University of Alberta

The Influence of Land-cover Type and Vegetation on Nocturnal Foraging Activities and Vertebrate Prey Acquisition by Burrowing Owls (*Athene cunicularia*).

By

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Abstract

Studies of habitat selection by foraging animals assume patterns of animal presence correlate with successful foraging, without explicit evidence this is valid. I used GPS dataloggers and digital video recorders to determine precise locations where nocturnally foraging Burrowing Owls captured vertebrate prey. I compared land-cover type selection patterns using a presence-only Resource Selection Function (RSF) to a model that incorporated prey capture locations (CRSF). I also compared net prey returns in each cover type to better measure reward relative to foraging effort. Finally, I measured vegetative conditions at foraging and random locations. The RSF method did not reflect prey capture patterns, and cover-type rankings from this model are inaccurate. Burrowing Owls successfully forage across all cover types, albeit where vegetation is relatively sparse, with highest net energy returns in native grass. Conservation efforts for Burrowing Owls should focus on ensuring heterogeneity of plant heights and densities across the landscape.

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Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

1.1. Study species and conservation issues

1.1.1. Previous research

The Burrowing Owl (*Athene cunicularia)* is currently listed as endangered in Canada (COSEWIC 2006), a classification that has persisted since 1995 (Wellicome and Haug 1995). Estimates of the extent of the population decline in Canada are as high as 90% over the 1990's, when annual decreases were approximately 20% (Skeel et al., 2001; Wellicome and Holroyd 2001). More recent trends indicate some stability in the population (Wellicome pers. comm.), albeit at numbers approximately one tenth of those reported in the 1970s. The current geographic range of the Burrowing Owl in Canada is approximately 60% of its historical range (Figure 1). The most commonly attributed cause of the decline is habitat degradation, with approximately 75-80% of Canada's native grassland in the prairie provinces converted to non-native vegetation, primarily for the purposes of agriculture (Wellicome and Haug 1995). Many studies have contributed to our understanding of the Burrowing Owl population decline (Haug & Oliphant 1990; Wellicome 2000; Poulin 2001; Sissons et al 2001; Todd et al 2003; Sissons 2003; Shyry 2005; Poulin and Todd 2006; Floate et al 2008; Manalo-Stevens 2010). However, despite the breadth of research, the mechanism by which habitat degradation may have influenced the Burrowing Owl decline has not been implicitly identified. Through a feeding experiment, Wellicome (2000) demonstrated a positive relationship between the amount of food that pairs receive and the number of offspring they raise to fledging age (41 days). This suggests that low reproductive success may be caused by low prey abundance or availability. Conversion of native grassland to non-native vegetation types has been shown to affect the density of some small mammal species (Basquill and Neilsen 1999), and to limit access of avian predators to their prey because of differences in vegetation type and structure (Bechard 1982). Foraging success of raptors may be negatively affected by decreased small mammal abundance and/or availability, and has been hypothesized to be a key factor influencing population growth rate of Burrowing Owls.

1.1.2. Prey Abundance

Poulin (2003) suggested Burrowing Owl populations may depend on meadow vole (*Microtus pennsylvanicus)* irruptions for increases to occur. He based his hypothesis on the observation that the only recent increase in Burrowing Owl numbers occurred in a year following an outbreak of meadow voles. Poulin (2003) further speculated that loss and fragmentation of native grassland may have reduced the frequency of meadow vole irruptions such that "boom" reproduction years for Burrowing Owls may also have been reduced. While an appealing hypothesis, whether changes in meadow vole outbreaks as a result of agriculture conversion are the reason for Burrowing Owl declines has not been established.

Poulin and Todd (2006) demonstrated that the primary prey source of Burrowing Owls in all years tends to be small mammals, with insects, earthworms, amphibians, birds and reptiles contributing the remainder. In south-central Saskatchewan, where agriculture predominates, deer mice (*Peromyscus maniculatus)* are the most common small mammal species found in Burrowing Owl pellets (Ray Poulin, unpub. data). In Alberta, where ranching predominates, Burrowing Owl pellets contain higher percentages of voles

(*Cricetidae)* (Ray Poulin, unpub. data). Thus, Burrowing Owls seem capable of switching their diets toward what is available. Multiple small mammal trapping studies demonstrate that deer mice are much more abundant in farmland and roadside ditches than in native prairie (Wellicome 2000; Sissons et al., 2001; Poulin 2003; Sissons 2003; Hennin 2010). Given the flexibility in diet selection shown by Burrowing Owls, it remains unclear how owl demography is affected by shifts in small mammal communities caused by native prairie conversion.

1.1.3 Prey Accessibility

The conversion of native grassland to non-native cover types may negatively affect Burrowing Owl foraging via the introduction of taller, denser vegetation than was historically typical. Tall or dense vegetation may obscure prey items, or physically prevent an individual from acquiring prey. Therefore, despite the abundance of prey in non-native cover, it may be virtually inaccessible. If this is the case, foraging may be restricted to remaining native grassland patches where these vegetative conditions permit the owls to access their prey. This may require increased travel to reach suitable patches, or intensive use by multiple individuals may reduce the prey supply significantly. Alternatively, foraging may occur where abnormally obstructive vegetation exists, although it may require greater effort. Consequently, an adult's daily energetic consumption may be high, which may limit foraging and affect the number of prey items returned to the brood.

1.2. Measuring foraging success

1.2.1 Foraging patterns

How accessible prey items are to a foraging animal is difficult to measure. Some researchers have been able to determine the characteristics and conditions common to when and where prey are caught (Wakely 1978; Bechard 1982; Masman et al 1988; Preston 1990; Canavelli et al 2003; Chipman et al., 2008). However, for cryptic or nocturnally foraging species, such techniques are not possible. In such situations, researchers rely on technology to remotely monitor the animal's movements, the most popular of which is a VHF transmitter and receiver. Haug and Oliphant (1990), Sissons et al., (2001) and Sissons (2003) each used VHF transmitters to record nocturnal movements of Burrowing Owls. In all of these studies, proof of foraging success was not established. Instead, patterns of foraging "success" were interpreted from a Resource Selection Function (Manly et al., 2002), whereby disproportionately greater use of habitat categories relative to their availability was deemed "selection". In these papers, "selected" habitats were presumed to convey a positive effect on Burrowing Owl fitness based on the assumption that spending proportionately more time in a specific land-cover type increases foraging success. Consequently, the conclusions of these studies are based on assumptions concerning the animal's behaviour and presumed foraging success, and are perhaps inaccurate. Current conservation efforts aimed at increasing the foraging success of Burrowing Owls in Canada are based on the above studies, and may therefore be misguided if selection indices do not tell us where Burrowing Owls are actually successful at foraging.

1.2.2. Scale of selection patterns

Johnson (1980) identified 4 spatial scales at which animals select resources; 1) “first order selection” of a geographic range 2) “second-order selection” of a home-range 3) “third-order selection” of habitat elements within the home range, and 4) “fourth-order selection” of food items within a habitat element.

Selection patterns in foraging studies are often determined at the third order level. At this level, plots of land are often categorized based on perceived vegetative homogeneity within a spatial boundary encompassing the area in which the animal is thought to be able to forage. While selection of local sites within large-scale cover types may be linked to the habitat itself, third-order selection patterns are likely the result of finer-scale processes. Restricting analysis to a single scale of selection may not identify the ultimate processes behind observed patterns, limiting scientific understanding of the underlying relationships. If the goal of selection research is to identify, protect, and manage habitat elements to enhance a species' survival, deficiencies in our understanding of the linkages between different scales of selection may limit the efficacy of conservation actions. Coarse third-order measures may not identify the features that actually influence foraging success. Indeed, large-scale descriptions of land-cover types (i.e. grazed grassland, wheat field) are rarely homogeneous. In the prairie landscape, native pastures contain a multitude of grazing pressures or other disturbances that create subtle differences within or among pastures. Similarly, agricultural fields are often loosely categorized into cropland, despite the significant differences among crop types, as well as the heterogeneity inherent to even the same crop with different amounts of rainfall, fertilizer and soil types.

Burrowing Owl foraging may be influenced entirely by fine scale 3rd-order characteristics, in which case management at a coarser scale may be inefficient. Management for fine-scale conditions within all or some cover types may be more effective and more easily implemented than promoting one vegetation type over another. Current conservation efforts include conversion of cropland to native grass. However, if Burrowing Owls avoid non-native land-cover types simply because the vegetation precludes prey capture, a more efficient solution may be creating areas within these cover types where prey accessibility is high, rather than completely converting it to native grass.

1.3. Study Area

This study took place in Alberta and Saskatchewan during the summers of 2009 and 2010. The study area roughly extended from the towns of Hanna and Medicine Hat, Alberta, to the towns of Kindersley, Maple Creek, and Weyburn, Saskatchewan (Figure 1). The study area is predominated by the mixed-grassland ecoregion. Land-use consists primarily of cattle ranching in Alberta, and agriculture in Saskatchewan. Where native grass is present, it is dominated by needle and thread (*Stipa comata*), wheatgrasses (*Agropyron sp*.), blue grama (*Bouteloua gracilis*) and June grass (*Koeleria macrantha*). Agriculture consists of wheat types, oilseeds, coarse grains and pulse crops. Tame pastures within the home-ranges of the Burrowing Owls in this study consist entirely of crested wheatgrass (*Agropyron pectiniforme*).

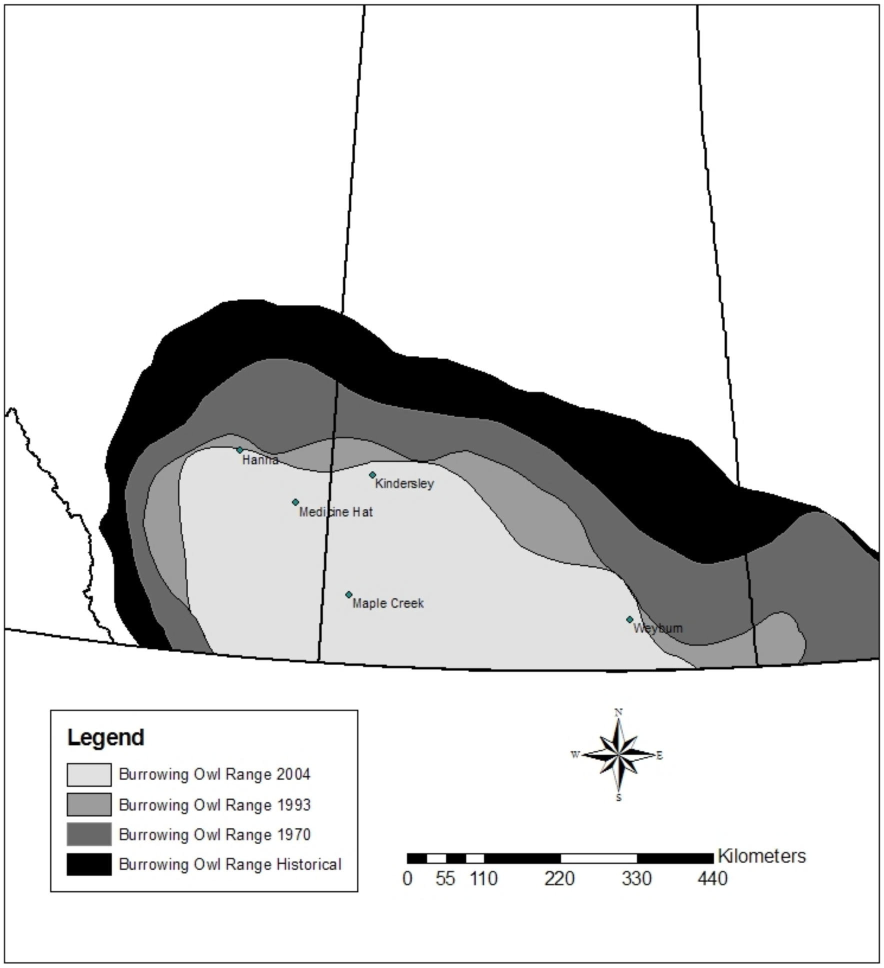

Figure 1.1. Contraction in the range of the Burrowing Owl, in the Canadian Prairies, over time.

1.4. Thesis overview

Although Haug and Oliphant (1990), Sissons et al. (2001) and Sissons (2003) each measured nocturnal patterns of use, there is still uncertainty as to how non-native vegetation types affect Burrowing Owl foraging in Canada. In addition to the problems listed above, these studies had small sample sizes (Haug and Oliphant – n=6 owls; Sissons et al (2001) – n=4 owls; Sissons (2003) – n=11 owls). Further, land-cover types within each study area consisted almost entirely of agriculture (Haug and Oliphant 1990;

Sissons et al. 2001) or native grass (Sissons 2003), thus adequate comparisons between types were not possible within each individual study. Here, I use GPS dataloggers to measure the precise foraging path of 18 nocturnally foraging Burrowing Owls in home ranges with both native grassland and crops in southern Alberta and Saskatchewan. The dataloggers allow me to identify different foraging behaviours, as well as prey capture sites.

In Chapter Two I examine coarse-scale Burrowing Owl third-order selection patterns. More specifically, I compare the traditional method of measuring these patterns (i.e., the use of data points without a measure of behaviour or resource use) against models that describe where prey were actually captured. Additionally, I compare foraging effort among land-cover types using time-spent, distance-travelled, and energy consumed as measures of effort, relative to the prey captured, as alternative measures of foraging-habitat suitability.

In Chapter Three I examine the fine-scale 3rd-order selection patterns of Burrowing Owl foraging sites. Specifically, I compare the vegetative characteristics at random points with points where owls were flying, hover-hunting, and where they successfully caught prey.

In Chapter Four I summarize the results of my thesis and discuss recommendations regarding the management of each of the cover types included in my study.

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Chapter 2: Using Vertebrate Prey Capture Locations to Identify Cover Type Selection Patterns of Nocturnally Foraging Burrowing Owls

2.1. Introduction

Management of wildlife often involves protecting, enhancing, or creating habitat elements considered important or essential to some component of a species' ecology (Walters 1991). Frequently, the focus of habitat conservation is to ensure that sufficient food resources remain available for the target species. In order to conserve the proper habitat element(s), a thorough understanding of the foraging ecology of the target species is necessary. Typically, this is achieved by remotely collecting movement data from an individual of the species, analyzing its spatial patterns relative to its available choices, and ranking the selection of habitat elements accordingly.

