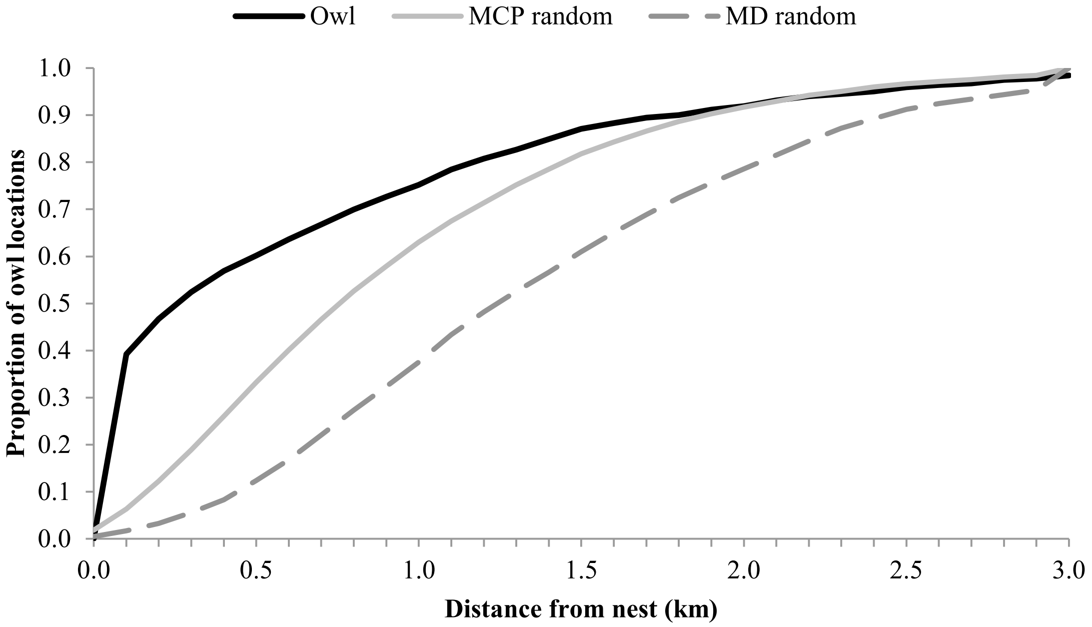

Figure 4.3. The average cumulative proportion of adult male Burrowing Owl locations, 100% minimum convex polygon (MCP) random locations, and maximum distance (MD) random locations with increasing distance from nest.

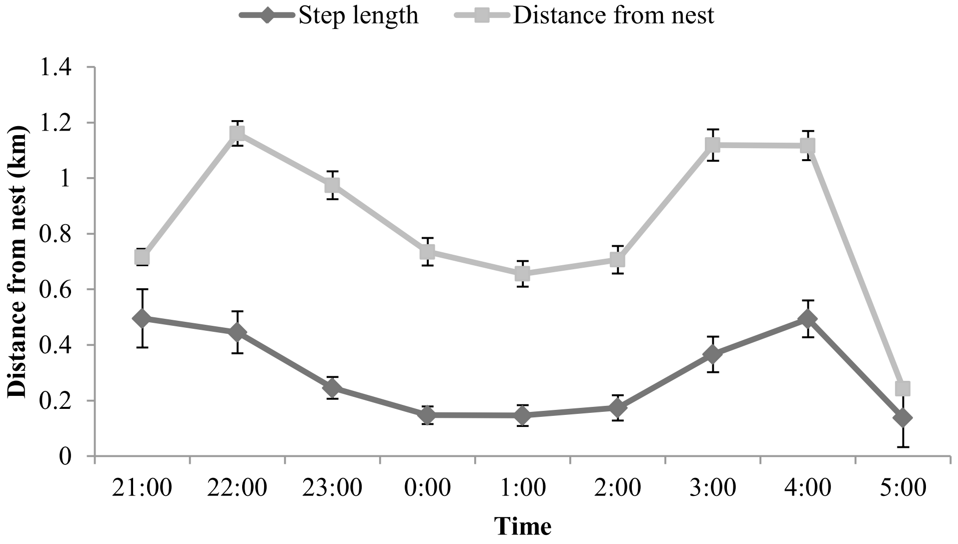

Figure 4.4. Average distance from nest and average step length (distance between consecutive owl locations) for each hour of the nocturnal period. Average was calculated for each individual, then averaged across all individuals. Error bars are 95% confidence intervals.

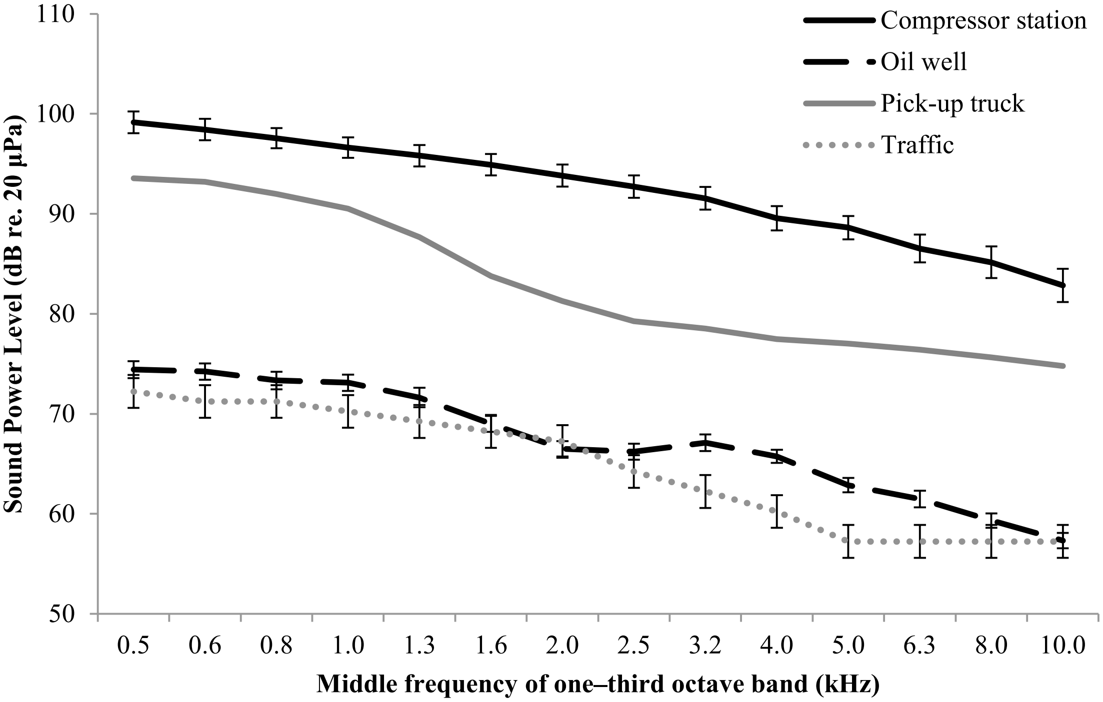

Figure 4.5. Average sound power level of 38 compressor stations , 44 oil wells (35 pump jacks and 9 screw pumps combined), and average hourly continuous energy equivalent sound power level of traffic (L_{eq} (1hr)) on 14 roads for each one-third octave band from 0.5 kHz to 10 kHz.

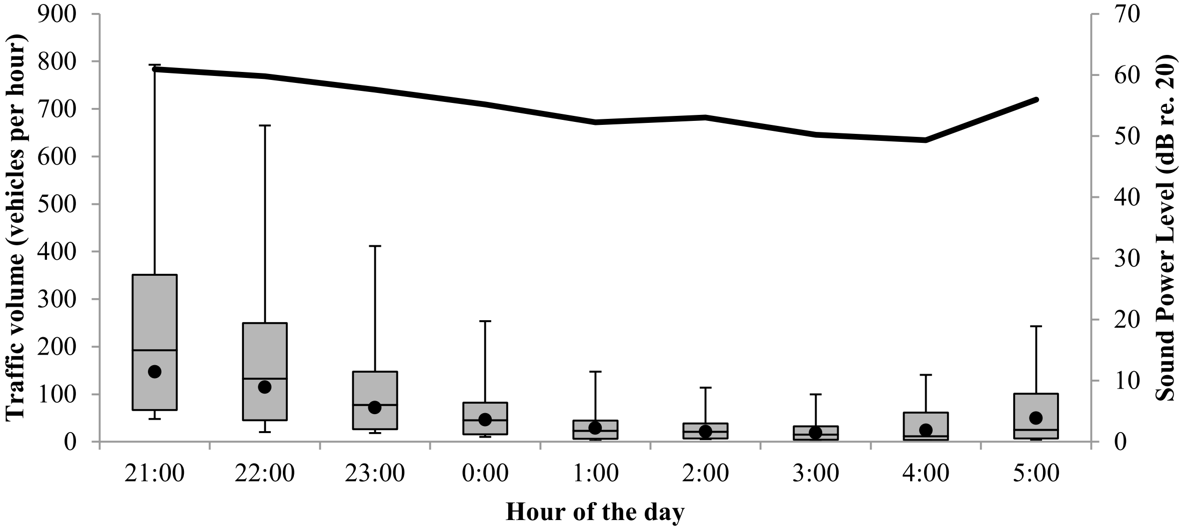

Figure 4.6. Hourly traffic volume (box plots) and average hourly continuous energy equivalent sound power level (solid line) of traffic (in 2.5 kHz one-third octave band) on 14 paved roads near Burrowing Owl nests where owls were tracked with GPS dataloggers. Upper limit of box is third quartile, middle line is median, lower limit of box is first quartile, whiskers represent minimum and maximum and black dot is average.

