

**THE EFFECTS OF LANDSCAPE COMPOSITION AND
CONFIGURATION ON BARN OWL (*TYTO ALBA*)
DISTRIBUTION, DIET AND PRODUCTIVITY IN THE
FRASER VALLEY, BRITISH COLUMBIA**

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the Department of Biological Sciences

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SIMON FRASER UNIVERSITY
Spring 2010

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Abstract

Modern agricultural practices and urban development have altered agricultural landscapes resulting in the loss and degradation of habitat for wildlife. Barn owls are one of many farmland birds experiencing population declines across much of their range. I examined how changes to the agricultural landscape and current landscape composition and configuration have impacted barn owl site occupancy, diet and productivity in the Fraser Valley, B.C. Long-term and current site occupancy was influenced by increases in traffic exposure and the length of highways within their home range. I argue this results because highway traffic increases adult mortality. In contrast, productivity was influenced by the amount of impermeable surface, a pattern mediated by impacts on diet quality (%voles in diet). My work suggests that survival and productivity are influenced by two different aspects of the agricultural landscape, and points to the importance of considering both when managing barn owl habitat.

Keywords: Landscape ecology; distribution; reproductive success; diet, barn owl; urbanization; grassland

Dedication

*To my mum, for her endless support in all my
endeavours*

Acknowledgements

I would like to begin with a huge thank you to my two supervisors, Dr. David Green and Dr. Elsie Krebs. They have been excellent mentors, exercising patience and making themselves available when I needed help and support. I also owe gratitude to the other members of my committee, Dr. John Elliot and Dr. Isabelle Côte, for their valuable expertise and constructive criticisms. I would also like to acknowledge my colleagues from the Centre for Wildlife Ecology who were very supportive throughout my degree and full of suggestions when called upon.

I offer a special thank you to all the field assistants who have helped me in my research: Veronique Connolly, who used her valuable experience to help me during my first field season, and Darwin Ma and Richard Chea, for their enthusiasm in the field and for working diligently to tease apart 1,524 pellets! I also owe gratitude to all the volunteers who pitched in, particularly Sean McCann, Ildiko Szabo and David Cunnington. It was also a great pleasure to work in the field along side fellow SFU grad, Kirstin Webster.

I appreciate the generosity offered me by Lorraine Andrusiak, sharing her data and knowledge on barn owls in the Fraser Valley. I am also thankful to two local organizations, OWL rehab centre and Delta Farmland Wildlife Trust, who both helped me establish contact with land owners. Further, I offer gratitude to all these land owners for letting me on their properties to conduct my research; without their consent this research would not have been possible.

A big thank-you to owl expert and friend Denver Holt, his generosity and enthusiasm, has widened my horizon and knowledge about owls.

Last but not least, I would like to thank my boyfriend Tim, my family and friends for their support, encouragement and putting up with me throughout this process.

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1: General Introduction

The composition and configuration of landscapes are dynamic and change over time as a result of natural and cultural processes (Brandt et al. 2002).

Naturally occurring processes such as succession, wildfires, floods, and climate change, differ in the frequency, intensity and scale at which they operate. Hence certain landscapes are dominated by a higher frequency and intensity of landscape- shaping processes than others. Landscape-level processes will contribute to the spatial patterning of different habitats. Depending on the species' ecology and habitat requirements, this spatial habitat pattern will influence the distribution and abundance of species.

In order to understand the factors impacting the distribution and abundance of species, landscape ecologists frequently examine how patterns of occupancy across the landscape correlate with the composition and configuration of habitats (Lindenmayer and Fischer 2006). While this approach can identify habitat composition and context required for a species to be present, it does not necessarily determine the landscape features required for species persistence. Thus, in order to sustain viable populations, it is also important for landscape ecologists to identify which features of the landscape correlate with breeding success or productivity of a species. An integrated approach examining both species patterns of habitat occupancy and productivity will facilitate the development of effective management strategies.