The most common method of evaluating the importance of a habitat element to a species is the Resource Selection Function (RSF; Boyce and McDonald 1999; Manly et al., 2002), a broad term describing a variety of statistical models that predict the likelihood of an animal's use of space. While a multitude of statistical techniques can generate a RSF, the basic design compares the characteristics at the animal's locations, termed "used" points, with randomly chosen locations that may not have been visited but were "available" to (i.e., had the potential to be used by) the animal within a biologically relevant spatial boundary (Boyce and McDonald 1999). Characteristics of points can be specific (e.g., species of plant) or general (e.g., broad land-cover type), but are generically termed resources. The use of each resource is compared to its availability, whereby resources used more than expected are deemed selected and therefore assumed to be important to the animal’s fitness, while those used less than expected are considered avoided, presumably making them less valuable. Based on these types of models, conservation groups tend to focus on increasing the amount of selected resources and/or minimizing avoided resources when protecting habitat (Johnson et al., 2004).

The RSF approach is common (Bader and Bednarz 2010; Boal et al., 2005; Bond et al., 2009; Burgess et al., 2009; Carrete and Donazar 2005; Henrioux 2000; Irwin et al., 2007; Glenn et al., 2004; Groce and Morrison 2010; Williams et al., 2011). However, users of this technique make several key assumptions. First, the use of the resource is assumed by the animal’s presence at a location. The types of behaviour engaged in by the animal at each point are not typically known. Thus, the specific resource exploited at any given time is also unknown, making it difficult to determine whether a habitat management strategy had created or protected the appropriate resources required by a species. Further, provided an animal is foraging while moving throughout the landscape, the RSF approach assumes that foraging is successful. A flaw of this logic is that animals foraging in low-quality habitat elements may require more time or effort to acquire food. Also, if an animal must cross large amounts of non-foraging habitat to reach food resources, there is the danger that the majority of locations will reflect movement through the sub-optimal habitat, rather than the habitat where successful foraging occurs. RSF models, when used naively, can create a very biased interpretation of what is high versus low quality foraging habitat.

The Burrowing Owl is an endangered species (COSEWIC 2006) that suffered a large population decline in Canada in the 1990’s (Wellicome and Holroyd 2001). While land-cover conversion of native grassland to agriculture is often identified as a causal factor in the decline, the mechanism by which this occurs is unclear. Wellicome (2000) found that supplemental feeding of Burrowing Owls resulted in increased reproductive success compared to concurrently un-supplemented control owls. This suggests that reduced food abundance or accessibility may limit the number of chicks produced, which over time has resulted in a decrease in the size of the owl population in western Canada. If food availability is lower in agricultural cover types than in native grassland, the increase in agriculture will likely lower average reproductive output relative to what occurred historically.

Haug and Oliphant (1990), Sissons et al., (2000) and Sissons (2003) have attempted to quantify where on the landscape Burrowing Owls acquire food. However, the crepuscular/nocturnal foraging habit of this species means that these studies suffered from the problems associated with using an RSF approach to assessing foraging-habitat selection. Consequently, the effects of native and non-native cover types on the foraging ecology of the Burrowing Owl remain ambiguous. What is needed to effectively identify high-quality foraging habitat is a method of identifying precise locations on the landscape where animals are found and simultaneously identifying those locations where the animal obtains specific types of prey. Ideally, the amount of foraging effort exerted should also be quantified.

In this chapter, I present four model types that describe space use by Burrowing Owls and examine how interpretation of what is important foraging habitat depends on the model used. The first model is a standard RSF that uses presence-only locations, temporally spread in time to ensure statistical independence, but where the behaviour at each location is unknown. Used locations are compared against random "available" locations within the home range to determine the importance of land-cover types. The second technique is similar to the first, except only true resource acquisition sites (i.e., places where Burrowing Owls were known to have captured prey) comprise "used" locations, and is termed the Capture Resource Selection Function (hereafter, CRSF). As >90% of Burrowing Owl prey deliveries are vertebrates by biomass, (Poulin and Todd 2006), they are the focus of this study. The remaining models each examine the prey return per unit effort in each land-cover type, and are collectively referred to as Return vs Effort (hereafter, RVE) models. The first examines the locations of prey captures relative to the rest of the owl's foraging path; a used/unused design termed a Prey Capture Function (hereafter, PCF). The others evaluate prey return per unit effort in each cover type, using time-spent (hereafter, TSF), distance travelled (hereafter, DTF) and energetic consumption (hereafter, ECF) as measures of effort.

2.2. Methods

2.2.1. Field Methods

I studied the nocturnal foraging behaviour of male Burrowing Owls across the prairie portions of southern Saskatchewan and Alberta, during the months of June and July, in 2009 and 2010. Nests were located in early May via diurnal and nocturnal call-back surveys, followed by visits to prospective burrows. Nests were monitored weekly using underground infrared cameras that permitted me to accurately estimate hatch dates based on an early-to-mid-clutch egg counts (see Wellicome 2005 for a description of this technique). Trapping of male Burrowing Owls occurred at least 7 days post-hatch of the eggs to minimize nest abandonment while still allowing capture of males that become less aggressive as the summer progresses.

Males were trapped at nest or roost burrows using either bow-nets (Northwoods Falconry) or one-way walk-in traps (Winchell 1999). Typically, a dead mouse or bird was placed within the trap to attract the owl. I also buried a wildlife caller nearby that played a male territorial Burrowing Owl calling sound. The volume of the caller was kept low to reduce the likelihood of attracting or disturbing the female. Once caught, males were weighed and fitted with an aluminum Fish and Wildlife leg band. Dataloggers were attached as a “backpack” using half-weave Teflon ribbon. Teflon ribbons were secured to the datalogger using light-weight packing tape containing a tear-proof fiberglass cross-weave to prevent the owls from forcibly removing or damaging the datalogger. The entire assembly weighed approximately 8g. To minimize risk from predators, males were returned to their nest burrows to recover from handling stress and datalogger attachment.

To record prey deliveries at the nest burrow, I set up Digital Video Recorders (DVRs). Setup consists of a security-style DVR powered by four 6-volt deep-cycle marine batteries. Connected to the DVR were two infra-red, waterproof, security cameras. One camera was placed at the burrow mouth, opposite the mound, permitting an unobstructed view of the delivered prey item as the owls tend to carry prey in front of their bodies as they enter the burrow. The second camera was placed approximately 1 meter from the burrow, filming "over-the-shoulder" of the first camera. This camera functioned as a backup in case an accurate identification could not be made on the first camera, and to detect prey deliveries occurring just off the mound. The DVR records a date and time stamp on the screen that was synchronized with the datalogger time.

I attempted to re-trap owls three to four days after logger attachment, when the datalogger battery was likely depleted. Trapping did not exceed two hours, and 1-2 dead mice were left in the burrow mouth to offset the lack of foraging caused by trapping/handling. Occasionally, owls forcibly removed the dataloggers themselves, and some of these were recovered fortuitously at or in burrows.

I documented the predominant features within a 3.2 km radius around each nest, recording land-cover types, roads, and potential perches, which included fencelines, signposts, and petroleum structures suitable as perch sites. Land-cover types were classified as either “Cropland” (actively growing crop at the time), “Native Grass” (vegetation predominantly native species), “Roadway” (includes both the road surface and associated ditches, if present), “Stubble” (inactive cropland with remnants of previous season’s harvest), “Tame Grass” (vegetation predominantly introduced grass species), “Tame Hay” (vegetation harvested for the production of hay – typically alfalfa species), “Water Body” (permanent body of water) and “Wetland” (area associated with permanent or ephemeral water body, but covered with emergent vegetation). The radius is based on the maximum movement distance recorded by any one owl.

2.2.2. Dataloggers

I recorded male locations at a rate of 1 fix every 2 seconds from 21:00 to 07:00 as the male forages primarily during crepuscular hours, with peak activity periods around 22:00 and 04:00 (Haug and Oliphant 1990; Sisson 2003; Poulin & Todd 2006). Though it is customary in use vs. availability studies to choose an interval that ensures statistical independence of points, it is impossible to identify capture sites without knowledge of the entire foraging paths. The dataloggers recorded 3-dimensional locations (latitude, longitude, and altitude), speed, angle of 2-dimensional movement, and degree of precision. Accuracy of the logger is very high, with 95% of all locations falling within 4.2m when recorded for 24-hours in a fixed position (Dell'arricia et al. 2010).

2.2.3. Identification of Capture Sites

I viewed the DVR footage and noted all prey deliveries occurring during the time dataloggers recorded owl movement, noting specifically the time of delivery. For each recorded delivery, I used ArcMap to assess the movement data of the corresponding male, observing first if the male was present at the nest at the time of delivery, and then examining all behaviour patterns occurring 10 minutes prior to delivery of food at the nest. If I judged the male, not the female, to be the deliverer of the prey, I searched for clusters of points immediately preceding the direct flight to the nest, and classified such clusters as capture clusters. The location within the cluster immediately preceding flight represented the capture site (Figure 2.1). Any deliveries that I suspected the male transferred off-camera were included. If the male returned to the nest but did not appear on camera and the female flew out of view for a short period (less than 15 seconds) but returned with vertebrate prey, I assumed the female got the prey from the male. Deliveries occurring when the male was not present at, or near, the nest were not included, nor were those preceded by the male's presence at a known roost. Burrowing Owls routinely cache prey in roost burrows. Consequently, these deliveries were most likely cache retrievals, not prey captures.

As the time on both the DVR and datalogger were synchronized for each owl, the male's presence at the nest was always confirmed in the datalogger data, and in the video data. Therefore, I am confident that the movement data away from the nest is an accurate representation of the male's movements. Field observations of foraging owls during crepuscular periods were the basis for assuming the cluster of points preceding direct flight to the nest indicate of prey captures, as the observed owls spent several seconds either subduing their prey, or ensuring it was sufficiently incapacitated to return to the nest.

I identified the species of prey as accurately as possible from the DVR footage. Because Burrowing Owls carry their prey in their beaks as they enter the nest burrow, an unobstructed view of the prey was common. However, occasionally moisture or debris on the camera lens made identification of prey to the species level impossible. In these instances, the prey was assigned to broader categories, such as "mouse" or "small mammal" or in very small number of cases "vertebrate". All of these deliveries are included in the analysis because I was confident the item was not an invertebrate.

2.2.4. Resource Selection Function

I used logistic regression as an estimating function to generate the RSF, incorporating the individual owl as the random effect parameter. This accounted for variation in each owl's foraging strategy and available land-cover configuration (Larsen et al., 2000). Used points were compared against random "available" points. Used points were sub-sampled from the owl's movement locations, excluding those less than 50m from the nest, as points within this radius tend to reflect behaviours other than foraging (Haug and Oliphant 1990). Points were sub-sampled at an interval of 10 minutes. Based on the datalogger data, owls routinely fly upwards of 40-50 km/h, thus they are capable of crossing their entire home-range within 10 minutes. Consequently, I consider the sub-sampled points indicative of the owl's choice to be in that location, rather than a reflection of autocorrelation with the previous location. Only Cropland, Native Grass, Roadways, Stubble, Tame Grass, and Wetlands were included as land-cover types, as all others were not present within the 3.2km radius of every owl.

I used ArcMap to generate 500 random points within 3.2 km of each owl's nest. For each random and used point, I recorded land-cover type, distance to nest, distance to nearest road, and distance to nearest cover type edge. As a central-place forager, a male Burrowing Owl must return to its nest once prey is captured, and many central-place foragers are presumed to forage near to the nest to minimize energy expenditure (Andersson 1981). Edge is defined as the line of transition between two non-similar land-cover types. Frequently, edges correlate with a change in vegetation type and structure, as from grazed to ungrazed pastures, or from agriculture to grassland. Such edges may offer higher prey abundances as prey species from both land-cover types may be present. For each distance variable, I performed a fractional polynomial (fracpoly) analysis, which identifies the most parsimonious non-linear transformation of the variable. I then incorporated the fracpoly-recommended transformations for each variable into the multivariate model. I compared this model to linear, non-linear (i.e., quadratic and cubic) and land-cover-type-only models using Akaike's Information Criteria (AIC). I report the odds ratios for each dependent variable, where values >1 indicate selection, and values <1 indicate avoidance.

2.2.5. Capture Resource Selection Function

The construction of the CRSF was similar to the most parsimonious RSF model except used points represented vertebrate prey capture sites rather than any location where the owl was observed. All capture sites from two nests were excluded from the

RSF and CRSF analyses because the land-cover configuration around the nest did not include one or more of the three predominant types on the Canadian prairies (i.e., native grassland, cropland, and stubble). It is not possible to model an individual's selection between cover types when cover type variation does not exist.

2.2.6. Prey Capture Function

The PCF is an adaptation of a used/unused design, where unused points are represented by locations where the owl was present but did not capture prey. Unused points consist neither of the capture cluster, nor flights to the nest made with prey. Points within 50m of the nest were also excluded for the reasons listed previously. Used points in this analysis represented sites where prey was captured. Thus the design of this model could more accurately be described as capture/no capture. Random effects logistic regression was used to fit the model.

2.2.7. Electivity

In the logistic regression models, conclusions regarding land-cover selection are relative to a reference category. I chose native grass as it is the predominant land-cover type in owl home ranges, and because it is the only native cover type included in the model. However, these models do not permit a sufficient understanding of the selection patterns of Burrowing Owl use of native grass in and of itself. Therefore I also determined the electivity index for each cover type. Electivity is an index of selection where scores >0 indicate selection, and scores <0 indicate avoidance. The electivity model did not include distance parameters, rather it was intended to provide a categorical understanding of Burrowing Owl land-cover type selection.

The complex and non-linear transformations of the distance variables made interpretation of the logistic regression results challenging. For clarity, I grouped the distances into 150m-wide bins, and calculated the electivity index for each bin.

2.2.8. Time-spent Function, Distance-travelled Function, and Energetic Consumption Function

I compared the number of prey items returned in each cover type against the amount of time spent foraging in that land-cover types (TSF), as well as the distance travelled (DTF). Time spent and distance travelled are based on all nocturnal foraging locations, excluding those within 50m of the nest, capture clusters, and return flights to the nest made with prey. Distance travelled in each land-cover type was calculated by measuring the step-length between points in ArcMap.