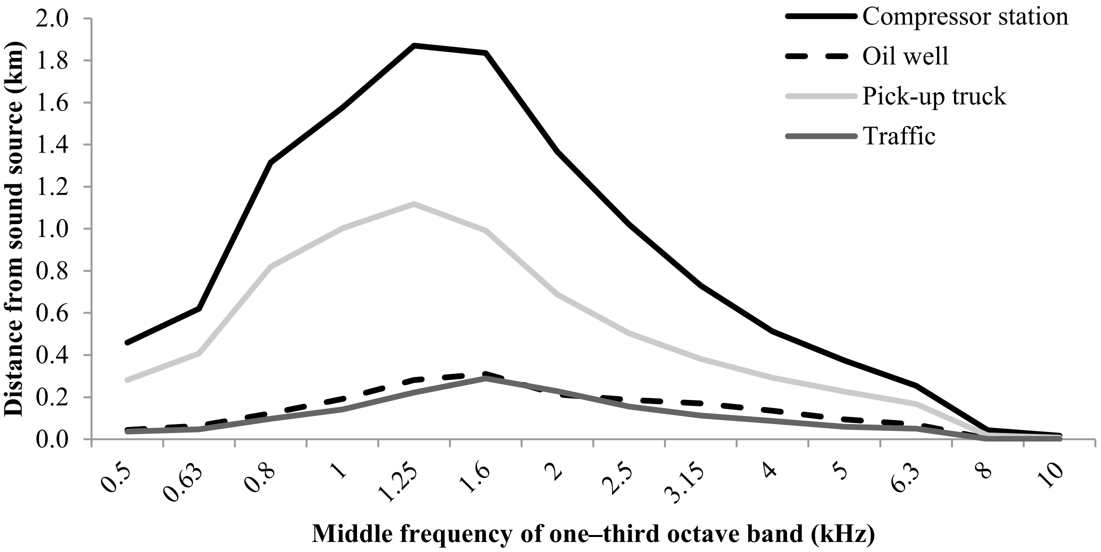

Figure 4.7. Distance at which a Burrowing Owl can detect each of four sound sources in the 2.5 kHz one-third octave bands. Sound levels used in the calculations were the average sound power levels of compressor stations and oil wells and the average continuous energy equivalent sound power level were calculated across all hours for traffic for each road, and then averaged for all roads. Calculations assume no barriers between source and receiver (owl) and wind to be negligible.

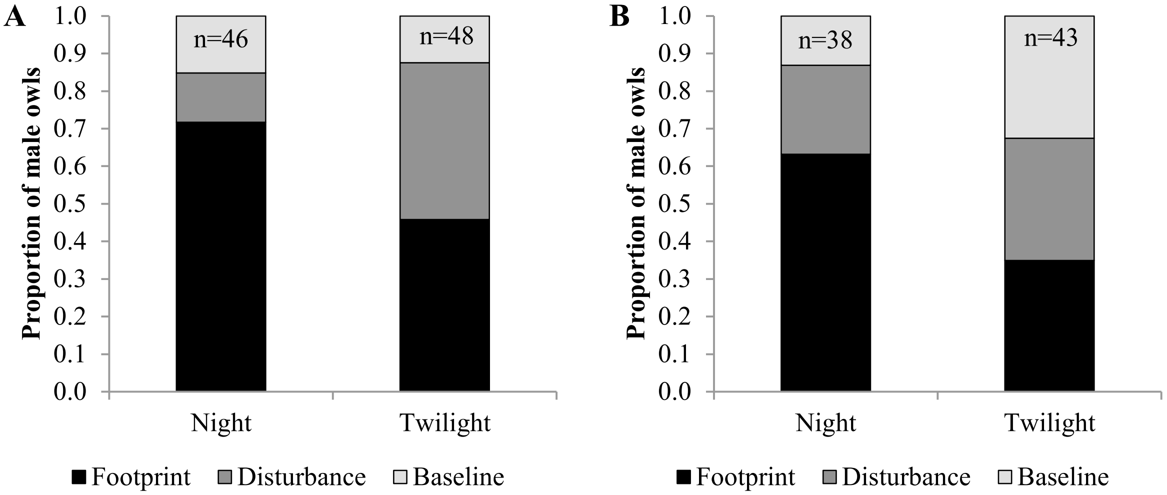

Figure 4.8. Proportion of owls with the baseline, disturbance, or footprint model as the best model, when defining available area as (A) maximum distance travelled from the nest or (B) the 100% minimum convex polygon.

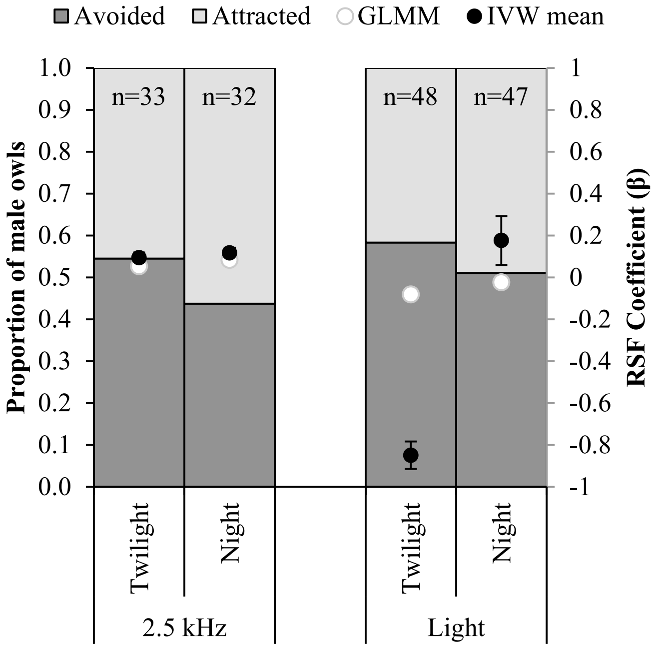

Figure 4.9. Using the maximum distance the owl travelled from the nest as the definition of available, the inverse variance weighted mean (IVW) and generalized linear mixed model (GLMM) RSF coefficients (β) and proportion of owls attracted to (β > 0) or avoiding (β < 0) sound (2.5 kHz) and light. Bars are related to left y-axis and circles and error bars are related to right y-axis. Error bars are 95% confidence intervals.

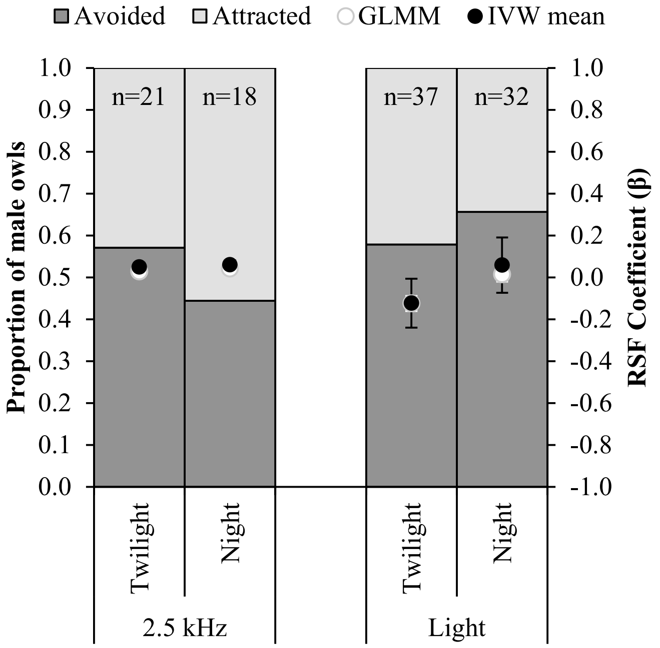

Figure 4.10. Using 100% minimum convex polygon (MCP) as the definition of what was available, the inverse variance weighted mean (IVW) and generalized linear mixed model (GLMM) RSF coefficients (β) and proportion of owls attracted to (β > 0) or avoiding (β < 0) sound (2.5 kHz) and light. Bars are related to left y-axis and circles and error bars are related to right y-axis. Error bars are 95% confidence intervals.