Three aspects of landscape change are known to negatively impact individual species: habitat degradation, habitat loss, and habitat subdivision and isolation. Habitat degradation is defined as “the slow decline or attrition of habitat suitability” (Lindenmayer and Fischer 2006). This process negatively affects species via declines in food and/or shelter. However, the effects of habitat degradation can be difficult to detect, especially when only examining habitat occupancy. For example, habitat degradation may not be detected in a long-lived species, since it will continue to be observed in the habitat despite the fact that it may have lower productivity. This pattern has been observed in species dependent on cavities for nesting. Reduced cavity availability often due to human activities such as logging and clearing, will reduce breeding, but this impact may not be detected quickly because of long lived individuals in the population continue to be observed in the habitat (Newton 1994).

Habitat loss is simplest to detect at a landscape scale, and habitat loss due to human activities is known to be the primary cause in the decline in species worldwide (Fahrig 2003). The loss of habitat also implies that remaining viable habitat is fragmented into smaller patches with lower levels of connectivity. Living in smaller isolated patches leaves species with multiple challenges. Over the short term, fragmentation may reduce foraging efficiency and increasing home range size (Redpath 1995). Dispersal movements may be restricted across fragmented landscapes due to increased mortality (Matthysen et al. 1995; Banks et al 2004; Stow and Sannucks 2004). Increased isolation will enhance the risk of extinction (Levins 1969).

Birds are an excellent group for examining the effects of habitat-threatening processes, as they generally operate on larger spatial scales than other groups of species. All three aspects of landscape change can potentially negatively impact their breeding and lead to a shorter breeding season, reduced weight of fledglings, and reduced fledging success (Hinsley et al. 1999; Zarette et al. 2000). In addition, landscape change may also alter species interactions by increasing competition for reduced resources between species (Piper et al. 2002), increasing predation and (nest) parasitism, particularly at boundaries of vegetation remnants (Paton 1994; Robinson et al. 1995; Lahti 2001), or disrupting mutualistic interactions (Cordeiro and Howe 2003).

Within the last century, humans have had a major impact on landscapes (Lindenmayer and Fischer 2006). The pattern of human modification of the landscape is non-random, and in the majority of cases the most productive landscapes are modified first. Original habitat patches are therefore found in less productive and more inhospitable terrain, often at higher elevations and on steeper gradients, with lowland and coastal areas converted to agricultural production (Landsberg 1999; Daily 2001) and urbanization (Luck et al. 2004)

Habitat conversion has particularly impacted grassland habitats. Currently, ~ 90% of grassland in developed countries has been lost to due agriculture and urbanization (Earthtrends 2009). Human population growth has catalyzed two major shifts in the agricultural landscape: increased homogeneity (Benton et al. 2003) and the total loss of agricultural landscape due to urbanization (Theobald 2001). Homogeneity, both on spatial and temporal

scales, is a result of agricultural intensification (i.e. use of agrochemicals, modernized machinery) reducing the structural complexity of agricultural landscapes, resulting in large, heavily utilized, monoculture fields (Fuller 1995; Krebs et al. 1999; Wilson et al. 2005). Urbanization has led to the direct loss of the agricultural landscape, but also degrades and subdivides the remaining agricultural landscape into smaller patches due to infrastructure development, housing and industrial complexes (Underhill and Angold 2000; Forman et al. 2003; Filippi-Codaccioni et al. 2008). Both agricultural intensification and the overall loss of habitat due to urbanization have been implicated in the declines in range and abundance of many birds associated with the agricultural landscape (Fuller et al. 1995; Krebs et al. 1999; Peterjohn 2003; Brennan and Kuvlesky 2005; Donald et al. 2006; Filippi-Codaccioni et al. 2008).