All locations >50m from the nest were classified into one of four foraging-related behaviours: Flying, Perching, Hovering, or Walking. Fly points were defined as those with a speed >= 5 km/h. When owls run to chase insects (Thomsen 1971; Coulombe 1971), it is unlikely that their speed exceeds 5 km/h. Perch points are stationary points (< 5 km/h) within 15m of a known perch location. Hover hunting tends to occur in one location for less than 30-45 seconds (pers. obs.). However, to account for the possibility that an owl occasionally hovers for a longer period, hover points are clusters of points < 2 minutes in duration. Clusters of points were considered distinct if they were separated by two or more consecutive fly points. Walking represents clusters of points > 2 minutes in duration showing directional movement. If the cluster of movement was contained within a circle with a 10m radius, I assumed the owl was stationary and therefore not foraging. Although an owl that is stationary and on the ground may be scanning for prey, it is more likely resting, as few prey will be detected from such a position given the limited search radius.

I assigned all Burrowing Owl points a caloric value (cal/sec) based on the behaviours occurring at that time. Caloric values were based on Andersson's (1978) calculations for a 200g bird. I corrected the energetic consumption to 160g to represent mean Burrowing Owl mass. Consequently, perch points were assigned a value of 0.48 cal/sec, walk points 0.96 cal/sec, fly points 3.2 cal/sec, and hover points 4.8 cal/sec. Bautista et al., (2001) found the caloric consumption during walking in starlings (*Sturnus vulgaris*) was 1.6 times that of perching. As Burrowing Owls may run, I increased the estimated walking caloric value to 2 times that of perching to account for a more energetic method of foot-travel. Caloric value of prey items was assumed to be 34 kcal/g, based on an average mass of 22.1g (from this study: 80% mice x 20g + 20% voles x 26g) and an average caloric value of 1.6Kcal/g (Fleharty et al., 1973). I assigned an average value despite the fact that some deliveries were identified to species level as there was no objective way to determine individual prey mass or caloric value. Indeed, identifying the caloric value of prey items was not the intent of this model. Rather, it is a coarse measure of the caloric return versus consumption, and I argue an average value is sufficient to permit an accurate comparison between foraging tactics and land-cover types.

2.3. Results

In 2009 and 2010, I trapped and attached dataloggers to 40 owls (23 in 2009; 17 in 2010). Of these, 36 were recovered. However, six nests had DVRs that did not function properly while the datalogger was recording, and 12 had no vertebrate prey deliveries during the period when the DVR or datalogger recorded data. The remaining loggers (18) successfully recorded foraging data and had at least one vertebrate prey delivery occur while the datalogger was recording. All dataloggers recorded for less than two nights (Night 1 - Mean Datalogger Operating Time (MDOT) = 10.3 hours (SD 1.2); Night 2 - MDOT = 5.1 (SD 2.8); Total - MDOT = 15.4 (SD 2.5), with a total recording time for all owls of 278 hours (Night 1 = 186 total hours; Night 2 = 92 total hours).

I successfully identified 112 vertebrate prey captures (Mean= 6.2; range= 1-14). Over 78% of captures were the result of hover hunting (Figure 2.2) and most captures occurred in native grass, followed by cropland, stubble, roadways, tame grass, and wetlands. The average distance-to-nest for all capture sites was 895m (SD 662). Just under half of all captures (47%) occurred >800m from the nest and 17% of captures occurred >1600m from the nest. Fewer than 10% of captures occurred <200m of the nest (Figure 2.3).

In native grass, owls captured a greater diversity of prey types (Table 2.1), and this land-cover type was the main source of voles (80%), and amphibians (75%). Mice dominated captures in stubble and cropland. Over half of all captures (58%) were confirmed as mice, followed by unidentified small mammals (15%), voles (13%), amphibians (11%) and unidentified vertebrates (3%). Confirmed species identification was possible for 32 prey items, and consisted of deer mouse (15), meadow vole (9), Northern-grasshopper mouse (5), sagebrush vole (2), and olive-backed pocket mouse (1). Further, 10 anuran prey deliveries were confirmed, although identification of species was not possible from the DVR footage.

2.3.1.Hourly Behaviours

Burrowing Owls spent between 10 and 30 minutes engaged in high-energy foraging (flying and hovering), depending on land-cover type, with the remainder spent low-energy foraging (perching and walking) (Table 2.6). The ratio of time spent low-energy foraging compared to high-energy foraging was approximately 2:1; however foraging was not balanced across all hours. Figure 2.4 demonstrates high-energy foraging accounted for a greater proportion of time spent during crepuscular hours (22:00 and 04:00), with the least activity occurring around 05:00 and 06:00. Prey captures occurred at least four times more often during high-energy foraging than low-energy foraging for each cover type (Table 2.6), with roads an exception. Low-energy foraging dominated owl behaviour in most land-cover types, with the exception of wetlands and cropland (Table 2.6).

2.3.2.Distance to Feature

The results of the logistic regression models are reported in Table 2.3. The general trends for the distance variables are quite consistent, regardless of the feature (nest, road, edge) measured (Figures 2.6, 2.7 & 2.8). The RSF and CRSF models tend to show decreasing selection for a location with increasing distance to feature, with the highest scores for the nearest bin. The PCF model, however, shows increasing selection with increasing distance to feature up to a certain distance, beyond which selection shows either no trend or decreasing selection.

2.3.3.Use/Availability Models

Rankings of the degree of use of each land-cover type tend to mirror the rankings of its availability (Figure 2.5), with roads a notable exception. Burrowing Owls spent approximately 17% of their time on roads, despite roads occupying only 1% of the available foraging area. Electivity in the RSF model was highest for roads at 0.87, with stubble second at 0.05. All other electivity scores were below zero, indicating avoidance of these cover types. Rankings based on RSF electivity were Roadways > Stubble > Wetlands > Native Grass > Cropland > Tame Grass (Table 2.7).

Vertebrate prey captures occurred less than expected in each cover type except in stubble and on roadways (Figure 2.5). CRSF electivity was highest on roads and stubble; however, the strength of selection of roads dropped to 0.60, whereas stubble increases to 0.35, as compared to the RSF. Cover type rankings based on CRSF electivity were Roadways > Stubble > Cropland > Tame Grass > Native Grass > Wetlands (Table 2.7).

The inclusion of distance parameters in the logistic regression models changed the RSF ranking considerably, as Burrowing Owls avoid native grass compared to all other land-cover types, except for tame grass and roadways (Table 2.3). Based on odds ratios, cover type rankings in the RSF logistic regression model were Stubble > Wetland > Cropland > Roadways > Native Grass > Tame Grass. In contrast, the CRSF displays different patterns than the RSF. Based on CRSF odds ratios, the rankings were Stubble > Roadways > Cropland > Tame Grass > Native Grass > Wetlands. However, only stubble showed a statistically significant difference from native grass (Table 2.3); thus apart from stubble, the ranking of the remaining cover types was relatively arbitrary.

2.3.4. Return vs Effort Models

The PCF electivity scores demonstrate that, relative to where Burrowing Owls spend their time, selection patterns differ from the use/availability models. Rankings based on PCF electivity were Tame Grass > Stubble > Cropland > Native Grass >

Wetland > Roadways, with positive scores for only the first three cover types. The inclusion of distance variables in the logistic regression models again alters the relationship, as no cover type is selected relative to native grass, although wetlands are avoided (Table 2.3).

In the TSF model, rankings of cover types are Cropland > Tame Grass > Stubble > Native Grass > Wetland > Roadways. Roadways saw almost as many hours of use as stubble, yet 3.5x more prey captures occurred in stubble. Wetlands and tame grass saw very little use, and the fewest captures, although the prey return rate for tame grass was high.

The DTF demonstrates that Burrowing Owls travelled most extensively through native grass and cropland, but the rate of return was highest in stubble (Table 2.4). Although more time was spent foraging in stubble relative to cropland, the distance travelled in the former was half of that in the latter. At minimum, a Burrowing Owl needs to travel over 2.5km in order to capture vertebrate prey, regardless of cover type, and on average will need to travel 4.9 km prior to making a successful capture (Table 2.4). DTF rankings are Stubble > Tame Grass > Native Grass > Cropland > Roadways > Wetlands. In the ECF, net energy is not a reflection of the actual caloric consumption attained by the male, as the prey was delivered to the nest and presumably fed to the chicks. Rather it is intended as a coarse-measure of foraging efficacy. Net high-energy foraging was positive in all cover types, with the exception of roadways (Table 2.5). Net low-energy foraging was positive in all cover types except wetlands and tame grass. Based on net energy returns of high-energy foraging only, cover type rankings are Tame Grass > Stubble > Cropland > Native Grass > Wetland > Roadways. Based on low-energy foraging net returns only, the cover rankings are Cropland > Native Grass > Roadways > Stubble > Wetland = Tame Grass, with the latter two seeing no prey captures. Based on combined high and low-energy net returns, cover type rankings are Native Grass > Cropland > Stubble > Roadways > Tame Grass > Wetland. Table 2.6 presents the rankings of each cover type from each use/available and RVE model.

2.4. Discussion

2.4.1. Foraging Behaviours:

Although previous studies discuss Burrowing Owl hover-hunting as a foraging method, its degree of use has not been described. Martin (1973) considered hover-hunting a seldom used behaviour, even when food requirements of the chicks were high. However, Thomsen (1971), Coulombe (1971), and Haug and Oliphant (1990) assumed hover-hunting representative of an owl searching for high calorie (i.e., vertebrate) prey. This study demonstrated that high-energy foraging (i.e., hover-hunting and flying) accounted for 33-50% of an owl's foraging behaviour depending on the land-cover type, and 78% of vertebrate prey acquisitions. While Masman et al., (1988) found an increase in hover-hunting with increased brood-hunger in kestrels (*Falco tinnunculus*), the consistency of the crepuscular patterns observed in this study (Figure 2.4) and others (Poulin and Todd 2006; Haug and Oliphant 1990), suggest the increase in hover-hunting around the hours of 22:00 and 04:00 are indicative of increased prey activity or availability, not brood hunger. Given the marked difference in hourly capture rate between high and low-energy foraging, hover-hunting is likely employed to maximize the number of deliveries, rather than minimize caloric expense, as is typical for most species during the breeding season (Norberg 1977). However, the energetic return on high-energy foraging is similar to low-energy foraging in this study, possibly refuting the hypothesis that the latter is more energy efficient.

Because of the high energetic demands of hover-hunting, perching and walking may allow the owl to recover energy while still being able to search for prey. Alternatively, perch-hunting may be intentional, in that the owl chooses to remain in a single location and scan for prey. Norberg (1977) and Andersson (1978) conclude less-efficient foraging methods should be chosen at times of low prey density and detectability. Thus the reduction in activity levels around 00:00 and 06:00 (Figure 2.4) probably reflect a lack of available prey or suboptimal foraging conditions, rather than necessary rest periods. Walking may be used primarily for low-energy self-provisioning, such as feeding on insects. Coulombe (1971) found foot chases were largely used for catching arthropods during the day, and Butts and Lewis (1982) concluded the short vegetation around black-tailed prairie dog (*Cynomus ludovicianus*) colonies facilitated foot chases for arthropods. Additionally, Swainson's Hawks (*Buteo swainsoni*) have been observed running in pursuit of insect prey (Canavelli et al., 2003). Similar to perch-hunting, this behaviour will inherently permit incidental capture of vertebrates, some or all of which are likely returned to the nest. It is also possible that the male is consuming vertebrates and not returning them to the brood. However, Burrowing Owls are reported to return decapitated prey to the nest (Troy Wellicome pers. comm.), suggesting the male ingests a portion of the prey to recover energy spent foraging, but returns the majority of that prey item to the brood. No prey items were observed to be decapitated in this study however.

2.4.2. Distance to features

In use/availability models, selection tends to be highest for the most proximal distance bin, with a general trend of decreasing selection with increasing distance from each feature examined. However, in the PCF models, the proximal bin typically has the lowest electivity score, with an increasing trend spanning several bins, followed by a decrease in the most distant bins. A lack of foraging, or successful foraging, near the nest may be the result of one or more influences. First, the proximal food supply may have been decimated previously in the breeding season if Burrowing Owls tend to capture proximal prey to reduce energy consumption, reminiscent of Storer-Ashmole's halo (Storer 1952; Ashmole 1963; Elliot et al., 2009). Second, Burrowing Owls may avoid proximal foraging in order that this prey supply either remain for occasional foraging by the female, or persist until the juveniles are capable of self-provisioning. Finally, historical Burrowing Owl nests throughout much of their range were strongly associated with black-tailed prairie dog colonies (Sidle et al., 2001), which would result in a more gregarious nesting structure than is typically observed in Canada currently. Prior to the population decline in Canada, Burrowing Owls likely encountered conspecific neighbours more readily. Consequently, the proximal prey supply around Burrowing Owl nests may have been reduced because of the number of neighbouring owls, requiring adults to distance themselves from the colony or a conspecific's core territory in order to find vertebrate prey. The pattern observed in this study may simply reflect an evolutionary tactic of a species accustomed to a more gregarious situation, and thus a reduced proximal vertebrate prey supply.

The degree of use and relative lack of prey return near roads and edges suggest these features are either sub-optimal foraging locations, or that Burrowing Owls are engaged in non-foraging behaviours when near roads. Meunier et al. (2000) hypothesized that Eurasian Kestrels (*Falco tinnunculus*), which have a foraging strategy similar to the Burrowing Owl, selected for roadways because of the abundance of perches in these areas. However, Burrowing Owls appear to distance themselves from roads and edges when acquiring the majority of their prey, despite the abundance of prey that typically exists in roadside ditches (Sissons et al., 2001; Poulin 2003). Note that edge in this study was measured on a large scale, and defines the boundary between two land-cover types. I did not measure edge on a finer-scale, such as the transition between a patch of grazed grass and an ungrazed patch. It is possible that such "edges" may heavily influence Burrowing Owl foraging patterns. This relationship, however, was not discernible given the resolution of habitat elements in this study and remains untested.

2.4.3.Use/Availability Models

Comparisons between the RSF and CRSF demonstrate that the data collection process used in the RSF, which does not permit interpretation of the behaviour at each point, limits understanding to space-use patterns only, rather than prey capture patterns. The RSF model indicates that owls significantly select for most land-cover type relative to native grass. Yet the CRSF, using prey capture sites, demonstrates that only stubble is significantly selected relative to native grass, with all others showing no statistical difference from native grass. Consequently, space-use patterns are not analogous to resource selection patterns if the measured resource is vertebrate prey. Recommendations to land managers regarding the suitability of the land-cover types based on the conclusions from the RSF method could have included deeming native grass as among the least optimal cover types, or the promotion of roads or wetlands as heavily utilized, and a positive influence on Burrowing Owl foraging success. However, the use of roads or wetlands is seldom for the purposes of active foraging, and prey return rates are among the lowest in these cover types. Further, native grass consistently ranks equal or above several land-cover types in the CRSF and each RVE model.