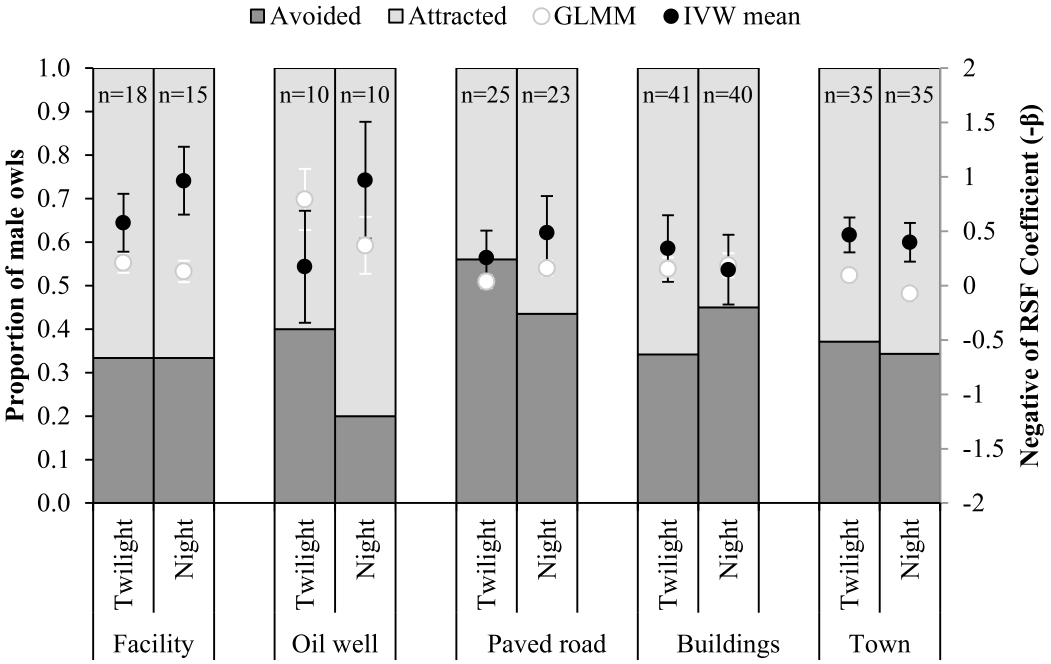

Figure 4.11. Using the maximum distance the owl travelled from the nest as the definition of available, the inverse variance weighted mean (IVW) and generalized linear mixed model (GLMM) RSF coefficients (-β) and proportion of owls attracted to (-β > 0) or avoiding (-β < 0) compressor stations, oil wells, paved roads, buildings, and towns. This figure shows variables that were the distance to the nearest feature, so the negative of the RSF coefficient is presented so the direction of the sign (positive vs. negative) corresponds to owl response to the feature (attracted vs. avoided). Bars are related to left y-axis and circles and error bars are related to right y-axis. Error bars are 95% confidence intervals.

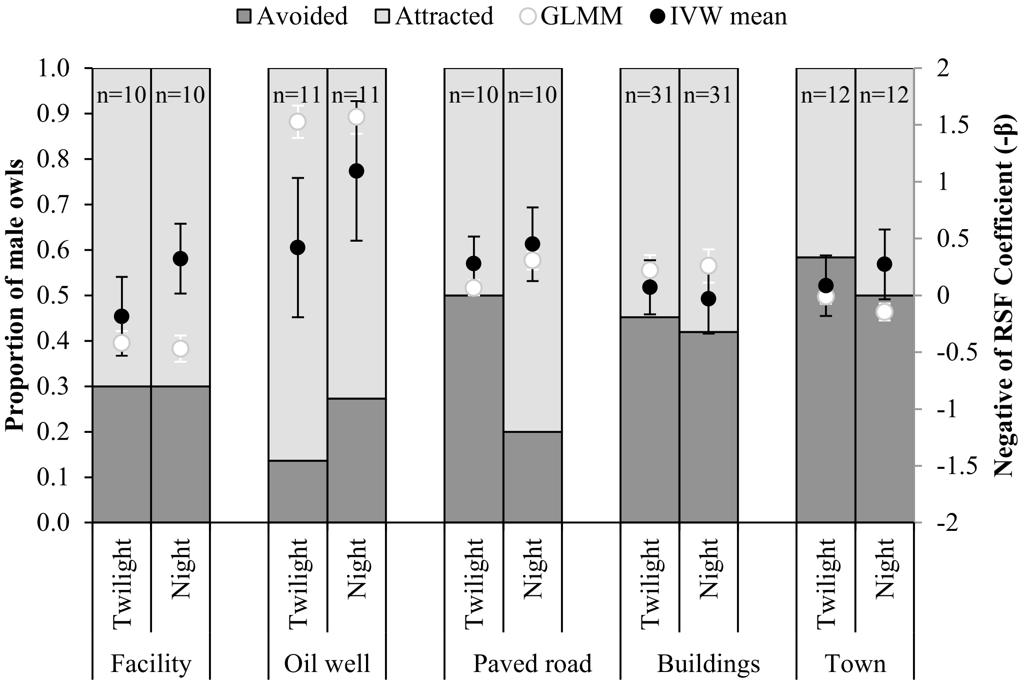

Figure 4.12. Using 100% minimum convex polygon (MCP) as the definition of what was available, the inverse variance weighted mean (IVW) and generalized linear mixed model (GLMM) RSF coefficients (-β) and proportion of owls attracted to (-β > 0) or avoiding (-β < 0) compressor stations, oil wells, paved roads, buildings, and towns. This figure shows variables that were the distance to the nearest feature, so the negative of the RSF coefficient is presented so the direction of the sign (positive vs. negative) corresponds to owl response to the feature (attracted vs. avoided). Bars are related to left y-axis and circles and error bars are related to right y-axis. Error bars are 95% confidence intervals.

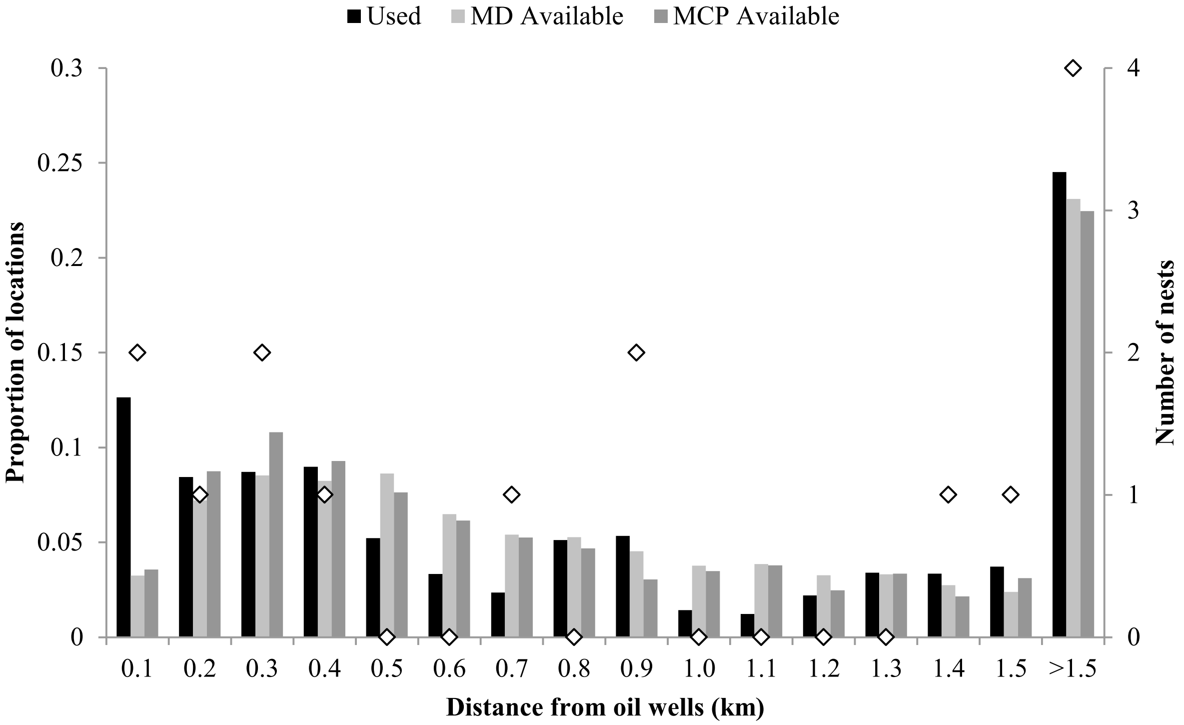

Figure 4.13. Proportion of owl locations (Used), random locations within the maximum distance travelled radius (MD Available) and random locations within the 100% MCP (MCP Available) within each 0.1-km distance bin of oil wells. Also, the number of owl nests with the nearest oil well within each 0.1-km distance bin (diamonds). Bars relate to left y-axis and diamonds relate to right y-axis.