The barn owl (*Tyto alba*) is one of the affected farmland birds, closely associated with agriculture for centuries and globally distributed. However, over the last 25 years, range contractions and population declines of barn owls have been documented in both North America and Western Europe (Colvin 1985; Toms et al. 2001). Barn owls are limited in their ranges by colder temperatures (Edwards 1987), thus, southern Canada is the northern extent of the species' distribution in North America. In Canada, barn owls occur in two geographically separated populations an eastern population (Ontario), and a western population (British Columbia). The eastern population has been listed as endangered since 1999 (COSEWIC 2001), and in the west, barn owls have been listed as a species of Special Concern since 1983 (COSEWIC 2001). The western population is

predominantly found in south western British Columbia in the Fraser Valley (Campbell et al. 1990). Degradation, loss and fragmentation of the agricultural landscape have been implicated as having a negative influence on barn owl populations in Europe and the US (Colvin 1985; Taylor 1994). The loss of grassland may also change the available prey community (Butet 2001; Aschwanden et al. 2007). In addition, urbanization leads to more highways that fragment the agricultural landscape, and increase the risk of barn owl vehicle collision (Ramsden 2003; Boves 2007). In western Canada the extent to which changes in landscape composition and configuration, and how current landscape features impact barn owl distribution, diet and productivity remain unclear.

In this thesis, I examine how landscape composition and configuration impacts barn owl distribution, diet and productivity. In order to assess how landscape features influences the distribution of barn owls, in Chapter 2, I compare how the current distribution of barn owls has changed in relation to surveys conducted 15 years ago, and examine how changes in landscape features (i.e. grass cover, urban development and traffic volume) over this time period correlate with changes in the distribution of barn owls across the Fraser Valley. In addition, I evaluate which aspects of the current landscape appear to influence whether suitable roost/nest sites are active. Since early European settlement in the 19th Century, the Fraser Valley has mainly consisted of agricultural land, but over the last 35 years the area has undergone considerable land use changes (Boyle 1997). The main trends being a shift from grassland-

associated agriculture (Statistics Canada 2006) and increased urbanization (BC Stats 2007)

The degradation, loss and fragmentation of barn owl habitat can lead to a decline in roost/nest sites, food availability or increased mortality. Together these processes may lead to reduced abundance, as investigated in Chapter 2, or it may reduce successful reproduction (Lindenmayer and Fischer 2006).

Thus, presence alone does not give a clear indication of whether a population is healthy and self-sustaining in the long term, or if the current landscape is so degraded that the population represents a reproductive sink. In order to examine what features of the landscape influences productivity, I assess in Chapter 3 how the current landscape composition and/or configuration impacts barn owl diet and/or productivity, and whether diet quality influences the productivity of nesting barn owls in the Fraser Valley. In Chapter 4, I discuss the relevance of these results for barn owl conservation in the Fraser Valley, presenting a list of management recommendations, and suggestions for future research for how to further elucidate the impacts of landscape fragmentation on barn owl survival and productivity.

2: Effects of Past and Present Land Use Patterns on Site Occupancy and Nesting of the Barn Owl *Tyto alba* in the Fraser Valley, British Columbia, Canada

2.1 Abstract

Population declines of farmland birds over the last two decades have been linked to changes in agricultural practices and urbanization that lead to the loss and fragmentation of grassland habitats. I investigated how changes in grass cover (i.e. hay, pasture, set aside and grassland), urban development and increased exposure to motorised traffic over the last 15 years have influenced the long-term occupancy of roosting and nesting sites and the current distribution of barn owls in the Fraser Valley, British Columbia, Canada. Land use was characterized using data from field surveys, digitized ortho photos and classified data layers. I quantified land cover within a 1 km radius (3 km^2) of potential nesting and breeding sites, since this is the estimated home range of a barn owl. As expected, over the last 15 years there were considerable changes in the land cover surrounding potential nest/roosting sites. Grassland cover declined by 53%, increases in urban development doubled the amount of impermeable surface cover, and traffic exposure on highways increased by 33%. In addition, the numbers of suitable nest/roost sites decreased as old wooden barns or large single standing trees were removed. To assess which landscape variables best predict site occupancy by barn owls, I evaluated models relating landscape

variables to occupancy using Akaike's Information Criterion for small sample sizes (AICc) and Akaike weights. I found that long term occupancy of sites by barn owls was mainly influenced by increases in the traffic exposure on highways, and that the current occupancy of sites by barn owls was predicted primarily by the length of highways within a 1 km radius of a site. Since vehicle collisions are a source of mortality for barn owls, these results suggest that highway mortality may limit the distribution of barn owls in the Fraser Valley, and points to the need for further research investigating the population impacts of highways as well as methods to reduce mortality of barn owls along highways.