The ability to identify true resource selection patterns permitted me to demonstrate that intensive use of some cover types does not equate to intensive acquisition of vertebrate prey there. A RSF approach analogous to that employed here, if used on a species showing similar foraging strategies and interpreted as indicative of successful foraging, will likely show comparable inaccuracies. While some species may show intensive use of those land-cover types that offer the highest return of resources relative to foraging effort, it is not always the case. Unless it is explicitly proven that the pattern of space-use consistently reflects the pattern of resource acquisition in question, the conclusions of an RSF model like that employed in this study provide an inaccurate or incomplete understanding of the 3rd order selection patterns of the target species.

2.4.4. Return vs Effort Models

The goal of the RVE models was to demonstrate the foraging success of Burrowing Owls in each land-cover type to better understand the effect each type may have on Burrowing Owl fitness. Although the CRSF model includes prey acquisition locations, inferring that selection patterns are indicative of each cover type's impact on fitness may be less accurate or less informative than a RVE model that measures prey return relative to foraging effort. However, a coarse RVE model such as the PCF may oversimplify the effects of each cover type on Burrowing Owl fitness. In this model, only wetlands were significantly avoided relative to native grass, with all other cover types showing no selection patterns. The resulting conclusion is that the prey return relative to foraging effort in native grass and cropland are equal, as is each cover type's effect on fitness. However, a lack of statistical significance does not necessarily equal a lack of biological significance. The incremental differences observed in the return rates between the cover types in the TSF, DTF or ECF models, if consistent throughout the nestling phase, can result in very different amounts of prey return. For example, cropland is not selected relative to native grass in the PCF, yet in native grass Burrowing Owls capture approximately 0.8 prey items per hour. In cropland, that number is 1.1. If the available foraging times for males throughout the nestling stage are simplistically set to 9 hours each night for 30 nights, and restricted to a single cover type, the total deliveries for an owl foraging in native grass would be approximately 216, and 297 in cropland. Further, the effort to obtain these items in native grass would be approximately 1.4 times higher than in cropland (Table 2.5). While the PCF ranks these two cover types equally, there may be a significant advantage for an owl foraging in cropland with 81 more prey items returned to the brood. Conversely, if net caloric return is considered the most accurate measure of foraging success relative to effort, and if prey rates for both high-energy (HE) and low-energy (LE) foraging methods are included, native grass has the highest overall net gain, and is therefore the most optimal cover type (Table 2.5).

Comparisons between the results of space-use selection patterns in this study with others from the Burrowing Owl literature were confounded by inconsistencies with the classification of cover types by researchers. "Grass-forbs" areas in Haug and Oliphant (1990) included hayland, roads, ungrazed pasture, and uncultivated areas. Gervais et al., (2003) included stubble fields in the "grass" category, and wetlands and roads in "other", despite the fundamentally different vegetative characteristics of these areas. Further, my study has demonstrated the danger in interpreting patterns of selection when resource use is not explicitly demonstrated. For example, Sissons (2003) recommended wetlands and associated edges as important for foraging, yet my study demonstrated this cover type provided very low prey returns. Both Sissons et al., (2001) and Haug and Oliphant (1990) found owls avoided cropland, but in my study cropland shows some of the highest capture rates of prey. Sissons (2003) concluded owls may target the edges between large-scale cover types, yet my results suggest foraging males tend to distance themselves from these areas when engaged in their primary foraging behaviours.

As each of these studies recorded locations at fixed intervals and did not measure behaviour, approximately half of their data inevitably represent an owl that is not actively foraging. Indeed, Sissons' (2003) conclusion regarding edges and the selection for rights-of-way in Haug and Oliphant (1990) are likely a result of this fact. As Haug and Oliphant (1990) only recorded owl locations when the individual was stationary, high-energy foraging was almost certainly not occurring. Consequently, the conclusions of these studies should be restricted to land-cover type selection patterns of nocturnal space-use, rather than patterns of successful nocturnal foraging.

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Table 2.1. Summary of vertebrate prey captures for each land-cover type. "Small mammal" refers to an item that was positively identified as a small mammal, but could not be categorized further. "Unknown" deliveries were identified as vertebrates, but could not be categorized further.

Cover Type	Vertebrate Prey Types					
	Vole	Mouse	Small Mammal	Anuran	Unknown	Total
Native Grass	12	8	8	8	1	37
Wetland	0	0	1	1	0	2
Tame Grass	1	3	0	0	0	4
Tame hay	0	0	1	0	0	1
Cropland	1	28	1	1	0	31
Stubble	1	20	6	0	2	29
Roadways	0	6	0	2	0	8
Total	15	65	17	12	3	112

Table 2.2. Evaluation of candidate models of Burrowing Owl space-use patterns. "Dn" refers to distance to nest, "Dr" distance to roads, and "De" distance to edge. The numerals in the model terms for the fracpoly-recommended models refer to transformation 1 or 2. The most parsimonious model is in *italics*.

Model Name	Model Terms	k	AICc	ΔAICc	Model Likelihood
Cover type only	Covtype	2	4736.6	2370.4	0
Linear distance	Dn + Dr + De + Covtype	5	2753.1	386.9	0
Distance-squared	$Dn + Dn^2 + Dr + Dr^2 + De + De^2$ + Covtype	8	2597.6	231.4	0
Distance-cubed	$Dn + Dn^3 + Dr + Dr^3 + De + De^3$ + Covtype	8	2664.2	298.0	0
Fracpoly-recommended	*Dn1 + Dn2 + Dr1 + Dr2 + De1 + De2 + Covtype*	*8*	*2366.2*	*0.0*	*1*

Table 2.3. Comparative results of random-effects logistic regression for the Resource Selection Function, Capture Resource Selection Function and Prey Capture Function. "Dn" refers to distance to nest, "Dr" distance to road, and "De" distance to edge. The numbers identify the first and second fracpoly-recommended transformations. Native grass is the reference category and is omitted from the table. Odds ratio values of >1 indicate selection, whereas values <1 indicate avoidance, relative to the reference category.

Variable	**Resource Selection Function**				**Capture Resource Selection Function**				**Prey Capture Function**			
	OR	**SE**	**Z**	***p***	**OR**	**SE**	**z**	***p***	**OR**	**SE**	**z**	***p***
Dn1	0.10	0.01	-29.70	0.000	0.96	0.03	-1.40	0.162	0.89	0.19	-0.57	0.566
Dn2	1.00	0.00	-0.75	0.451	0.01	0.00	-12.29	0.000	0.64	0.08	-3.80	0.000
Dr1	1.01	0.00	5.69	0.000	1.03	0.04	0.78	0.437	1.63	0.21	1.73	0.085
Dr2	1.00	0.00	4.78	0.000	0.24	0.29	-1.20	0.229	0.55	0.54	-0.61	0.541
De1	0.00	0.00	-9.58	0.000	1.01	0.00	-2.48	0.013	46.11	134.63	1.68	0.093
De2	121405	156316	9.09	0.000	1.01	0.00	3.47	0.001	0.00	0.00	-1.96	0.050
Wetland	2.41	0.687	3.09	0.002	0.76	0.58	-0.36	0.721	0.20	0.15	-2.07	0.038
Tame Grass	0.973	0.316	-0.08	0.935	1.18	0.70	0.28	0.781	1.01	0.59	0.02	0.982
Cropland	2.38	0.425	4.87	0.000	1.36	0.44	0.95	0.340	1.04	0.34	0.11	0.915
Stubble	6.20	1.21	9.32	0.000	3.74	1.21	4.08	0.000	0.84	0.30	-0.49	0.624
Roadways	1.89	0.698	1.73	0.083	1.41	1.32	0.36	0.715	0.84	0.48	-0.31	0.759

Table 2.4. Summary of results of Time Spent Function and Distance Travelled Function for each cover type.

	Time Spent Function						Distance Travelled Function		
Cover Type	% Captures	% Used	% Available	Total Hours Foraging	# Captures	Capture Rate/Hour	Distance Travelled (km)	Captures per km	Metres to capture
Native Grass	33	31	41	47	37	0.8	151	0.24	4.1
Wetland	2	4	4	6	2	0.4	22	0.09	11.0
Tame Grass	4	3	6	4	4	1.0	15	0.26	3.9
Cropland	28	19	32	29	31	1.1	146	0.21	4.7
Stubble	26	22	15	34	29	0.9	75	0.39	2.6
Roadways	7	21	1	32	8	0.2	49	0.16	6.2

Table 2.5. Results of Energetic Consumption Function. High-energy foraging (HE) includes flying and hovering. Low-energy foraging includes perching and walking. Energy return ratio is acquired:consumed.

Cover Type	Energy Consumption (Kcal)					Net Energy (Kcal)						Energy Return Ratio	
	Fly	Hover	Perch	Walk	Total	Hover	Perch	Walk	HE	LE	HE + LE	HE	LE
Native Grass	61.7	158.8	28.9	9.2	258.6	1191.2	39.1	126.8	833.5	165.9	999.4	4.8	5.3
Wetland	9.2	30.5	0.3	3.5	43.5	59.5	-0.3	-3.5	28.3	-3.8	24.5	1.7	0
Tame Grass	6.6	16.0	3.3	0	25.9	164.0	-3.3	0	113.4	-3.3	110.1	6.0	0
Cropland	46.9	113.0	4.7	22.6	187.3	1012.0	131.3	45.4	690.0	176.7	866.7	5.3	7.5
Stubble	37.6	114.8	7.7	23.6	183.6	1010.2	26.3	78.4	697.6	104.7	802.3	5.6	4.3
Roadways	21.6	48.8	18.6	40.3	129.3	-48.8	117.4	95.7	-70.4	213.1	142.7	0	4.6

Table 2.6. Summary of the rankings of each cover type for each model. The total represents a sum of the rankings, with lower scores reflecting higher model rankings. Log/reg refers to logistic regression. HE refers to high-energy foraging, LE refers to low-energy foraging.

Cover Type	RSF Electivity	CRSF Electivity	PCF Electivity	RSF Log/Reg	CRSF Log/Reg	PCF Log/Reg	TSF	DTF	ECF - HE	ECF - LE	Total
Native Grass	4	5	4	5	5	3	4	3	1	3	37
Wetland	3	6	5	2	6	6	5	6	5	6	50
Tame Grass	6	4	1	6	4	2	2	2	4	5	36
Cropland	5	3	3	3	3	1	1	4	3	2	28
Stubble	2	2	2	1	1	5	3	1	2	4	23
Roadways	1	1	6	4	2	4	6	5	6	1	36

Table 2.7. Breakdown of average hourly foraging behaviours for each cover type, as well as the number of captures resulting from each behaviour. High-energy (HE) includes flying and hovering, and low-energy (LE) includes perching and walking. Ratio is LE:HE for minutes, and the reverse for captures.

Cover Type	Fly	Hover	Perch	Walking	HE	LE	Captures/Hour	Ratio	
Native Grass	9	16	30	5	26	34	1.09	1.33	Minutes
	-	0.91	0.06	0.12	0.91	0.18		5.18	Captures
Wetland	13	28	3	16	41	19	0.54	0.46	Minutes
		0.54	0.00	0.00	0.54	0.00		0.00	Captures
Tame Grass	10	16	34	0	26	34	1.17	1.29	Minutes
		1.17	0.00	0.00	1.17	0.00		0.00	Captures
Cropland	12	20	8	20	32	28	1.56	0.87	Minutes
		1.26	0.20	0.10	1.26	0.30		4.17	Captures
Stubble	9	19	13	19	28	32	1.37	1.14	Minutes
		1.18	0.05	0.14	1.18	0.19		6.25	Captures
Roadways	4	6	24	26	10	50	0.29	4.77	Minutes
		0.00	0.15	0.15	0.00	0.29		0.00	Captures

Table 2.8. Comparative results of cover type rankings for Resource Selection Function, Capture Resource Selection Function and Prey Capture Function based on electivity models and odds ratios as reported by the logistic regression models

Cover Type	Electivity	Ranking	Odds Ratio	Ranking
Resource Selection Function				
Native Grass	-0.09	4	1.00	5
Wetland	-0.05	3	2.41	2
Tame Grass	-0.37	6	0.97	6
Crop	-0.11	5	2.38	3
Stubble	0.05	2	6.20	1
Roadways	0.87	1	1.89	4
Capture Resource Selection Function				
Native Grass	-0.18	5	1.00	5
Wetland	-0.33	6	0.76	6
Tame Grass	-0.16	4	1.18	4
Crop	-0.07	3	1.36	3
Stubble	0.35	2	3.74	1
Roadways	0.60	1	1.41	2
Prey Capture Function				
Native Grass	-0.04	4	1.00	3
Wetland	-0.21	5	0.20	6
Tame Grass	0.29	1	1.01	2
Crop	0.07	3	1.04	1
Stubble	0.26	2	0.84	5
Roadways	-0.64	6	0.84	4

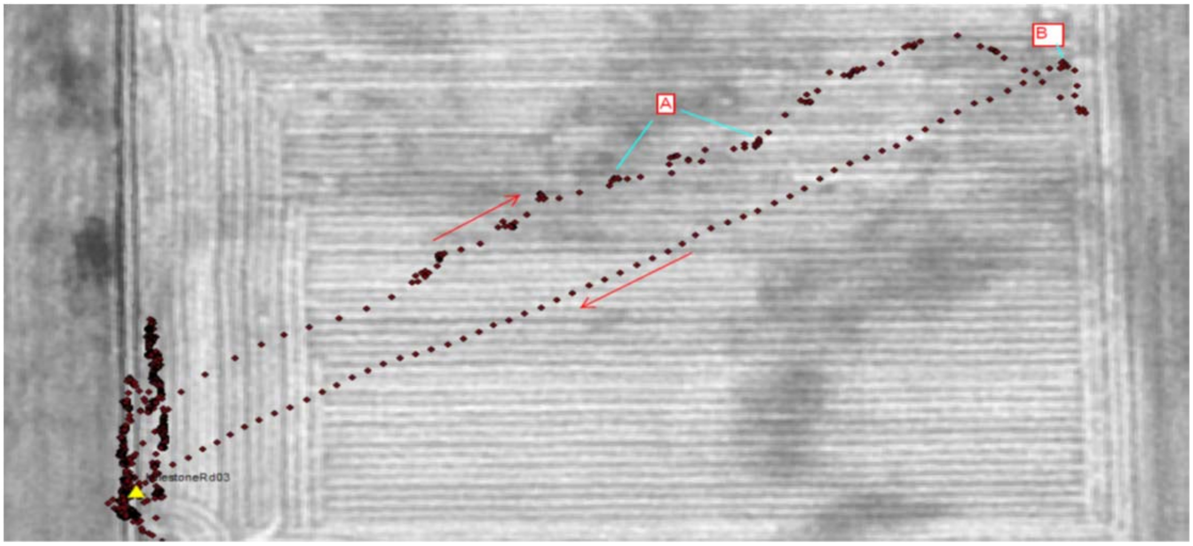

Figure 2.1. Flight path of foraging burrowing owl showing examples of hovering clusters (A) and the prey capture site (B). Red dots represent movement locations and the yellow triangle represents the nest. Red arrows indicate direction of travel. The movement locations are overlaid onto satellite imagery.