4.5 References

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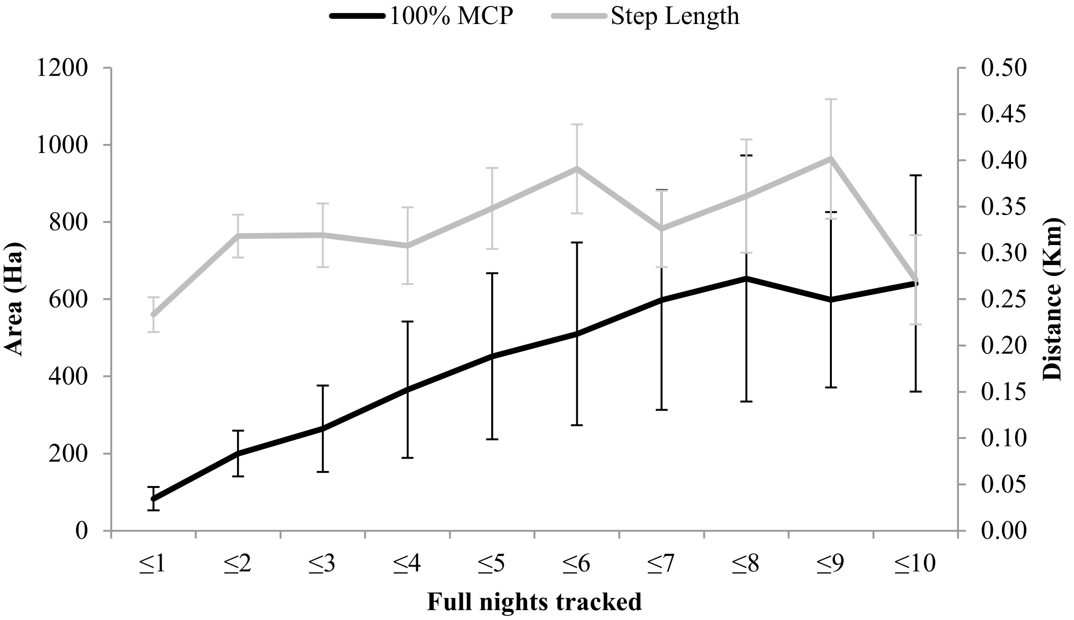
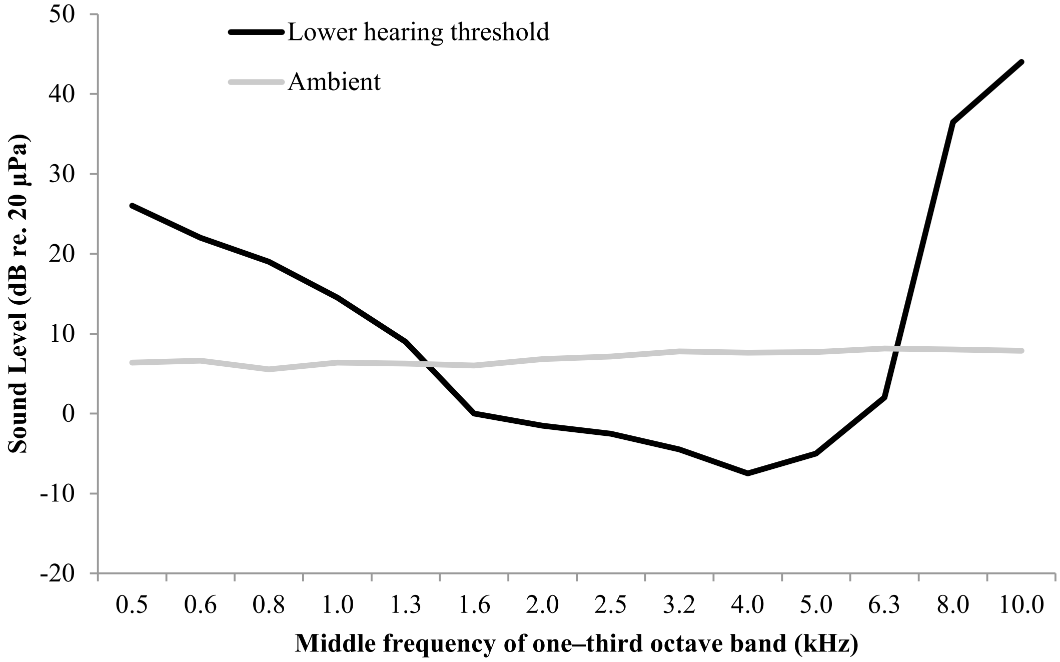
Appendix 4.1. Cumulative average adult male Burrowing Owl nocturnal foraging area measured with 100% minimum convex polygon (MCP) and average step length (distance between consecutive owl locations) by the number of nights tracked. Owls were tracked with GPS dataloggers while nesting in Alberta or Saskatchewan, Canada. Error bars are 95% confidence intervals.



Appendix 4.2. Lower hearing threshold of Eastern screech owl (adapted from Brittan-Powell et al. 2005) and ambient sound level for each one-third octave band from 0.5 kHz to 10 kHz. Owls can hear sounds that are louder than ambient sound or are above their lower hearing threshold.



CHAPTER 5. LINKING BURROWING OWL NOCTURNAL RESOURCE SELECTION TO REPRODUCTIVE SUCCESS

5.1 Introduction

Animals use resources depending on preference and availability. Availability is the accessibility of a resource to an animal (Johnson 1980). If a resource is equally available and used in equal quantities, there is no preference. Preference for different resources by different species is what enables species to occur sympatrically (Rosenzweig 1981). However, most resources are not equally available to organisms, so it is difficult to determine habitat preference. Instead, the use of resources is compared to availability in order to determine resource selection (Manly et al. 2002a). Resource selection is often used in ecology and conservation biology to identify important resources or habitat features for a species. This approach assumes animals select resources that best meet their needs and that habitat elements that are selected are of high quality and provide a benefit for fitness.

There are numerous challenges and potential sources of errors when examining resource selection by an animal. Selection can be confounded by the area defined as available (Beyer et al. 2010), number of random locations used (Baasch et al. 2010), sample of animals trapped and tracked (Carter et al. 2012), and mismatch between spatial (Boyce 2006, Chalfoun and Martin 2007) and temporal (Hebblewhite and Haydon 2010) scale of sampling and landscape features. These types of issues are common in ecology, and can result in incorrectly identifying landscape features as less important (if avoided) or more important (if attracted to) for a species, which may lead to erroneous or even harmful management actions. This could be quite damaging to a population, especially for threatened and endangered species.

While thousands of studies have identified landscapes features that species are attracted to and avoid, the underlying mechanisms causing selection and the consequences to fitness have rarely been evaluated (Slaght et al. 2013, Kniowski and Gehrt 2014). If the goal of management actions is to stop a population decline and eventually to recover that population, there needs to be a clear link between how attraction and avoidance of landscape features influences population processes. Demonstrating that individuals whose selection behaviour deviates from the population mean also have differential fitness is a common way of making the connection between selection behaviour and habitat quality (Aldridge and Boyce 2007, Bloom et al. 2013).

We tracked adult male Burrowing Owls (*Athene cunicularia*) while they foraged at night during the breeding season. We examined the relationship between their selection of landscape features (land-cover and anthropogenic infrastructure) and reproductive success (nest survival and fledging rate). We tracked the male because the male defends the nest burrow and does almost all of the hunting during most of the breeding season (Poulin and Todd 2006), so his pattern of resource selection has the greatest potential to influence the success of the nesting attempt. Most importantly, landscape features used by the male owl at night could influence the amount of prey captured and delivered to the nest, which could affect the number of juveniles that fledge (Wellicome et al. 2013).

Based on timing of arrival, we have demonstrated that Burrowing Owls preferred nest sites that were surrounded by high proportions of land-cover types that had large amounts of bare ground (annual crop fields and road surfaces) in the spring (Chapter 2). They also fledged more juveniles when they had more of these land-cover types around their nest (Chapter 2). The choices owls made at this scale (second-order) are important when considering resource selection (third-order) because availability becomes particularly restrictive when an animal is constrained to an area while breeding, such as a den or nest (Rosenberg and McKelvey 1999). Annual crop and road surfaces have lots of bare ground, which results in greater ability to capture prey (Marsh et al. 2014b). The relationship between lots of bare ground around the nest and increased fledging rate may therefore be linked to increased prey captures and deliveries to the nest, resulting in more juveniles fledging (Wellicome et al. 2013).

Owls capture more prey in areas with more bare ground and shorter, less-dense vegetation (Marsh et al. 2014b), likely because of higher availability of small mammals which make up 90% of the biomass they consume (Poulin 2003). This is interesting because highest small mammal abundance is in areas with tall, dense vegetation (Poulin 2003, Sissons 2003). Owls capture more deer mice (*Peromyscus maniculatus*) in landscapes dominated by annual crop fields and more meadow voles (*Microtus pennsylvanicus*) and sagebrush voles (*Lemmiscus curtatus*) where their nests are surrounded by a greater proportion of native grassland (Heisler et al. 2013). This variation in prey abundance and availability across the landscape results in opportunities for owls to select particular areas when they are hunting. Evidence suggests that owls are likely limited more by availability than abundance of prey (Marsh et al. 2014b), so owls that choose to hunt in areas with vegetative characteristics conducive to accessing prey should capture more prey. Choices owls make while hunting and the amount of prey brought back to nests affects fledging rates because almost all individual nestling mortality (i.e. partial brood loss) results from food shortage (Wellicome et al. 2013), so if the nesting attempt is successful, more owlets should fledge from nests with more prey. Thus, we predict owls will select land-cover types that have a lot of bare soil (annual crop and road surface) and will have greater nest survival and fledge more juveniles.

5.2 Methods

Using call play-back surveys in early May, we found 521 Burrowing Owl nests in the grasslands of Alberta and Saskatchewan, Canada from 2007 to 2010. Nests were visited once per week throughout the breeding season until the juveniles fledged (35 days after hatching). At a sample of these nest sites, 84 adult males were captured with either a one way walk in (Winchell 1999) or bow-net (Bloom 1987) trap and had a seven gram GPS datalogger (TechnoSmArt, Guidonia Montecelio, Italy) attached with Teflon ribbon in a backpack style configuration. Three lures (dead mouse, speaker playing a Burrowing Owl primary call, and Burrowing Owl decoy) were used in various combinations to capture each owl. Once the dataloggers were attached, the owls were released into their nest burrow. The dataloggers were upgraded by the manufacturer each year, resulting in differing options and program schedules over time (one location every two seconds [2009 and 2010], 15 minutes [2007, 2009, and 2010] and hour [2008]). The following data were stored on internal memory within the GPS datalogger: latitude, longitude, speed, altitude, dilution of precision, Greenwich Mean Time, and date. Owls were re-trapped after approximately twelve days to remove the datalogger and download the data. To ensure the highest quality data, only owl locations with a dilution of precision (≤ 1.5), speed (≤ 64 km/h), and altitude (> 20 m below and < 80 m above the elevation of the owl's nest) were used. One location every 15 minutes (2007, 2009, and 2010), or else one location every hour (2008), was selected for these analyses. A test of the accuracy of the datalogger showed that over 95% of the locations were within 4.2 m when tested in a fixed location for 24 hours (Dell'ariccia et al. 2010).