2.2 Introduction

Agricultural landscapes provide important habitat for many plant and animal species. Traditional farming practices such as crop rotations and the maintenance of hedgerow and grassy verges produced a structurally varied landscape capable of maintaining levels of biodiversity similar to that of many natural ecosystems (Bignal and McCracken 1996; Altieri 1999). However, changes in agricultural practices over the last 50 years (i.e. use of agrochemicals, modernized machinery) have reduced the structural complexity of agricultural landscapes, resulting in large, heavily utilized, monoculture fields and an overall reduction in the quality of land as habitat for wildlife.

In addition to changes in agricultural practices, in many areas agricultural land has been lost and fragmented due to urbanization and its associated infrastructure (Underhill and Angold 2000; Forman et al 2003). Infrastructure such as roads and railways can negatively impact wildlife due to increased

mortality from collisions with vehicles, restricted access to resources through the barrier effect, or because populations are subdivided and isolated into smaller and more vulnerable fractions (Forman et al. 2003; Jaeger 2005). All these changes have been implicated in the declines both in range and abundance of many species associated with agricultural landscapes (Matson et al. 1997; Söderström et al. 2001; Robinson and Sutherland 2002; Benton et al. 2003; Filippi-Codaccioni et al. 2008).

There is accumulating evidence that farmland birds are particularly sensitive to changes in agricultural practices. In Britain, 86% of farmland birds have shown range contraction over the last 40 years (Fuller et al. 1995). Similar trends have been reported from elsewhere in Europe and North America (Krebs et al. 1999; Peterjohn 2003; Brennan and Kuvlesky 2005; Donald et al. 2006). However, no single factor appears to be responsible for the observed range contractions and population declines. In the case of the corn bunting (*Miliaria calandra*) and the tree sparrow (*Passer montanus*) population declines have been linked to a reduction in winter survival due to loss of a key winter food supply provided by quickly disappearing fallow grain fields (Siriwardena et al. 2002; Wilson et al. 2007). In contrast, lapwing (*Vanellus vanellus*) declines appear to be linked to higher rates of nest predation resulting from increased grazing intensity on marginal grasslands. The reduced cover in intensely grazed fields makes lapwing ground nests more conspicuous and vulnerable to predation (Chamberlain and Crick 2003). The variation in underlying causes for population declines of farmland birds has led some authors to argue that more

species-specific research is required in order to design appropriate conservation measures (Fuller et al. 1995; Peterjohn 2003).

The barn owl (*Tyto alba*) is an iconic farmland bird that for centuries has been associated with humans and agriculture (Bunn et al. 1982). However, barn owls are now experiencing range contractions and declines across their range (Colvin 1985; Toms et al. 2001; Sauer et al. 2008). In Britain, where they have been studied most intensively, their numbers are reported to have dropped by 69% over the last 50 years (Toms et al. 2001). Four factors are argued to have contributed to barn owl population declines. First, the loss of moderate-length grassland over the last 50 years is thought to have decreased small mammal populations and reduced prey availability (Colvin 1984; Taylor 1994). Second, old wooden barns have been converted into inaccessible steel barns and old trees have been removed as part of field enlargement programs, resulting in the loss of nesting/roosting sites (Taylor 1994; Ramsden 1998). Third, the increased urbanization of agricultural areas has increased both the number of roads and traffic volume, and consequently increased barn owl road mortality (Ramsden 2003; Preston and Powers 2006). Finally, second-generation anticoagulant rodenticides, which are more concentrated and toxic, metabolize slower in the liver of targeted rodents, exposing barn owls to the risk of secondary poisoning by consuming rodents with residues of rodenticides (Newton et al. 1991).