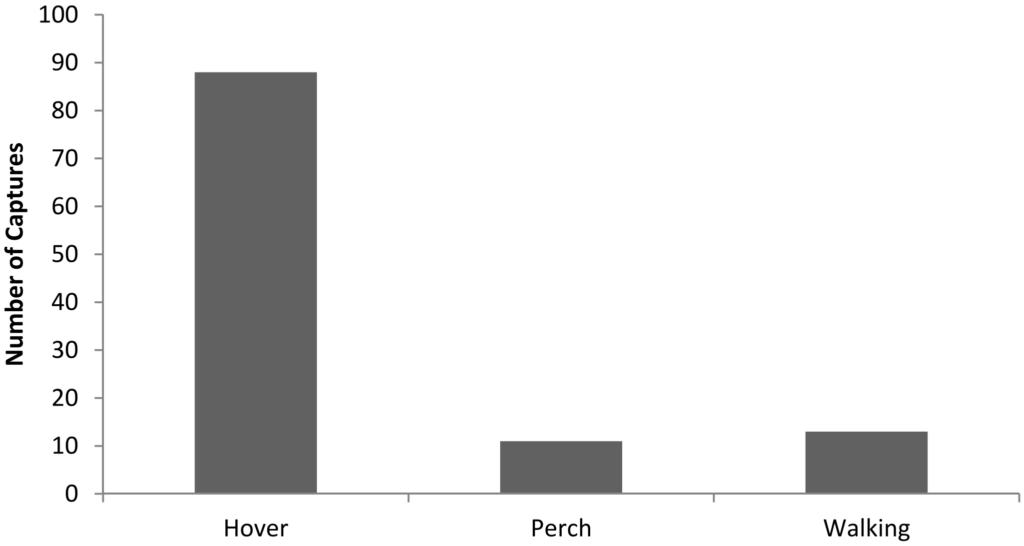

Figure 2.2. Total number of prey captures for each foraging method.

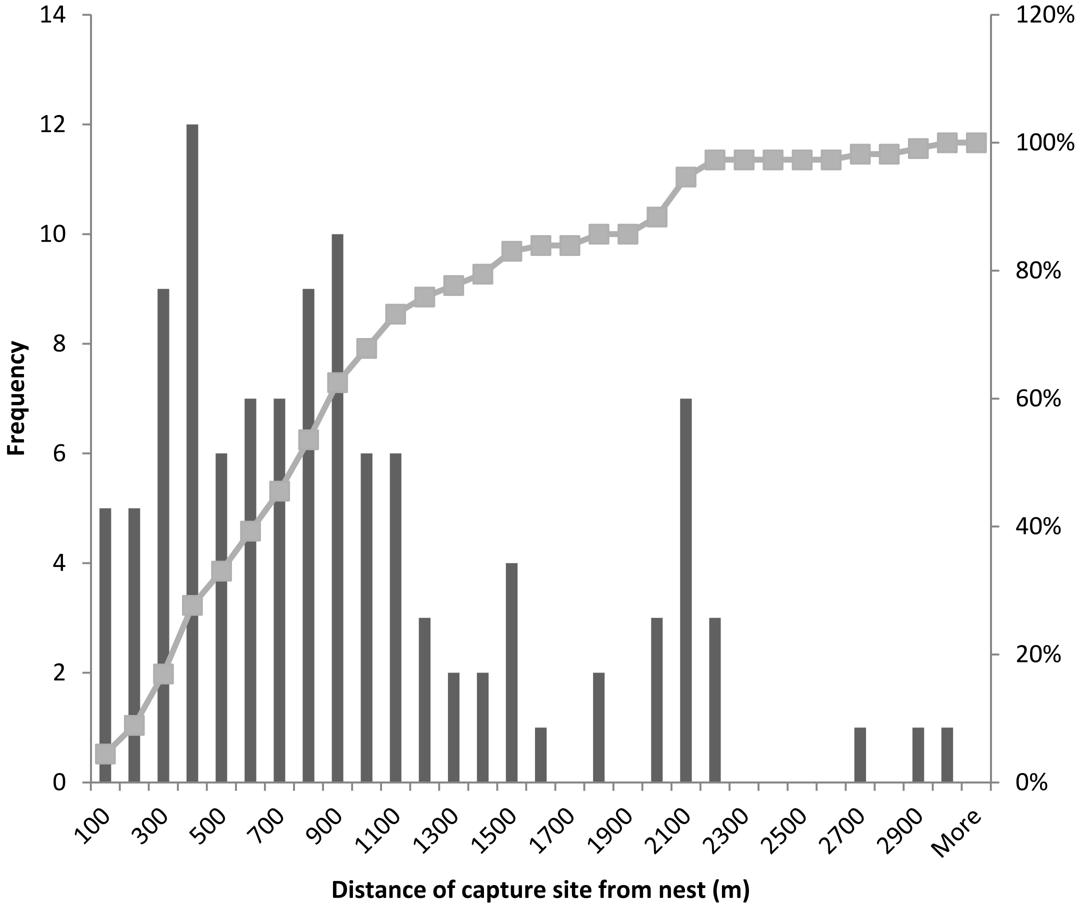

Figure 2.3. Distance from capture site to the nest. The boxed line represents the cumulative percentage of captures at each distance bin.

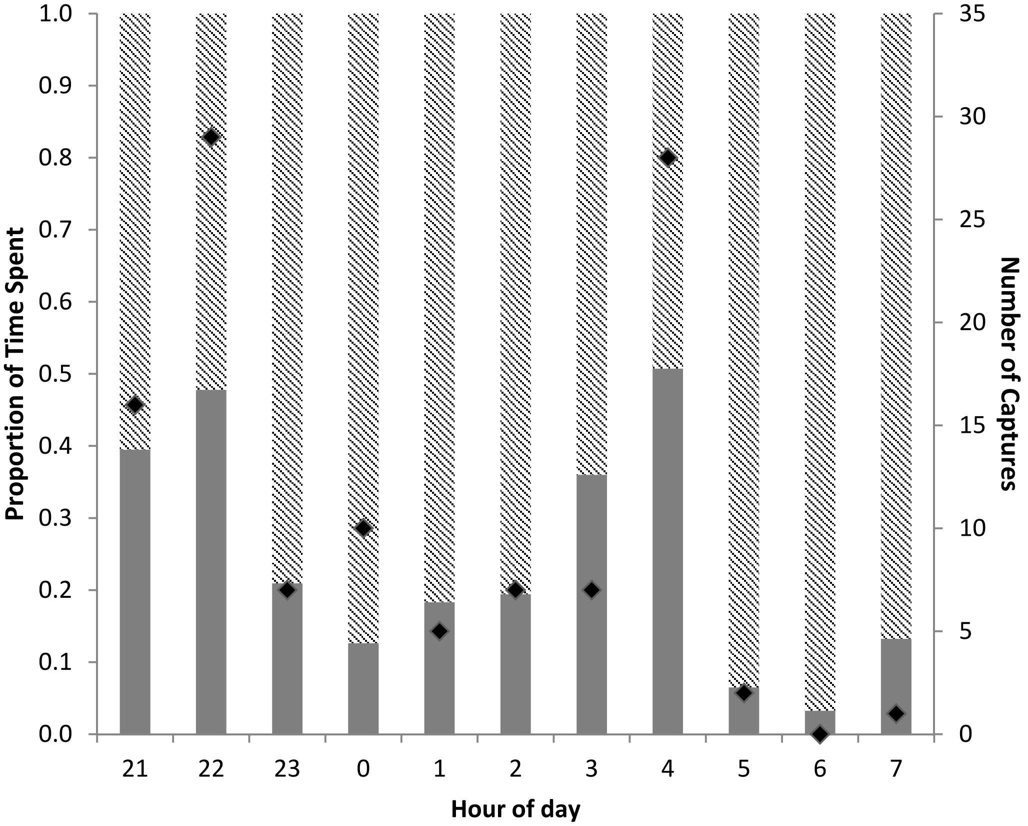

Figure 2.4. Proportions of high-energy (solid) and low-energy (hatched) foraging behaviours, as well as the total number of prey captures (diamonds) per hour of nocturnal foraging. Hours are recorded using a 24-hour clock. High-energy foraging consists of flying and hovering. Low-energy foraging consists of perching and walking.

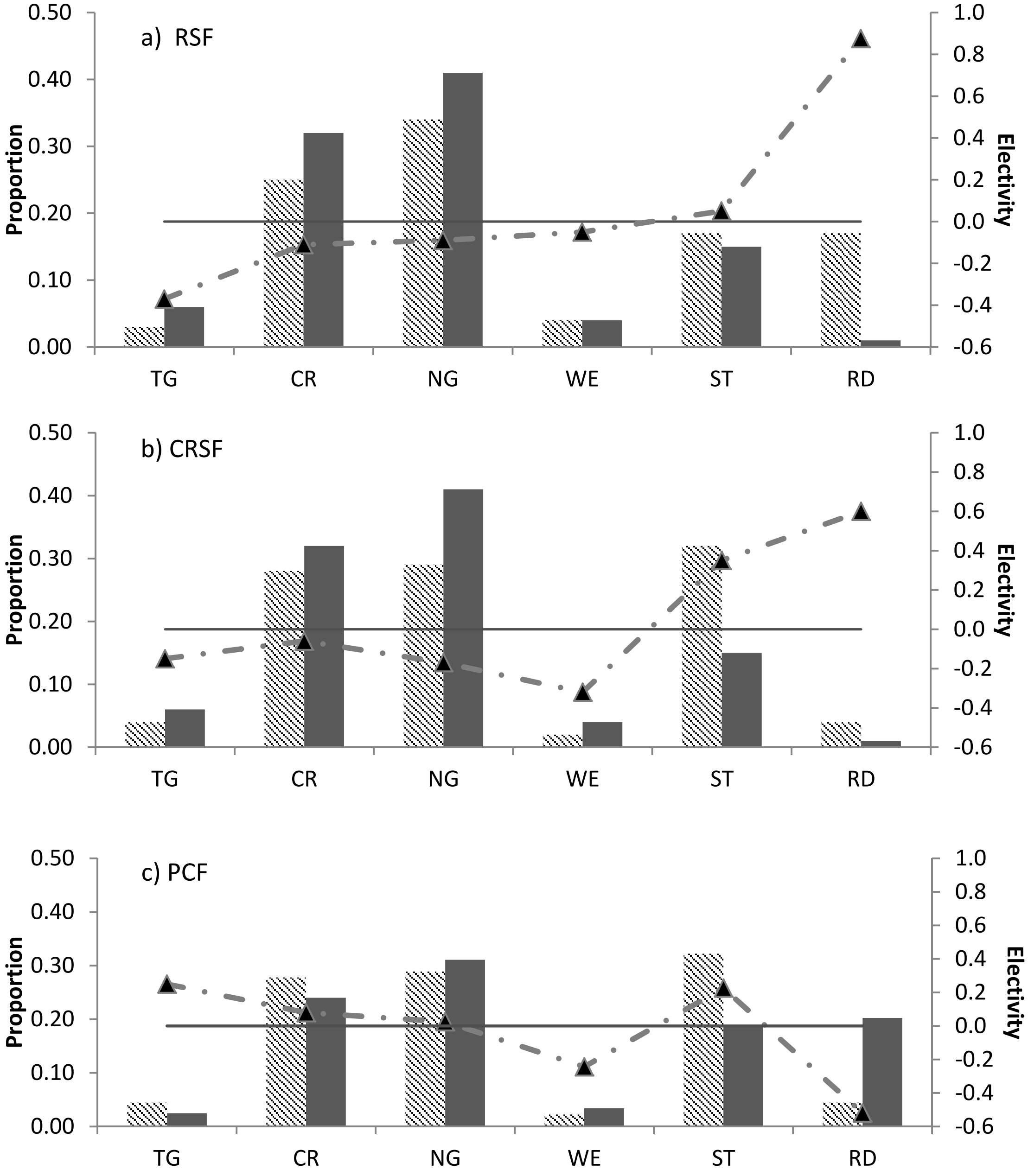

Figure 2.5. Proportions of use (hatched columns) and availability (solid columns), and electivity scores (dark triangles) for each land-cover type for the a) Resource Selection Function, b) Capture Resource Selection Function and c) Prey Capture Function. Electivity scores >0 (solid horizontal line) indicate selection, whereas scores <0 indicate avoidance. TG=Tame Grass, CR=Cropland, NG=Native Grass, WE=Wetland, ST=Stubble, RD=Roadways.