Each year, land-cover (permanent cover [native and tame grassland], annual crop, riparian area [sparse vegetation and seasonally dry], road, water bodies [standing water all year], buildings [residential and agricultural buildings], shrubs and trees) were recorded on aerial photographs. These aerial photographs were digitized in a GIS environment onto SPOT5 imagery (2006 coverage). All data were collected by trained field staff in possession of valid animal care approval, federal and provincial research permits and bird banding licenses (permit number 10796).

To ensure we used only locations from nocturnal foraging activities (Poulin and Todd 2006), only datalogger locations taken between nautical twilight start and end were included in our analyses. Owl activities vary considerably between the twilight and night period (Poulin and Todd 2006), so locations in these two periods were analysed separately. All locations between sunset and sunrise were categorized as night locations and all remaining locations that occurred between night and nautical twilight start and night and nautical twilight end were categorized as twilight locations. Sun position times were determined from the National Research Council of Canada website (http://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html). We excluded owl locations from the first night of tracking, because owls travelled shorter distances and had smaller home ranges during that night (Chapter 4).

5.2.1 Analysis

Prior to each analyses, data were evaluated for outliers, homogeneity, normality, collinearity among covariates, potential interactions, and independence of the response variable (Zuur et al. 2010). All models were validated by looking for influential observations, residual homogeneity, independence of covariates, normality of residuals, and spatial independence (Zuur et al. 2007). The relationships between residuals and covariates were examined for nonlinear responses and where appropriate (e.g. lay date in nest survival analysis), quadratic terms were tested. All variables were standardized prior to analysis.

5.2.2 Resource selection

We examined resource selection for each owl using the logistic discriminant function. We generated 5 random locations for every owl datalogger location within the one hundred percent minimum convex polygon (MCP). Land-cover and distance to nest burrow, nearest dirt road, gravel road and paved road were determined for each owl datalogger location and each random location. Distance to roads was limited to roads that were within five km of the outside edge of the 100% MCP. During the analysis, each random location was given one-fifth the weight of each datalogger location to adjust for the uneven ratio of datalogger to random locations (see Aldridge and Boyce 2007). Models contained distance to nest and land-cover with permanent land-cover being the reference category. The selection coefficients and variances for distance to nest and each land-cover type were estimated for each owl. Three more models were run for each owl which contained distance to nest, land-cover, and then one of: distance to dirt, gravel or paved roads. Distance to dirt road, gravel road and paved road were not combined into a single model because they were correlated ($r > 0.6$). Selection coefficients and variances were extracted from the distance to each road type for each owl from these models. These models were run for twilight locations and night locations, resulting in two sets of selection coefficients and variances reflecting owl selection of each land-cover type, nest burrow and each road type for each owl. Selection coefficients for distance variables (nest, dirt road, gravel road, paved road) were multiplied by -1 so that the response of the owl (selected versus avoided) matched the signs (positive versus negative) of the coefficients for land-cover variables.

5.2.3 Reproductive success

Selection coefficients were then used as variables in the nest survival and fledging rate analyses. The inverse of the variance of these selection coefficients were used as a weighting for these models. We also used these selection coefficients and variance to calculate the inverse variance weighted mean resource selection for each land-cover type and distance to nest and dirt, gravel and paved roads (Nielsen et al. 2009).

In a GIS (ESRI 2012), the area of the 100% MCP for each owl for each night as calculated. The area (ha) of the average nightly 100% MCP was then calculated for each owl, excluding the area of the first night the owl was tracked. The log of the area of the average nightly 100% MCP was used in all models because there were several owls that had very large nightly home ranges (outliers).

Burrowing Owl daily nest survival and fledging rate was examined in relation to owl selection of the nest burrow, land-cover types and roads. Daily nest survival was modelled using a weighted logistic exposure model (Shaffer 2004) in Program R (R Core Team 2014) with a generalized linear model and a custom logistic exposure link function (Herzog 2013, Bolker 2014). Each model contained the selection coefficient for one variable (land-cover type or distance to nest, dirt road, gravel road or paved road), year as a categorical variable, log of the area of the average nightly 100% MCP, and the date (Ordinal) the first egg was laid (clutch initiation date). The inverse of the variance of the selection coefficient was used as the weighting for each model. This weighting was used to account for the differing availability of the landscape features to each owl. The inclusion of clutch initiation date helps control for greater nest survival and number of juveniles that fledge from nests that began earlier in the season.

The number of owlets that fledged from successful nests was analysed using weighted zero-truncated Poisson regression. Nests were categorized as successful if at least one owlet fledged (reached 35 days of age). The number of offspring at that reached 35 days of age post-hatch was determined for each nesting attempt by recording the fledglings at the nest burrow for 18–24 hours when they were between 30 and 35 days of age. These videos were transcribed and the total number of owlets observed above ground at any one time was counted. Each model contained the selection coefficient for one variable (nest, land-cover type or road type), year as a categorical variable, log of the area of the average nightly 100% MCP, and clutch initiation date.

5.3 Results

We used data from 63 male owls that were tracked over an average of 4.7 nights (SD = 3.02, range = 2 – 10). The average nightly distance from the nest during twilight hours was 0.77 km (SD = 0.49) and 0.70 km (SD = 0.67) for night hours. All RSF models for owls converged when using the twilight locations, but the models using the night locations failed to converge for three owls. The majority of individual owls were attracted to all road types during night and twilight, except to paved roads during twilight hours (Figure 5.1). The inverse variance weighted (IVW) mean showed the same pattern as the proportion of owls attracted to roads (Figure 5.1). Owls were also attracted to road surfaces as a land-cover type (Figure 5.2). More than two thirds of owls avoided annual crop and the IVW mean showed significant avoidance of annual crop during twilight hours (Figure 5.2).

Fifty-five out of the sixty-three (87.3%) nesting attempts succeeded. Of the eight nests that failed, four had unknown causes of failure, three were depredated by American Badgers (*Taxidea taxus*), and one nest was flooded. An average of 4.5 owlets (SD = 2.17) fledged from successful nests and an average of 4.0 owlets (SD = 2.53) fledged from all nesting attempts combined.

There were no significant relationships between selection of landscape features or land-cover and fledging rate or nest survival (Appendix 5.1 & Appendix 5.2). Burrowing Owls had greater nest survival and fledged more juveniles when the males spent more time near the nest burrow, during both the night and twilight hours (Figure 5.3 & Figure 5.4).

5.4 Discussion

Burrowing Owl nest survival and fledging rates were each unrelated to selection of landscape features or land-cover. Our prediction that owls that selected landscape features with high prey availability would fledge more juveniles was not supported. Instead, we found that owls that were spending more time closer to the nest had greater nest survival and fledging rates and also had smaller home ranges. Admittedly, statistical power for nest survival analyses was low because of the limited number of nest failures.

Burrowing Owls deliver the highest amounts of prey during twilight hours (Poulin and Todd 2006, Marsh et al. 2014a). The amount of prey brought back to the nest, especially between hatching and fledging, greatly influences the number of juveniles that fledge (Wellicome 2000). One explanation for why selection for the nest was positively associated with reproductive success is that owls may be capturing more prey closer to the nest; however, a companion study found that few prey are captured close to the nest (Marsh et al. 2014a). An alternative explanation is that owls that spend more time close to the nest are more efficient at capturing prey. The most efficient hunters may be returning to the nest more often to deliver more prey in a shorter period of time resulting in more locations closer to the nest.

The relationship between selection of the nest burrow and nest survival and fledging rate was strongest during the hours in the middle of the night, but few prey deliveries are made in the middle of the night (Poulin and Todd 2006). Distance from the nest during night hours was more variable, meaning where individual owls chose to be in relation to the nest burrow varied more during the darkest time of the night when they were not actively hunting. Some owls were choosing to be closer to the nest and some were choosing to be further during this time. If owls were not delivering prey to the nest in the middle of the night, variation in the distance individual owls chose to be from the nest and their resulting reproductive success were likely related to their ability to detect and react to predators approaching the nest.

Greater nest survival where the adult male owls are selecting strongly for the burrow may be explained by the increased success of predator detection and deterrence that results from the adult male's proximity to the nest. Reproductive success can be greatly influenced by the ability of a parent to efficiently detect and react to threats (Gotmark et al. 1995, Magana et al. 2010). Recipients of warning calls often have greater survival (Griesser 2013). Male owls would not be able to actively defend their nest or vocally warn the female or young of approaching predators if they are away from the nest. This is especially true during the middle of the night because Burrowing Owls have poor night vision (Dice 1945) and, therefore, would need to be close to the nest to visually or aurally detect an approaching predator. Though cavity nesting birds have greater nest concealment, the incubating mate relies on the other sex to act as a lookout and signal when predators are present (Johnson and Kermott 1991). A nest predator can be detected earlier when the male is close to the nest and there is a greater opportunity to use defensive behaviour to repel threats (De Kiriline Lawrence 1967). American Badgers are nocturnal predators that regularly predate Burrowing Owl nests (Wellicome et al. 1997) and were responsible for the failure of at least three nesting attempts in our study. Burrowing Owls that spend more time during twilight and night hours closer to the nest may be able to effectively harass badgers and other nest predators and drive them away, a behaviour that was caught on film for at least one nest. Later in the season, it is also possible that the male owls can warn the female and owlets of an approaching ground predator so they can move to another burrow and escape being trapped in the burrow and predated.

Nests fledge more young when potential predators are actively repelled (Wiklund 1990). Male owls that are close to the nest could also detect and warn the owlets of approaching diurnal raptors (Swainson's Hawk (*Buteo swainsoni*), Northern Harrier (*Circus cyaneus*), etc.) during twilight hours and nocturnal raptors (Great-horned Owl (*Bubo virginianus*)) during the middle of the night. Adult Burrowing Owl predation by a raptor is responsible for less than 5% of nest failures (Fisher et al. 2015), but raptor predation of hatch year owlets is common (Wellicome 2000, Todd 2001). Predation risk may, therefore, be why male owls that select for the nest burrow during night and twilight hours fledge more young. Proximity to the nest would increase the male owl's ability to detect a predator and communicate the risk to the owlets quickly. Owlets that have more time to react to a predator would have a greater probability of surviving to fledge (Griesser 2013), resulting in greater fledging rates.

Even though owls had greater fledging rates when the landscape around their nest had greater quantities of land-cover with lots of bare ground (Chapter 2), selection of these land-cover types while foraging at night did not affect fledging rate for the sample of owls we tracked. This may be testament to the ability of this species to use a wide array of prey species. On a smaller scale (second-order of selection) than our study, Burrowing Owls do better when there is more land-cover with bare ground, likely due to greater overall prey availability (Chapter 2). On a larger scale (fourth-order of selection), a companion study found owls were able to capture prey in areas with high prey availability (short vegetation, bare soil) (Marsh et al. 2014b) within all land-cover types (Marsh et al. 2014a). In that study, adult male Burrowing Owls were tracked (1 fix every 2 seconds) as they hunted at night, while their prey deliveries were simultaneously recorded at their nests with a video camera (Marsh et al. 2014a, Marsh et al. 2014b). Marsh et al. (2014a, 2014b) were able to identify locations where prey were captured and compare land-cover type and vegetation characteristics at those locations to locations where they hunted but did not capture prey. Owls prefer nest sites surrounded by land-cover with greater average prey availability (Chapter 2), but land-cover type in the vicinity of their nests does not influence their reproductive success because they can capture prey within each land-cover type where there is high prey availability (Marsh et al. 2014b).

Selection is often used to identify those landscape features that are important for an organism. Our resource selection models showed considerable selection for roads of all types, yet selection of these features did not result in greater reproductive success. In fact, roads with high-speed traffic disrupted Burrowing Owls during the day (Scobie et al. 2014). We also found owls were avoiding annual crop fields while travelling at night, but more of this land-cover around the nest was correlated with more owlets fledging (Chapter 2). When prey capture sites were compared to other locations along a flight path, Marsh et al. (2014a) found high use of annual crop fields and a high ratio of energy used versus gained from prey captured. Management recommendations that were informed by the results of the conventional resource selection analyses alone may have resulted in actions that were harmful to Burrowing Owls. There is a clear need to link selection and fitness, especially for endangered species during the breeding season, before conclusions can be drawn about a selected landscape feature and habitat quality.

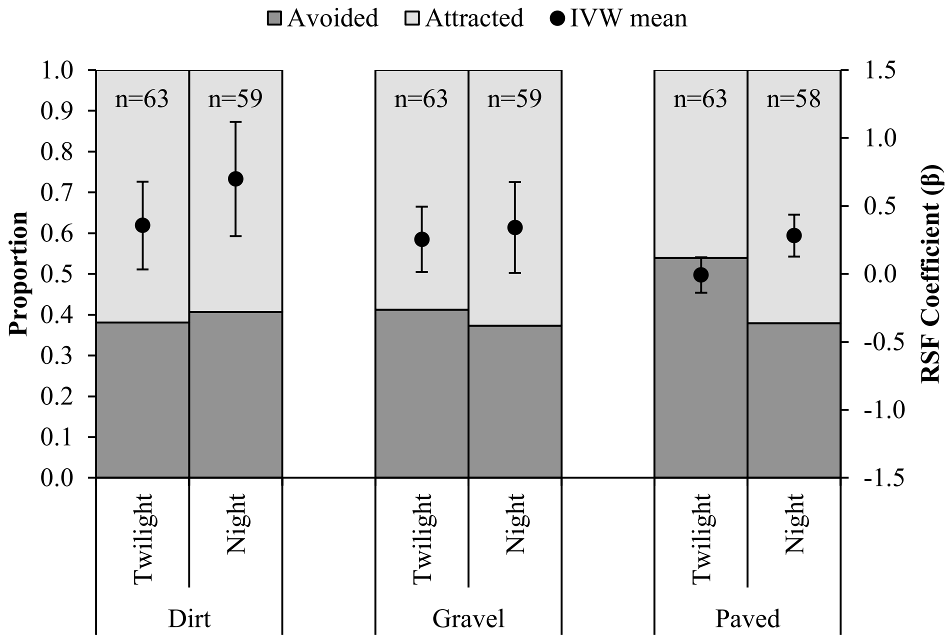


Figure 5.1. The inverse variance weighted mean (IVW) RSF coefficient (β) and proportion of adult male Burrowing Owls attracted to (negative RSF coefficient (β)) or avoiding (positive RSF coefficient (β)) dirt road, gravel roads and paved roads. Bars are related to left y-axis and circles and error bars are related to right y-axis. Error bars are 95% confidence intervals.

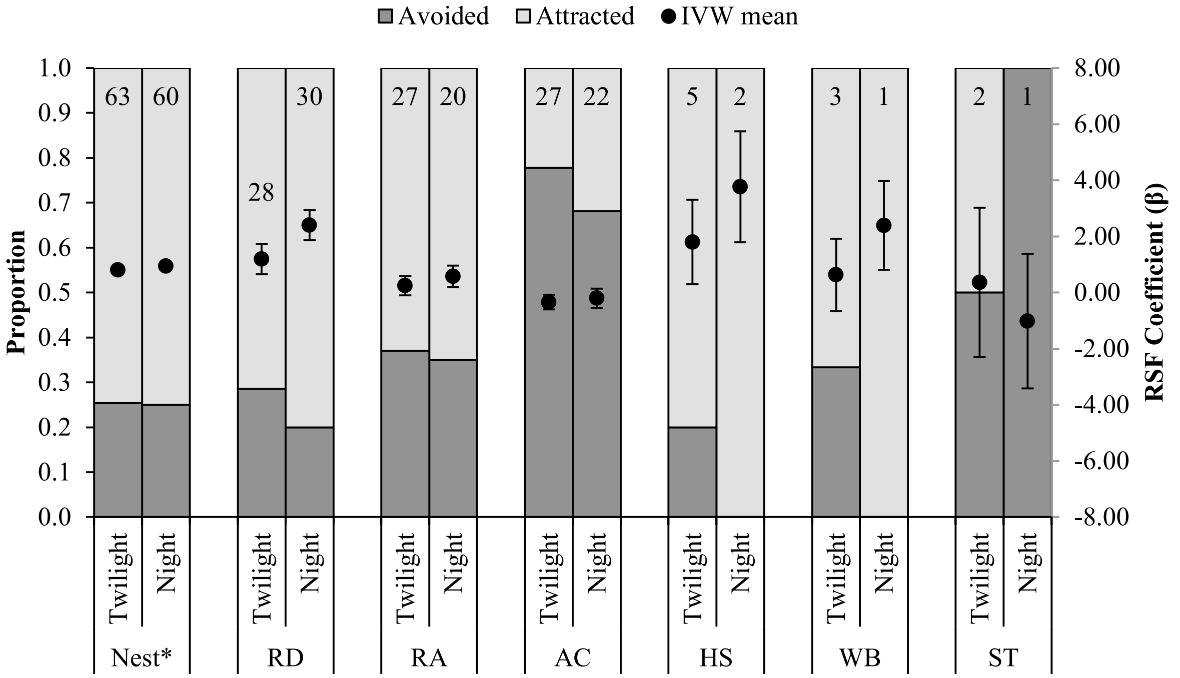


Figure 5.2. Adult male Burrowing Owl selection of the nest burrow and of each land-cover type, illustrated with both the inverse variance weighted mean (IVW) RSF coefficient (β) and the proportion of owls attracted to (positive RSF coefficient (β)) or avoiding (negative RSF coefficient (β)) each feature. Reference category is permanent cover (native and tame grassland). (RD= road, RA= riparian area, AC= annual crop, HS= human structures (buildings), WB= water body, ST= shrubs or trees). Bars are related to left y-axis and circles and error bars are related to right y-axis. Error bars are 95% confidence intervals. * negative RSF coefficient.