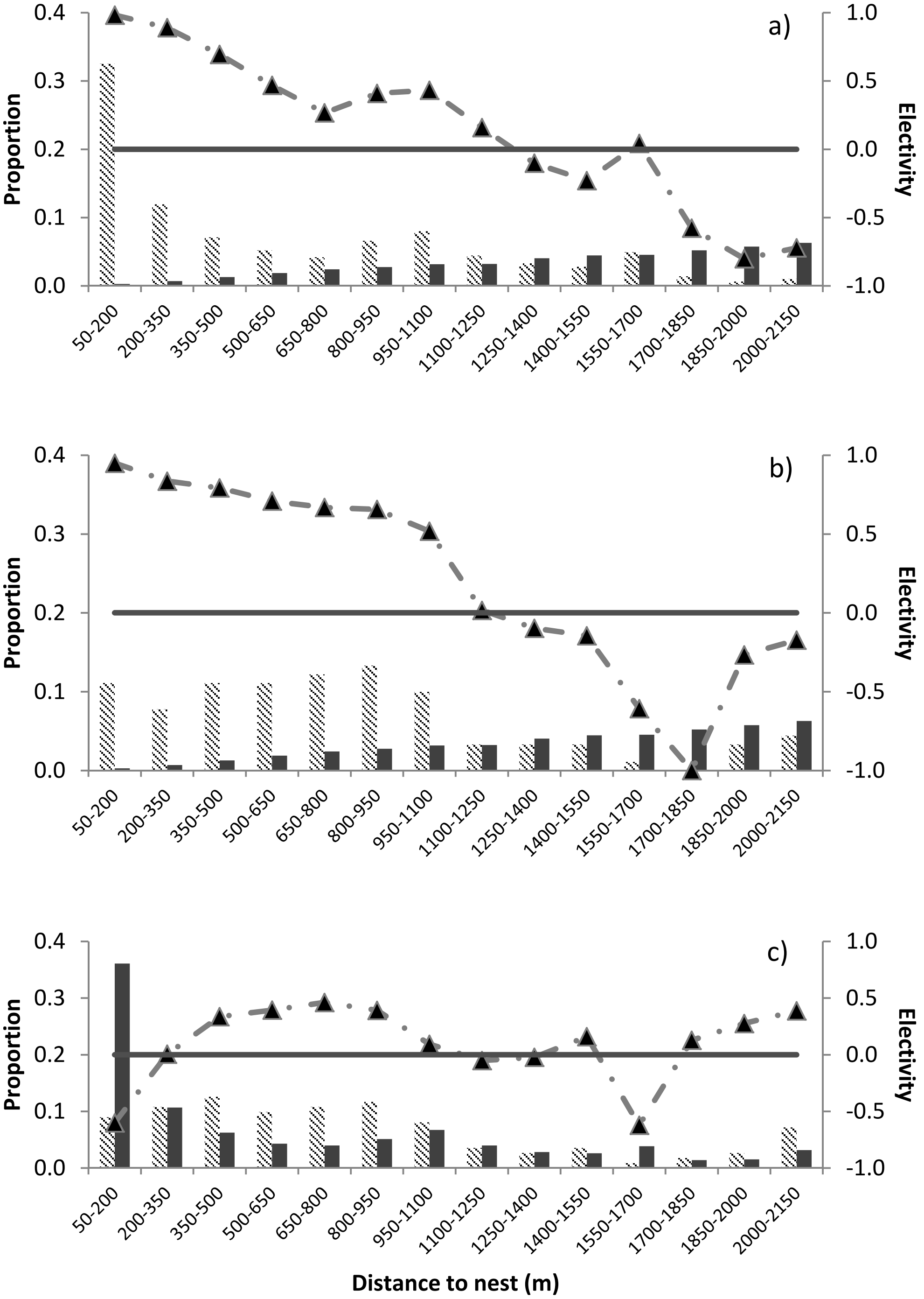

Figure 2.6. Proportions of use (hatched columns) and availability (solid columns), and electivity scores (dark triangles) for distance-bin relative to the nest for the a) Resource Selection Function, b) Capture Resource Selection Function and c) Prey Capture Function. Electivity scores of >0 (solid horizontal line) indicate selection, whereas scores <0 indicate avoidance.

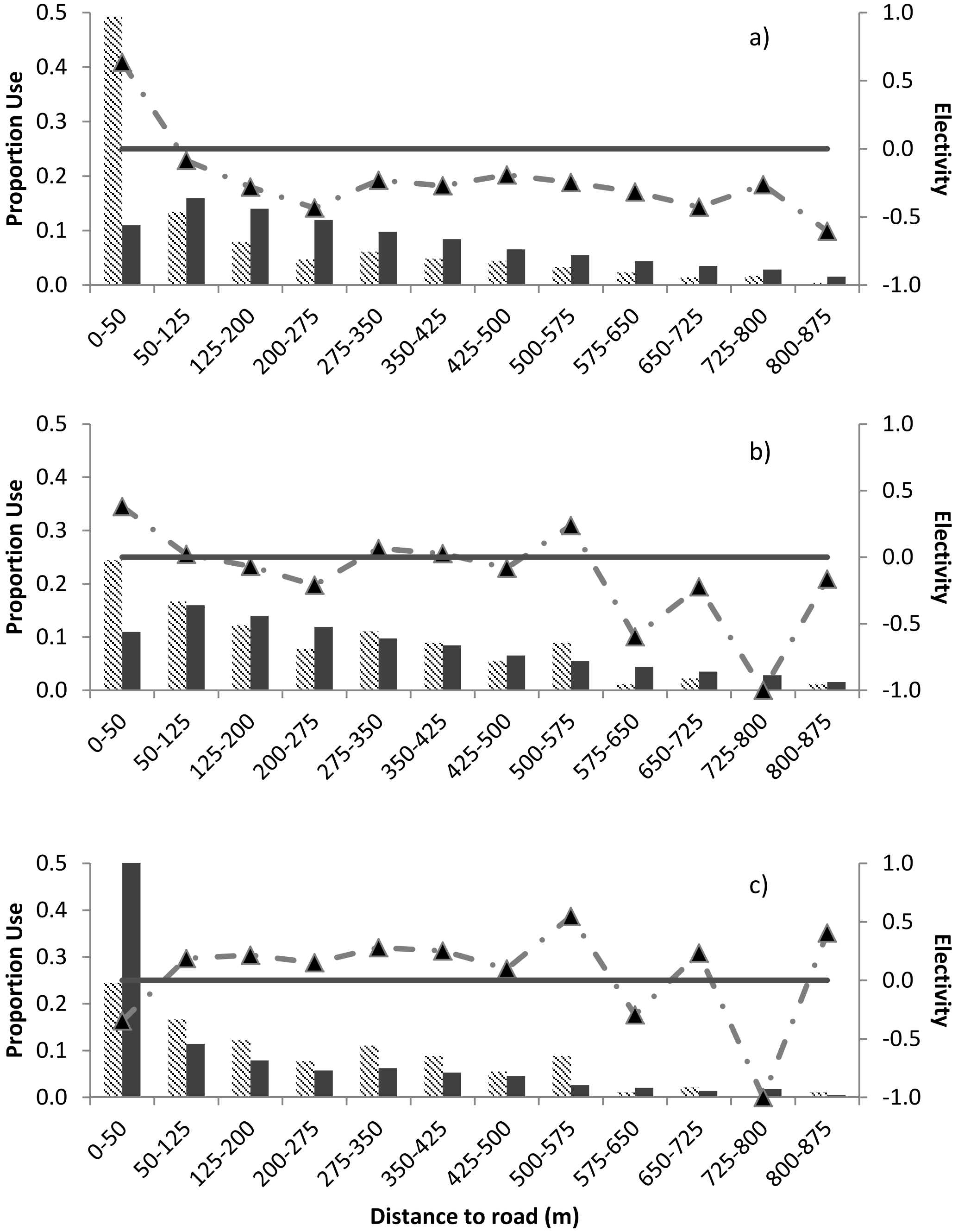

Figure 2.7. Proportions of use (hatched columns) and availability (solid columns), and electivity scores (dark triangles) for distance-bin relative to the nearest road for the a) Resource Selection Function, b) Capture Resource Selection Function and c) Prey Capture Function. Electivity scores of >0 (solid horizontal line) indicate selection, whereas scores <0 indicate avoidance.

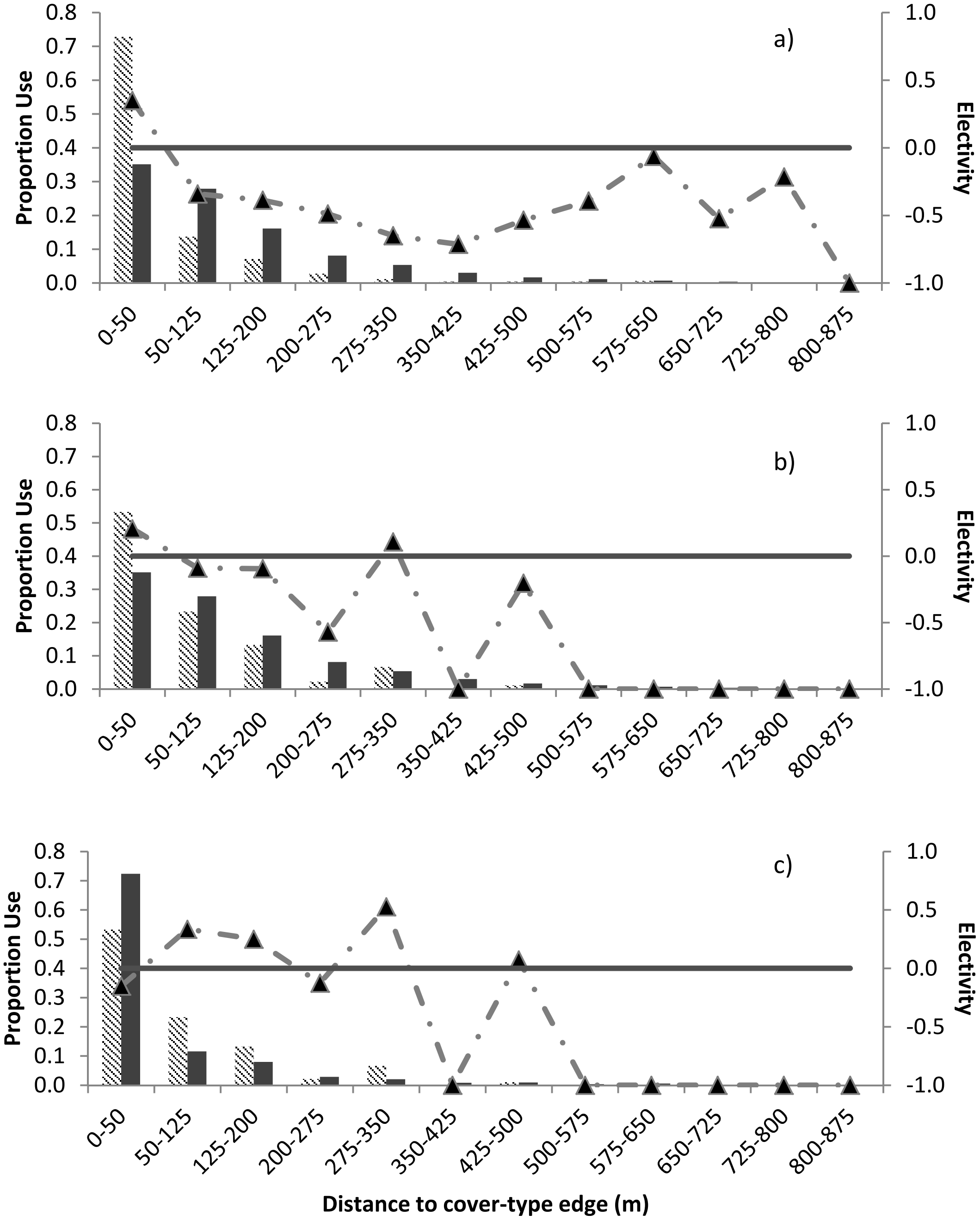

Figure 2.8. Proportions of use (hatched columns) and availability (solid columns), and electivity scores (dark triangles) for distance-bin relative to the nearest cover type edge for the a) Resource Selection Function, b) Capture Resource Selection Function and c) Prey Capture Function. Electivity scores of >0 (solid horizontal line) indicate selection, whereas scores <0 indicate avoidance.

Chapter 3: The influence of vegetation on Burrowing Owl nocturnal foraging behaviours and successful vertebrate prey capture

3.1. Introduction

The study of habitat selection has a long history (Rosenzweig 1991). Most studies of avian habitat selection have identified the environmental conditions for locations in which individuals of a species place their territories or home ranges relative to the environmental conditions available to the entire population (2nd order selection; Johnson 1980). However, recent technological advances in monitoring the movement of individuals have allowed ecologists to place more emphasis on understanding 3rd order selection. Combined with increasing availability of remote sensing data that describes general environmental conditions (i.e., vegetation type, soil type, terrain ruggedness), 3rd order studies have improved our understanding of what animals select (use more than available) versus avoid (use less than available) within their home range. A limitation of most 3rd order studies is that the underlying mechanisms causing animals to select or avoid certain environmental conditions are not determined (Rousseau et al., 2010).

Foraging success is often a good predictor of reproductive success and/or survival of birds, particularly raptors (Bechard 1982; Korpimaki and Wiehn 1988; Wellicome 2000). Understanding the environmental conditions that are associated with successful prey acquisition is crucial to understanding habitat selection. Knowledge of how environmental conditions influence raptor foraging is limited in some species by their nocturnal habits, which preclude direct observation. Most studies on foraging by cryptic animals have used spatially inaccurate VHF radio-telemetry data and coarse-level descriptions of environmental variation, which limits our ability to measure whether prey was actually captured or determine the exact scale at which selection is occurring. To fully understand 3rd order habitat selection requires spatially accurate locations and detailed assessment of the environmental conditions where individuals search, attempt to capture, and ultimately acquire prey. Such a fine-scale quantification of 3rd-order selection is more difficult to obtain, but are likely crucial for understanding patterns observed at coarser scales of selection.

The Burrowing Owl (*Athene cunicularia*) is a fossorial owl associated with grassland ecosystems in prairie Canada. The reproductive success of Burrowing Owls tends to be limited by the abundance and/or availability of food, primarily in the form of small mammal prey captured at night (Wellicome 2000; Poulin and Todd 2006). A previous study of habitat selection within home ranges occurring in native grasslands of Alberta concluded Burrowing Owls "select" for areas of higher prey density (Sissons 2003). Sissons (2003) based his conclusions on the fact that the approximate points (obtained via triangulation using VHF telemetry) where individuals were found within their nocturnal home range had higher Robel pole scores than random points. Higher Robel scores indicate taller and denser vegetation which has been correlated with increased relative abundance of small mammals within prairie ecosystems (Poulin 2003; Sissons 2003; Hennin 2010). However, studies of foraging raptors that can be tracked individually have observed exact foraging locations and found individuals spending more time in areas with lower vegetation density or plant cover (Wakely 1978, Bechard 1982, Chipman et al. 2008). Tall and dense vegetation may negatively affect foraging success by preventing detection of prey items, either visually or acoustically, or by creating a physical barrier that limits a raptor's ability to capture prey.

Understanding habitat selection at all levels is particularly important for Burrowing Owls as they are classified as endangered in Canada (COSEWIC 2006). Current recovery plans hypothesize creation of extensive areas of prairie with tall grasses as one of the conservation actions that would most benefit the foraging success of the species despite limited understanding of their fine-scale hunting patterns. Burrowing Owls likely use sight more than sound when foraging for vertebrates, as suggested by the reduced facial disk when compared with other owl species (Marti 1969). As well, Burrowing Owls likely experience a reduced ability to hear prey when engaged in a highly-active method of foraging such as hover-hunting (Andersson 1978), which is their primary method of foraging for vertebrates (Chapter II). Therefore, I focused exclusively on quantifying how vegetative structure might influence visual detection of prey.

My overall objective was to evaluate whether nocturnally foraging Burrowing Owls select areas where prey are more abundant or where prey are more likely to be captured. Specifically, I tested whether local vegetation structure where Burrowing Owls travelled, searched for prey, or captured prey, differed between each other and random locations within owl home ranges. My main assumption was areas with tall and dense vegetation had higher small mammal abundances but prey may be more difficult to detect or capture. Conversely, I assumed areas with shorter and sparser vegetation have less prey but that prey was more available to be captured.

3.2. Methods

3.2.1. Monitoring foraging paths

I studied the crepuscular/nocturnal foraging behaviour of male Burrowing Owls across southern Saskatchewan and Alberta, during the months of June and July, in 2009 and 2010. To evaluate nocturnal foraging paths I used GPS dataloggers that recorded locations at an interval of 1 fix per 2 seconds from 21:00 to 07:00 which includes peak periods of movement (Haug and Oliphant 1990) and prey capture (Poulin & Todd 2006). The datalogger records a 3-dimensional location (latitude, longitude, and altitude), speed, angle of 2-dimensional movement, and degree of precision. Accuracy of the logger is very high, with 95% of all locations falling within 4.2m when recorded for 24-hours in a fixed position (Technosmart Operating Manual 2007).

Each male Burrowing Owl typically had to be captured twice. First, I captured males with chicks between 7 and 20 days post-hatch to minimize nest abandonment and maximize male-capture success. Males were trapped at nests or known roosts using either bow-nets or one-way-door, walk-in traps (Winchell 1999). Typically, a dead mouse or bird was placed within the trap to attract the owl. I also buried a wildlife caller nearby that played a male Burrowing Owl calling sound. The volume of the caller was kept low to reduce the likelihood of attracting, or disturbing, the female. Once caught, males were weighed and given an aluminum Fish and Wildlife band and a datalogger. Dataloggers were attached as a backpack using half-weave Teflon ribbon. Teflon was secured to the datalogger with light-weight packing tape containing a tear-proof fiberglass cross-weave. As a precaution after handling, males were then returned to their nest burrows where they could recover from handling once dataloggers were attached. Where possible, owls were captured a second time, approximately 3-4 days later, to remove the datalogger and retrieve spatial data. Trapping did not exceed 2 hours for either session, and two dead mice were left in the burrow mouth to offset any lack of foraging that may have been caused by trapping and handling. Occasionally, owls forcibly removed the dataloggers; some of these units were recovered fortuitously, or through searches, near nest or roost burrows.

3.2.2.Determining foraging success

Though the dataloggers provided an exact movement path for approximately 2 nights, they did not indicate if owls had captured prey. To determine if prey were captured I concurrently positioned Digital Video Recorders (DVRs) at each nest burrow. A security-style DVR powered by four 6-volt deep-cycle marine batteries ran two infra-red, waterproof, security cameras. One camera was placed at the burrow mouth, opposite the mound, permitting an unobstructed view of delivered prey as owls tend to carry prey in front of their bodies as they enter the burrow. The second camera was placed approximately 1 meter from the burrow, filming "over-the-shoulder" of the first camera. This camera functioned as a backup in case an accurate identification could not be made on the first camera, and to detect prey deliveries occurring just off the mound. The DVR records a date and time stamp on the screen that was synchronized exactly with the time recorded on the data-logger.

DVR footage provided a record of the exact time of all prey deliveries occurring during the time when data-loggers recorded owl movement. For each recorded delivery, I used a GIS program (ArcMap) to look at the movement data of the male prior to each delivery to the nest. The first step was to determine if the prey delivery captured on video included the male. I then examined the movement path for the ten minutes prior to the delivery of prey at the nest. Specifically, I looked for clusters of points that preceded a direct flight to the nest that led to a prey delivery, hereafter termed capture cluster. The location within the cluster immediately preceding flight was considered the capture site. Prey items that I suspected the male transferred to the female off-camera were included if the male returned to the nest but did not appear on camera and the female flew out of view for <15 seconds and returned with prey. I assumed the female did not have time to catch the prey and thus attributed the capture to the male. Deliveries occurring when the male was not present at the nest were not included, nor were those preceded by the male's presence at a known roost. Males routinely cache prey in roost burrows, and as such, these deliveries may have been cache retrievals, not prey captures.

I identified each prey item to species with as much specificity as possible from the DVR footage. Because Burrowing Owls carry prey in their beaks as they enter the burrow, an unobstructed view of the prey was common. However, occasionally moisture or debris on the camera lens made identification to species impossible. In these instances, the prey item was assigned to broader categories, such as "mouse" or "small mammal" or in very small number of cases, "vertebrate". All of these deliveries are included in the analysis because I was confident the item was not an invertebrate. The majority of Burrowing Owl prey deliveries to nests are vertebrates by biomass, (Poulin and Todd 2006) and were therefore the focus of this study.

3.2.3. Evaluating vegetation conditions along the foraging path

I visited all capture sites recorded for each owl. I also visited 20 fly points per owl. At fly points owls were moving in a relatively straight line at a constant speed. I assume owls were hunting but had not detected prey. I also visited 20 locations where owls hovered. Hover points were clusters of points where owls moved at slow speeds and maintained a relatively constant altitude. Hover points did not result in prey being delivered to the nest. I assume owls had detected prey or were actively searching for prey but were not successful in capturing prey. Finally, I sampled locations that were randomly generated within a 3 km radius of each owl's nest. Although the total number of random points within each owl's home range differed among owls, the number of random points for an individual owl equalled its total used (i.e., hover, flight and capture) points. I navigated to each type of location using a handheld GPS that was accurate to 5 metres. At each location, a Robel pole measurement was taken to estimate a visual obstruction index based on the height and density of the vegetation (Robel 1979). Measurements were taken in the 4 cardinal directions and averaged. The Robel pole was marked in five cm intervals, and I recorded the highest interval that was obstructed. To estimate how vegetation might obstruct an owl's ability to view small mammal prey from above, I also measured the percentage of exposed ground (hereafter PEG) within a 5m radius of each location. Measurements consisted of a visual approximation of the percent-area of exposed ground in each of the four cardinal directions and were averaged for each point. Exposed ground includes not only bare soil, but ground covered by lichens, which offers no structural concealment for small mammals. While I found my Robel scores were correlated with my PEG measurements (Spearman's rho = -0.3449, $P<0.001$), I contend the former better describes visibility on an angle. When hovering, Burrowing Owls may be more likely to look straight down. Vegetation measurements were conducted within two weeks of recording the owl's position. No harvesting of crops or haying occurred during the time the position was recorded and the vegetation data collected. Grazing may have occurred but could not have been quantified. As my goal was to measure the influence of vegetative structure on foraging, points occurring on the surface of roads were not included.

3.2.4. Statistical Analyses

The Robel pole measures in 5 cm increments and if no vegetation obscures the entire 5-cm interval a score of zero is assigned. I had a high proportion of "zeroes" (38% of total). Evaluation of histograms before and after transformation indicated that Robel scores could not be normalized. Therefore, I conducted two separate analyses. First, I evaluated if the likelihood

of a Robel score of zero versus any other value differed between owl locations and random points using a generalized linear mixed model with a binary error family and logit link.
I then analyzed the Robel data with the zeroes removed. These data were treated as unbalanced two-dimensional panel data, and I constructed two models: in the first I used a generalized estimating equation with a Gaussian family and a log link; in the second, I ln-transformed the data, then performed a generalized least squares regression. For PEG, I also ran two models that were identical to those used on the Robel scores, except PEG measurements were logit transformed. I then created an index to examine if Burrowing Owls select for areas with higher PEG given similar Robel scores. To do this, I divided Robel measurements by PEG scores. Areas with low Robel and high PEG scores tend to have low index values, as a PEG score of 10%, for example, is represented by "10", rather than "0.1". In 2010, significant amounts of rainfall limited data collection. I tested for differences in my vegetation measurements between 2009 and 2010 using generalized least squares regression.

Individual birds were treated as random intercepts in all models. All statistical analyses were performed using STATA 9.2 (STATACorp 2007) and significance was set as $p \leq 0.05$.

3.3. Results

During 2009 and 2010, I quantified Robel and PEG values at 91 locations where prey were acquired, 271 fly locations, 263 hover locations, and 857 random locations. Overall, 70% of the data were collected in 2010 and 30% in 2009.

Neither Robel nor PEG measurements were statistically different between years (Robel – p=0.096; PEG – p=0.872). Locations used by owls were significantly more likely to have a Robel score of zero than random sites (OR=0.587; SE= 0.065; z=-4.79; p=0.000). Further, where

Robel pole scores were greater than zero, they were significantly lower at capture and hover locations, relative to random locations; fly locations, however, were not statistically different from random locations (Table 3.1). Relative to native grass, only cropland showed statistically higher Robel pole scores at all locations, with all other cover types showing no statistical difference (Table 3.1).

Capture, fly and hover locations contained significantly higher PEG, compared to random locations (Table 3.2). Relative to native grass, all land-cover type categories contain significantly higher PEG (Table 3.2).

Capture and hover locations had significantly lower Robel:PEG indices than random locations, whereas fly locations were not statistically different from random locations (Table 3.3). Tame grass and stubble had lower Robel:PEG ratios relative to native grass, while wetlands and cropland were not significantly different from native grass (Table 3.3).

3.4. Discussion

3.4.1. Foraging Strategy

When on hover-hunting forays, Burrowing Owls alternate between periods of direct, swift, flight and stationary hovering. Foraging theory for a pause-travel forager states that the animal initiates travel after hovering in order to distance itself from the previously searched location (Andersson 1978). My data suggest the Burrowing Owl may also fly over less-suitable patches where vegetative structure makes prey detection or capture less likely, as “fly” locations show higher Robel pole scores than capture or hover locations (Table 3.1). However, the vegetation at capture and hover locations did not differ. Additionally, where Robel scores between random and foraging locations were similar, the locations where owls hover or capture prey will tend to have higher percentages of exposed ground (Table 3.3). Consequently, the owl's strategy seems to be to fly over patches that offer less access to prey, hover when the vegetative structure indicates prey detection may be high, and capture prey when it is present. This does not imply that prey presence always results in a capture; rather the patterns suggest that Burrowing Owls hover over suitable patches and wait for prey detection, rather than hovering after prey is detected, although the latter may occur as well.

Burrowing Owls do not seem to forage simply where vegetation permits prey capture. The PEG scores for capture and hover sites in native grass are lower than the average random PEG scores for all other land-cover types (Table 3.3). Therefore, the Burrowing Owl seems to search for local areas that optimize both detection and capture of prey, relative to the surrounding vegetative conditions. Given that the average owl must travel several kilometers, regardless of the land-cover type, prior to capturing prey (Chapter II), this strategy of searching for local sites that offer relatively higher prey accessibility may optimize owls' chances of detecting and capturing spatially unpredictable prey.

Sissons (2003) concluded Burrowing Owl foraging locations were more likely to have higher Robel pole scores compared to random locations in native grass, and attributed this selection to increased prey abundance. Sissons' (2003) average random Robel score, which included all land-cover types in his study area, was 4.5cm, and the average "foraging" Robel score was 6.4cm. Native uplands, which equate to native grass in my study, predominated Sissons' study area. The average Robel scores for random points and used points in native grass in my study were 10cm and 5cm respectively. It is possible that the uplands in Sissons' study were grazed to the extent that prey were present only in taller remnant patches, requiring the owls to forage where small mammals were present, rather than available. However, Sissons' use of VHF technology, which permits neither the degree of accuracy of the GPS datalogger used here, nor the ability to determine the owl's behaviour at each point, almost ensures that owl locations were likely neither reflective of foraging behaviour, nor the actual foraging location.

Wakely (1978) found Ferruginous Hawks (*Buteo regalis*) were attracted to areas free of cover, similar to the results of my study where Robel pole measurements of “zero” were more likely associated with used points than available points. Further, Garratt et al., (2011) found kestrels (*Falco tinnunculus*) selected for areas of recently-cut grass as it offered better access to small mammal prey. Preston (1990), however, found red-tailed hawks (*Buteo jamaicensis*) and northern harriers (*Circus cyaneus*) avoided bare ground. Preston (1990) also found that red-tailed hawks responded to a composite of prey density and plant cover density. Although I did not measure the vegetative conditions of the area surrounding the locations used in my study, the pattern of foraging in areas of relatively less obstructive vegetation might indicate that Burrowing Owls exhibit similar patterns, requiring a mix of dense cover (i.e., areas of prey abundance) and sparse cover (i.e., areas of prey accessibility). Indeed, Wakely (1978) found that the small animals typically occupying areas of high accessibility were transients from adjacent areas with more cover.

3.4.2.Management Implications

While my results offer new and unique insight into Burrowing Owl foraging patterns, they do little to explain Burrowing Owl population trends. Mature cropland may be virtually inaccessible to foraging Burrowing Owls later in the breeding season; however, most chicks die from starvation within the first 20 days of the nestling stage (Wellicome 2000). In this study, owls were tracked when their chicks were between 7 and 20 days of age, and adults successfully captured prey in all land-cover types at this time. Consequently, it is difficult to conclude that the vegetative conditions in native or non-native cover types negatively affect Burrowing Owl reproductive success during this critical stage. It is possible that mature cropland forces Burrowing Owls, particularly inexperienced juveniles, to forage more extensively on roadways, increasing the risk of anthropogenic mortality. However, Shyry (2003) and Todd et al., (2003) concluded most juvenile mortality results from avian predation, with starvation and anthropogenic causes contributing relatively little.