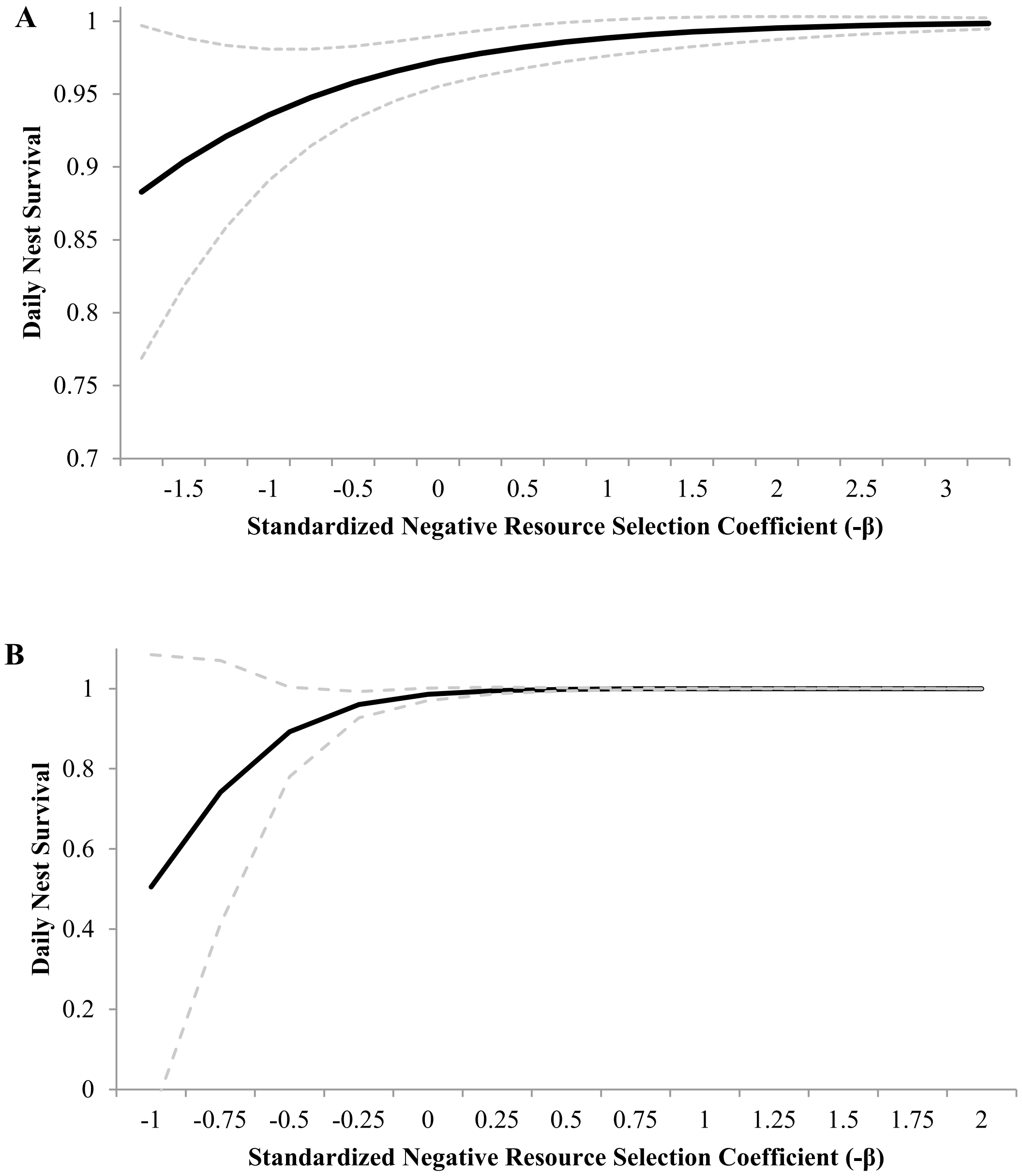


Figure 5.3. Male Burrowing Owl selection of the nest burrow during twilight (A) and night (B) hours, in relation to daily nest survival. Attraction to the nest increases as the negative resources selection coefficient increases. Grey dashed lines are 95% confidence intervals.

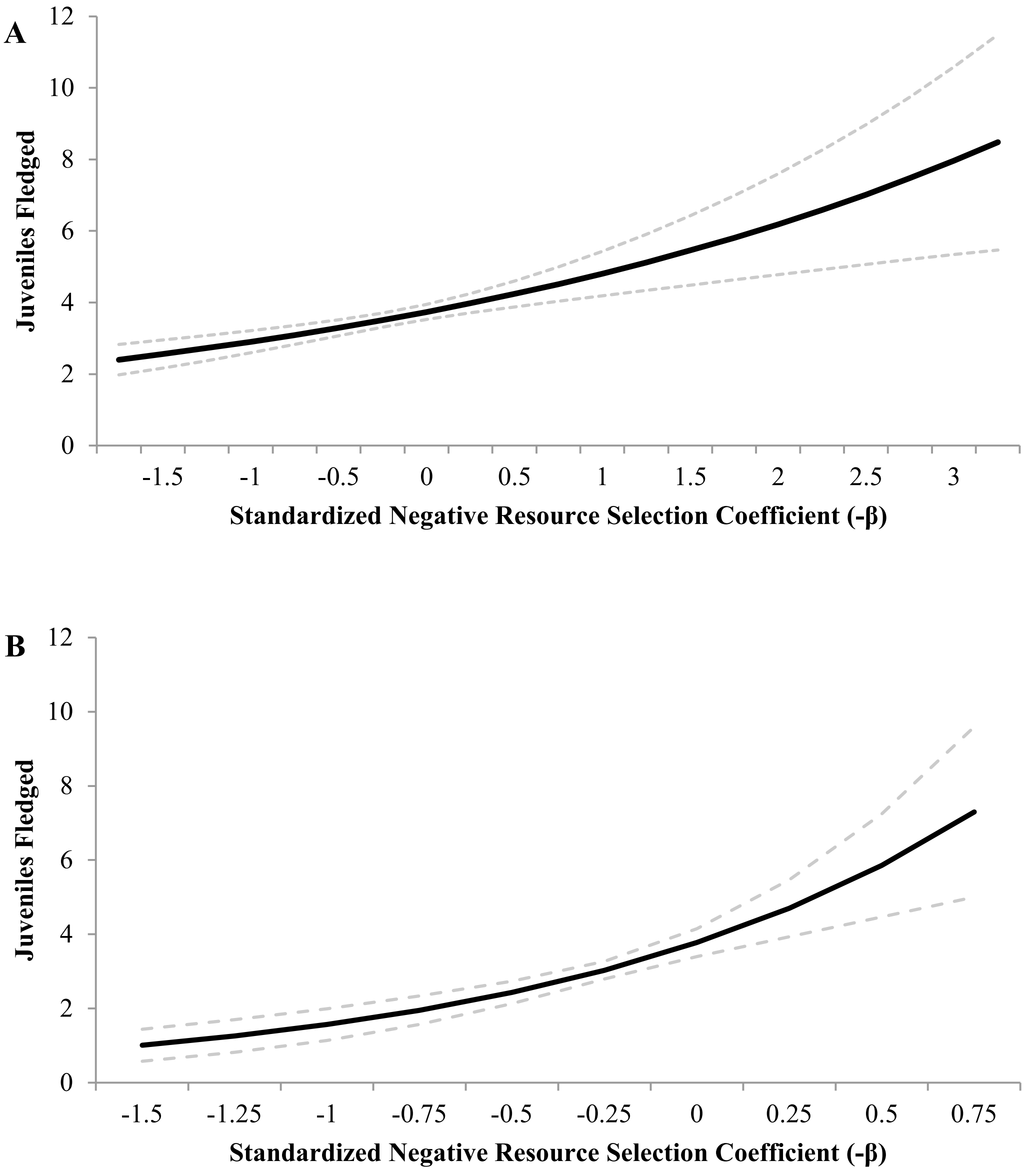


Figure 5.4. Male Burrowing Owl selection of the nest burrow, during twilight (A) and night (B) hours, in relation to the number of juveniles fledged. Attraction to the nest increases as the negative resources selection coefficient increases. Grey dashed lines are 95% confidence intervals.

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Appendix 5.1. Results of weighted general linear model with logistic exposure link examining relationship between nest survival and owl resource selection during night and twilight hours. All variables standardized.

				Lay Date		100% MCP Area		Nest Age		Intercept		
	Variable	**β**	**SE**	**β**	**SE**	**β**	**SE**	**β**	**SE**	**β**	**SE**	***n***
Night	Nest	2.62	1.04	0.12	0.24	1.17	0.21	-0.57	0.24	6.58	0.33	712
	Dirt road	1.2	2.38	0.29	0.67	1.73	0.98	-0.61	0.77	6.09	0.79	700
	Gravel road	-1.78	2.12	-0.11	0.59	1.11	0.80	-0.51	0.69	6.33	0.74	700
	Paved road	-2.42	2.31	-0.29	0.52	1.31	0.66	-0.78	0.67	7.55	0.75	692
	Annual crop	0.25	1.13	0.37	0.35	1.68	1.02	-0.51	0.50	5.66	0.80	308
	Road surface	0.77	1.30	-0.27	0.97	0.62	0.98	0.10	0.95	6.72	1.34	352
Twilight	Nest	0.71	0.30	-0.39	0.28	0.93	0.16	-1.09	0.29	6.81	0.27	744
	Dirt road	0.05	1.09	0.02	0.55	1.30	0.62	-1.49	0.79	6.38	0.77	744
	Gravel road	-0.22	1.85	-0.45	0.51	0.83	0.68	-0.77	0.66	6.92	0.77	744
	Paved road	-1.16	3.58	-0.46	0.37	1.26	0.58	-0.64	0.46	7.08	0.49	744
	Annual crop	-1.08	0.76	-0.14	0.47	0.84	0.54	-0.62	0.50	7.13	0.81	379
	Road surface	-1.72	3.71	-1.05	3.53	1.96	3.32	0.48	1.43	10.27	8.20	361

Appendix 5.2. Results of weighted linear zero truncated Poisson regression examining the relationship between the number of juveniles that fledged from successful nests and resource selection during night and twilight hours. All variables standardized.