Recent conservation efforts in Alberta and Saskatchewan include converting cropland to native grass. The efficacy of this effort with respect to increasing foraging success of Burrowing Owls is not clear. Chapter II illustrated that owls are as, or more, successful at catching prey in cropland or stubble as they are in native grass. Indeed, the results of this chapter indicate that conservation efforts aimed at improving successful foraging may be more easily implemented, and more effective, by ensuring each cover type offers sufficient prey accessibility. However, providing access to mature cropland requires landowner participation, as well as continuous effort and possible financial compensation. Many crop types may become so obstructive that Burrowing Owls likely cannot detect or access prey, whereas ungrazed native grass, which likely represents the most obstructive state, will likely still offer foraging opportunities. Thus, if cropland offers only ephemeral foraging opportunities, increasing amounts of native grass could benefit the owls by providing a more consistent foraging cover type.

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Table 3.1. Random-effects generalized estimating equation comparing Robel pole scores between random and used locations, and between different cover types. Random locations are the behavioural reference category and native grass is the cover type reference category. Both are omitted from the table.

	Variable	**Coef**	**SE**	**z**	***p***
Behaviour	Hover	-0.633	0.263	-2.41	0.016
	Fly	0.037	0.070	0.54	0.592
	Capture	-0.385	0.134	-2.87	0.006
Cover Type	Wetland	0.214	0.226	0.95	0.343
	Tame Grass	-1.933	2.343	-0.83	0.409
	Cropland	0.814	0.202	4.02	0.000
	Stubble	-0.060	0.271	-0.22	0.826

Table 3.2. Random-effects generalized estimating equation comparing percent exposed ground (PEG) between random and used locations, and between different cover types. Random locations are the behavioural reference category and native grass is the cover type reference category. Both are omitted from the table.

	Variable	**Coef**	**SE**	**z**	***p***
Behaviour	Hover	0.174	0.043	3.98	0.000
	Fly	0.066	0.029	2.3	0.021
	Capture	0.188	0.030	6.21	0.000
Cover Type	Wetland	0.409	0.078	5.29	0.000
	Tame Grass	0.723	0.092	7.85	0.000
	Cropland	0.634	0.091	7.69	0.000
	Stubble	0.833	0.091	9.2	0.000

Table 3.3. Random-effects generalized estimating equation comparing the ratio of Robel pole scores to percent exposed ground (PEG) between random and used locations, and between different cover types. Random locations are the behavioural reference category and native grass is the cover type reference category. Both are omitted from the table.

	Variable	Coef	SE	z	*p*
Behaviour	Hover	-0.870	0.202	-4.31	0.000
	Fly	-0.149	0.121	-1.23	0.220
	Capture	-0.665	0.130	-4.95	0.000
Cover Type	Wetland	-0.230	0.235	-0.98	0.329
	Tame Grass	-2.055	0.265	-7.74	0.000
	Cropland	-0.289	0.174	-1.66	0.098
	Stubble	-1.133	0.228	-4.98	0.000

Table 3.4. Average Robel pole, Percent Exposed Ground, and Robel:PEG index scores for random and behavioural points in each land-cover type. Robel pole scores are recorded in centimeters.

	Cover Type	**Random**	**Capture**	**Fly**	**Hover**
Robel Pole	Native Grass	10	5	10	7
	Wetland	12	7	13	8
	Tame Grass	1	1	2	1
	Cropland	23	12	23	15
	Stubble	9	5	10	6
Percent Exposed Ground	Native Grass	12	19	12	16
	Wetland	20	30	21	27
	Tame Grass	37	50	38	47
	Cropland	46	60	48	56
	Stubble	69	79	70	77
Robel:PEG Index	Native Grass	0.5	0.2	0.5	0.3
	Wetland	0.4	0.2	0.4	0.2
	Tame Grass	0.1	0.0	0.1	0.00
	Cropland	0.4	0.2	0.4	0.2
	Stubble	0.2	0.1	0.2	0.1

Chapter 4: GENERAL CONCLUSION

Current management strategies for the Burrowing Owl in Canada are based on research that attempted to quantify selection of land cover types during nocturnal foraging (Haug and Oliphant 1990; Sissons et al., 2001; Sissons 2003). However, these studies relied on technologies and analytical methods which may not accurately identify successful foraging sites, and therefore optimal cover types for foraging, thus the efficacy of conservation efforts were probably compromised.

In this thesis I collected nocturnal movement data that permitted the identification of various foraging behaviours, as well as the precise locations where prey items were captured. Consequently, the patterns of cover type selection I determined reflected true resource acquisition, and did not rely on the behavioural assumptions inherent in previous studies. I was also able to compare these patterns of cover type use with those determined by a coarse-scale approach that mimicked typical techniques used in many habitat selection studies to determine the latter's efficacy in representing prey capture patterns.

In chapter 2, I demonstrated that selection patterns observed when foraging is assumed at each location (i.e., RSF) did not match with those from a model where prey capture was proven at each location (i.e., CRSF). Thus, RSF-style models are likely inaccurate for this species if used to estimate foraging effort and success in each cover type. Burrowing Owls tend to focus much of their foraging around specific hours, and catch the majority of their prey using hover-hunting. However, an owl spends most of its time each night passively foraging or loafing. As a result, most nocturnal locations recorded in prior studies likely represent neither active, nor successful, foraging. It is possible that many other species exhibit similar space-use patterns, where significant amounts of time are spent engaged in non-foraging or unsuccessful foraging behaviours. If so, conclusions regarding habitat selection and optimality are likely incorrect if drawn from a model similar to the RSF implemented in my study.

Also in Chapter 2, I found that using logistic regression models that rank cover types based on use-versus-availability may inadequately identify optimal foraging land-cover types. A more appropriate measure of a habitat's optimality is the prey return received relative to foraging effort. The RSF and CRSF both ranked roads higher than native grass, whereas wetlands were ranked the same as native grass. In contrast, both roadways and wetlands were consistently proven in reward-versus-effort (RVE) models to be the least optimal habitats. Further, the RSF ranked all cover types above native grass, yet the RVE models demonstrate that prey return rates in native grass are comparable to all other cover types, and based on overall net energy gains, outranked all other cover types. Note that cover type rankings are based on prey returns from vertebrate prey only, as it is not possible to identify capture sites of insects from the datalogger data. However, as approximately 95% of the Burrowing Owl diet consists of vertebrates by biomass (Poulin and Todd 2006), it is unlikely that invertebrate prey acquisitions would affect cover type rankings significantly.

In Chapter 3, I examined fine-scale 3rd order selection patterns by measuring the vegetative characteristics at capture sites, as well as at sites where owls were flying or hovering. These used sites were compared to random sites within each owl’s home range. Sissons (2003) analyzed vegetation structure at points used by Burrowing Owls and found higher Robel pole scores than random sites. My results demonstrate the opposite, as owls both hover, and capture prey, where Robel scores and PEG are lower than random locations, a difference that is likely attributable to both the spatial accuracy of my data and the use of proven prey capture sites. Regardless of the land-cover type, Burrowing Owls consistently search for and capture prey in areas where the vegetation is more sparse than average. That is, Burrowing Owls forage for small mammal prey where they are most accessible, but perhaps not most abundant.

Consequently, it may seem counter-intuitive that the meadow vole irruption in 1997 (Wellicome 2000; Sissons et al. 2001; Poulin 2003) would positively affect Burrowing Owls given the owl’s preference for foraging in areas where vegetation is short and sparse, and the vole’s preference for tall, dense vegetation. However, it is possible that small mammal presence in these areas of high susceptibility may depend on high abundances. That is, if small mammal scarcity permits individuals to avoid areas where predators are more likely to detect and catch them, then low small mammal abundances will be reflected in poor foraging success, and ultimately in low reproductive success. Conversely, high small mammal abundances will force some individuals, such as juveniles, into areas where they are more vulnerable to predation (Dickman et al., 1991; Mappes et al., 1993; Meri et al., 2008).

4.1. Management Implications

Grasslands

A grazing regime that encourages small-scale heterogeneity of grass heights is likely to be the most beneficial to Burrowing Owls. While owls seem to search for areas where vegetation is sparse, transforming an entire pasture of native or tame grass to sparse-grass conditions through intensive grazing would likely decimate small mammal numbers, and significantly impact Burrowing Owl reproductive success. Edge et al., (1995) found a 50% decline in vole populations after large-scale mowing. Although little grassland in Canada is mowed, intensive grazing that removes patches of tall, dense vegetation will likely cause similar effects in small mammal populations. Further, vole abundances in Edge et al., (1995) declined in the absence of predation; therefore, the combined effect of mowing or intense grazing and increased predation from raptors will ensure small mammal populations will be lower. Conversely, too little grazing in native or tame pastures may also be detrimental to successful foraging, as the height and density of vegetation will prevent owls from accessing abundant prey. Stocking rates will be of particular importance in years or areas where pastures are of poorer quality, and will require more intensive management.

Cropland

Based on the results of my study, managing cropland early in the nestling stage may not need to take place, as vegetative structure did not prevent successful foraging. However, once mature, cropland will likely impede successful Burrowing Owl foraging, thus land-management will likely require creating small areas where the vegetation is either removed or trampled. Alternatively, narrow strips of land only a few meters wide could be left as stubble. Reducing the size of crop fields, without reducing the amount of crop planted, may be of some benefit as well. In other words, instead of planting crop across an entire ¼-section or section of land, alternating rows of crop and stubble approximately 100-200m wide would permit the same amount of crop to be planted. However, in the alternating-row scenario, a foraging owl would not have to go far to bypass cropland in favour of stubble. Additionally, such a scenario would not likely require additional management, such as trampling. What effect such a configuration would have on small mammal populations, is unknown. Further, the response to such recommendations from private landowners who are requested to alter their lands or farming practices in a way that may affect income for the sake of an owl would require some type of financial incentive to be implemented.

Stubble

Prey abundances in stubble are generally unknown, as small-mammal trapping studies analyze stubble and cropland together (Poulin 2003) or do not sample throughout the summer (Sissons et al., 2001). Thus, despite the bounty of food, recently-harvested fields likely offer to small mammals, it is not clear how an area showing no vegetative growth throughout the summer will affect small mammal population trends. Stubble may be the optimal cover type for vertebrate prey early in the breeding season, but its suitability later in the breeding season may diminish. If this is the case, the combination of a loss of stubble and active cropland as foraging cover types late in the summer could result in an average loss of 45% of the prey in the average owl's home-range because of changes in prey availability (Chapter II). Consequently, intra-seasonal trends of small mammal abundances in stubble should be investigated. However, I feel that increasing the amount of stubble available to a foraging owl, through the alternating-row scenario presented above, will have positive benefits on successful foraging.

Roads

Roads occupy only 1% of the average home range, yet Burrowing Owls spent approximately 17% of their time in this cover type. Although some vertebrate prey was caught on roads, the reward relative to the amount of time spent was the lowest among all cover types. Much of the time spent on roads appears to be walking or resting. Before efforts can be made to mitigate road use by Burrowing Owls, it is necessary to better understand their activities in this habitat. Adults may be feeding themselves when on roads because of higher insect availability (abundance and accessibility). If so, it may be necessary to mimic these conditions in safer cover types to minimize mortality. Further, juvenile owls would likely display similar foraging patterns, given their dependence on insect prey as they begin to forage themselves (Shyry 2003).

The focus on roads may, in part, stem from the abundance of prey often found in tall-grass ditches (Wellicome 2000; Sissons et al. 2001, Poulin 2003). As ditches themselves may not offer foraging opportunities due to the density of the vegetation, Burrowing Owls may be focusing on these areas because small mammals may occasionally venture out onto the road surface, which assuredly makes them easy to capture. Consequently, mowing of ditches may facilitate access to prey. However, the amount of available foraging area ditches encompass is very small, thus the amount of vertebrate prey these cover types contribute is likely similarly small. Therefore, the effect that managing ditches will have on the reproductive success of Burrowing Owls across Canada is likely minimal.

4.2. Future Research

The impetus for this study was to further investigate possible effects of non-native land-cover types on the Burrowing Owl population decline. Because much of the Great Plains throughout North America has been converted from native grass to agricultural cover types, the alteration of the conditions in which the Burrowing Owl evolved is often presumed to explain the population decline. Although loss of native grass may affect Burrowing Owls in multiple ways, I wanted to test the hypothesis that this loss reduces the availability of small mammals, which possibly results in fewer prey captures, fewer prey deliveries to the nestlings, fewer fledged chicks, and thus a decreased population.

I have demonstrated that non-native cover types do not impede successful vertebrate-foraging during the nestling stage. However, it is possible that non-native cover types, particularly cropland, impede successful foraging later in the year, but the largest contributor to chick mortality is starvation during the nestling stage (Wellicome 2000; but see Todd et al. 2003), not during the post-fledging stage. Therefore it seems unlikely that the population decline is a result of decreased foraging efficiency or success caused by the presence of non-native land-cover types. However, for a population increase to occur, a sufficient proportion of Burrowing Owl broods must receive enough food in order to survive. It is not known if prey availability is consistently high enough under current land cover configurations to permit this to occur.

Other potential effects of the continent-wide loss of native grass should not be dismissed. Each year, in many areas the majority of agricultural lands are ploughed at least once, effectively removing any burrows produced by fossorial mammals since the previous disturbance. Burrows are necessary for Burrowing Owls during breeding, migration, and over-wintering, and a lack of suitable burrows for nesting or safety from predators will likely have a negative effect on Burrowing Owls at all stages of their migratory cycle. It is also possible that only a fraction of the burrows produced each year by fossorial mammals are suitable for nesting, which makes the annual removal of burrows by ploughing all the more detrimental.

Much of the recent research on Burrowing Owls in Canada began in response to the population decline of the 1990's, which saw the estimated number of owls decline by 90%. However, many of the purported causes of the decline, such as the conversion of native grasslands to non-native cover types, occurred long before the 1980's and 1990's. It seems unlikely that the recent population trend is the result of processes that occurred gradually and long before the decline. More likely, more acute causes of mortality are responsible for such a precipitous drop in numbers. For example, the widespread of use of a multitude of highly toxic pesticides across North America in the 1980's and 1990's could very easily contribute to such a sharp drop in numbers, and future research on the Burrowing Owl should investigate such potential causal factors.

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