				Lay Date		100% MCP Area		Intercept		
	Variable	**β**	**SE**	**β**	**SE**	**β**	**SE**	**β**	**SE**	***n***
Night	Nest	0.88	0.16	-0.15	0.04	-0.23	0.04	1.62	0.05	53
	Dirt road	0.12	0.61	-0.10	0.11	-0.34	0.18	1.62	0.16	52
	Gravel road	-0.41	0.52	-0.17	0.09	-0.22	0.11	1.55	0.15	52
	Paved road	-0.36	0.36	-0.29	0.06	-0.41	0.06	1.66	0.07	51
	Annual crop	0.08	0.29	-0.11	0.07	-0.46	0.17	1.68	0.20	19
	Road surface	-0.19	0.19	-0.17	0.15	-0.19	0.13	1.42	0.18	25
Twilight	Nest	0.25	0.05	-0.27	0.03	-0.22	0.03	1.55	0.03	55
	Dirt road	0.20	0.26	-0.16	0.10	-0.27	0.13	1.71	0.11	55
	Gravel road	-0.02	0.26	-0.14	0.06	-0.19	0.07	1.68	0.08	55
	Paved road	-0.85	0.47	-0.23	0.04	-0.36	0.05	1.61	0.06	55
	Annual crop	0.16	0.11	-0.07	0.06	-0.17	0.08	1.50	0.08	24
	Road surface	-0.11	0.15	-0.22	0.16	-0.11	0.15	1.53	0.15	26

CHAPTER 6. DISCUSSION

In this dissertation, I examined the relationship between Burrowing Owls and the developed grassland landscape in which it lives in Alberta and Saskatchewan, Canada. The Burrowing Owl population continues to decline with no concrete answer as to the cause (Environment Canada 2012). One possible explanation for their continued decline was they may be stuck in an ecological trap caused by a preference to nest in lower quality habitat that results in lower fitness. In contrast, the landscape features that Burrowing Owls preferred during breeding (annual crop and road surfaces) were associated with the fledging of more juveniles (Chapter 2) - a result that is inconsistent with the ecological trap hypothesis. During the day, Burrowing Owls avoided roads with high traffic speeds, likely due to higher sound levels (Chapter 3), but during the night, their space-use patterns were influenced more by human infrastructure and resulting changes to the landscape than by the sensory disturbances (sound and light) produced by that infrastructure (Chapter 4). Also, Burrowing Owl resource selection of various landscape features at night did not predict their reproductive success (Chapter 5). Overall, I found no strong evidence that anthropogenic development on the grasslands is associated with maladaptive habitat preferences or has any negative effects on the current population's reproductive success. This dissertation adds to a body of evidence showing that Burrowing Owls are able to adjust to many different environmental situations at various temporal and spatial scales.

There is evidence that owls are still able to make a living on extensively modified landscapes at the fourth-order of selection. Burrowing Owls are able to capture prey almost equally in all land-cover types (Marsh et al. 2014a) as long as there are some areas with high prey availability (bare ground and/or short vegetation; Marsh et al. 2014b). Though Marsh et al. (2014a) did not make a link between fourth-order selection and reproductive success, it has been established that more prey delivered to the nest results in more juveniles fledging (Harrison et al. 2010, Wellicome et al. 2013).

Third-order selection typically involves tracking individual animals and examining the landscape features and land-cover types that they use in relation to what was not used or was available (Johnson 1980, Manly et al. 2002a). Several studies have tracked Burrowing Owls at night during the breeding season (Haug and Oliphant 1990, Sissons et al. 2001, Sissons 2003), but none have linked choices owls made at this scale with measures of fitness. I not only examined Burrowing Owl night-time space-use in relation to detailed landscape and sensory disturbance data with a resolution and accuracy never done before (Chapter 4), but I also looked for patterns in selection that explained nest survival and fledging rates (Chapter 5). Owls managed to make good choices, as measured by breeding season survival and reproduction, regardless of the extensively developed landscape on which they nest and the variety of choices available to them (Chapter 4 & Chapter 5). This adaptability is a sign that the Burrowing Owl is quite flexible in its habitat requirements and can make a living almost anywhere within their range.

Where an animal chooses to place their home range within the species' geographical range is second-order selection (Johnson 1980), and has been well studied for Burrowing Owls outside of Canada (Ortho and Kennedy 2001, Ronan 2002, Lantz et al. 2007, Crowe and Longshore 2013, Thiele et al. 2013), but less so for owls nesting inside of Canada (Stevens et al. 2011). Burrowing Owls in Canada are somewhat unique because they rely almost exclusively on American Badgers (*Taxidea taxus*) or Richardson's Ground Squirrels (*Urocitellus richardsonii*) for nest burrows. Stevens (2008) studied Burrowing Owl nests in Canada that were in abandoned American Badger or Richardson's Ground Squirrel burrows, but did not link habitat selection by individuals with their reproductive success. Instead, she looked for correlations between habitat selection indices and nest survival and fledging rate, with no correlations detected (Stevens 2008). We examined the preferred landscapes around Burrowing Owl nest sites surrounded by a broad spectrum of human development (Chapter 2). Changes to the landscape from human development have resulted in different predator and prey populations and potentially different environmental cues Burrowing Owls use to indicate high-quality habitat when choosing a place to nest. Despite extensive changes to the grasslands of Alberta and Saskatchewan, we found that the choices owls made at this scale resulted in greater reproductive success (Chapter 2).

The first-order of selection for Burrowing Owls determines their geographical range, which encompasses the Great Plains and extends south into Central America and west to the Pacific coast. Burrowing Owls are living in a diversity of grassland, steppe, desert, and savanna habitats within that area, but all rely on mostly small mammals for prey and burrows in which to nest. It seems that the primary habitat requirement needed by this this species is simply a grassland structure, access to prey and a burrow in which to nest. Overall, my results indicate that the Burrowing Owl in Canada has appropriate habitat available and reasonably high survival and reproductive success in this region relative to other areas of its range.

The question remains, why then is this species declining? Evidence suggests that high-quality habitat still exists in Canada (Chapter 2), but much of it is unoccupied. The decline of the Burrowing Owl population in Canada may be partially explained by more owls choosing to stay and breed in their wintering grounds (Macias-Duarte 2011), but something else must be causing the decline throughout its range.

There is one mechanism that acts at an extent large enough to be a possible explanation for the overall decline of the Burrowing Owl in Western North America. On average, Burrowing Owls lay nine eggs, but only fledge about 4.5 juveniles (Chapter 2), with almost 100% of individual nestling mortality (i.e. partial brood loss) due to food shortage (Wellicome et al. 2013). This may be caused by Burrowing Owls evolving to take advantage of changes in prey that are unpredictable within seasons (Wellicome 2005) or of periodic prey irruption years, which no longer occur in former frequency (Poulin 2003). Modifications made to the Great Plains after European settlement resulted in the extinction of one irruptive species (Rocky Mountain Locust (*Melanoplus spretus*); Lockwood 2010) and a reduction in the scale and frequency of irruptions of another (Meadow Vole (*Microtus pennsylvanicus*); Heisler et al. 2014). The potential influence of these irruptions on the Burrowing Owl was last observed in 1997 during a widespread Meadow Vole outbreak in the grasslands of Canada. That summer, eight juveniles fledged per nest on average, almost double the average from other years (Wellicome 2000). Also, after many years of decline, the number of pairs of owls increased significantly in the following year (Poulin et al. 2001). Further evidence that Burrowing Owls lay large clutches to take advantage of regular prey irruptions is that prey supplementation does not affect clutch size or hatching, but does result in significantly greater fledging rates (Wellicome et al. 2013). Prey irruptions may have occurred frequently enough to result in most Burrowing Owls laying large clutches every year. These prey irruptions occurred over large geographical areas impacting Burrowing Owls over these same extents. The subsequent population boosts would have then impacted even larger portions of the population range through natal dispersal by juveniles. The loss of irruptive prey events seems to have impacted Burrowing Owl populations at the same scale that declines are being observed. It would be very difficult to recommend conservation actions that would mitigate the loss of irruptive prey events because they were caused by major cumulative changes to the landscape and one of the key species (Rocky Mountain Locust) linked to these fluctuations is now extinct.

Climate change may have a role to play in the decline of the Burrowing Owl. Climate change may be contributing to the infrequent irregular irruptions of meadow voles that have been observed over the recent past. Meadow vole irruptions follow winters when there are long periods of thick (20+ cm) snow (Heisler et al. 2014). Warmer average temperatures during the winter could reduce the frequency in which snow conditions are right for meadow vole irruptions. Extreme weather events can directly negatively affect Burrowing Owl nest survival and fledging rate (Fisher et al. 2015). Productivity over the last thirty years has decreased by 12% due to nests failures during periods of heavy rain and lower survival of youngest brood members when it rains (Fisher et al. 2015), regardless of the abundance of small mammals. Adverse weather also influences adult survival during migration and on their wintering grounds (Wellicome et al. 2014a). Climate change predictions suggest that the grasslands will see an increase in frequency of severe storms and bouts of heavy precipitation (Mladjic et al. 2011), both of which are predicted to negatively affect Burrowing Owls throughout their range in North America (Fisher and Bayne 2014).

Burrowing Owls have flexible environmental requirements (Stevens 2008) that appear to be able to adjust to many of the changes humans have made to the landscape in which they breed. This dissertation adds to a body of evidence that suggests that as long as suitable nesting sites are available, that owls are able to forage and fledge young in Canada’s grasslands in a wide variety of land–cover types. The greatest contributions to their decline in Canada may be caused by the loss of prey irruptions and from increases in adverse weather conditions. These issues are best addressed at the scales at which they occur, which means international cooperation to reduce climate change and restoration of natural fluctuations that typify the grassland ecosystem.

6.1 References

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