Population trends are not well documented in North America, but based on breeding bird surveys the barn owl is thought to be declining by as much as 2% per year in western North America (Sauer et al. 2008). In Canada, the

northern extent of the barn owl's range in North America, the species is currently divided into two populations, an eastern population in Ontario, and a western population in British Columbia (Committee on the Status of Endangered Wildlife in Canada, COSEWIC). Since 1999, the eastern population has been listed as endangered, and since 1983, the western population has been assessed as special concern (COSEWIC 2001). Habitat loss is considered to be major cause of population declines in eastern Canada (Solymár and McCracken 2002).

There is little information on the factors influencing the distribution and abundance of barn owls in British Columbia and potential causes of decline have not been tested. To understand how land use changes may have impacted the distribution of western Canadian barn owls, I evaluate changes in grass cover, urban development and traffic volume in the Fraser Valley over the last 15 years, and assess whether these changes relate to changes in the distribution of barn owls over this period. In addition, I evaluate which aspects of landscape composition and structure appear to influence current occupancy of roosting and nesting sites.

2.3 Methods

Study species

The barn owl is widely distributed in temperate and tropical regions across the globe. In North America the barn owl is widespread in the USA, but their range in Canada is limited by colder climate and snow cover, and the species is primarily found in south-western British Columbia and southern Ontario (Cramp

1985; Snow and Perrins 1998). The historical status of barn owls in Canada is unknown but they were probably always present in small numbers in Ontario and British Columbia. Barn owls likely became more common following European settlement as forests were cleared and replaced with pastures and hay fields, and barns and other structures augmented the availability of nest and roost sites (Solymár and McCracken 2002).

In British Columbia, barn owls are predominantly found in the Fraser River Valley but lower densities are found on south-eastern Vancouver Island, the southern Okanagan Valley and the Creston Valley. Previous monitoring has focused on populations in the Fraser Valley (Andrusiak 1994) and on Vancouver Island (BC Field Ornithologists 2009). In conjunction with the former study (Andrusiak 1994), two programs investigating the use of nest boxes as a management tool for barn owls were undertaken in the Fraser Valley, demonstrating that nestboxes can be used to increase the number of nest and roost sites, and a genetic study, finding less genetic variation in the Fraser Valley population in comparison to other barn owl populations across North America (McLarty 1992). Other research on the barn owl in south-western British Columbia has mainly been confined to pellets studies (Cowan 1942; Dawe et al. 1978; Campbell 1983; Campbell et al. 1987)

Study Site

I monitored barn owls in the municipalities of Delta and Surrey, an area of 681 km² within the Fraser Valley, British Columbia, Canada (49° 8' 0" North, 122° 18' 0" West). The area is bounded by the Fraser River to the north, the US

border to the south, Georgia Strait to the west and the municipality of Langley to the east (Figure 1). This area is of key importance for migratory and residential farmland birds and encompasses important wildlife areas such as the Alaksen National Wildlife Area, Burns Bog and Boundary Bay. Prior to European settlement in the mid-nineteenth century, the floodplain would have been dominated by grassland and low shrub vegetation while higher elevations would have been covered primarily by coniferous forest (North and Teversham 1983). Since European settlement the area has traditionally been used for pasture and hay production, but over the last 35 years agricultural practices like vegetable, berry production and greenhouses have become more prevalent (Statistics Canada 2006). The human population of the Fraser Valley (Metro Vancouver and Fraser Valley Regional District) has increased by 400% since the 1960s (Boyle 1997). This has coincided with the removal of ~ 5000 ha (7.5%) of land from agricultural production in this area since 1974 (Agricultural Land Reserve 2009). Currently, 500 000 people are residing in the municipalities of Delta and Surrey (Statistics Canada 2006).

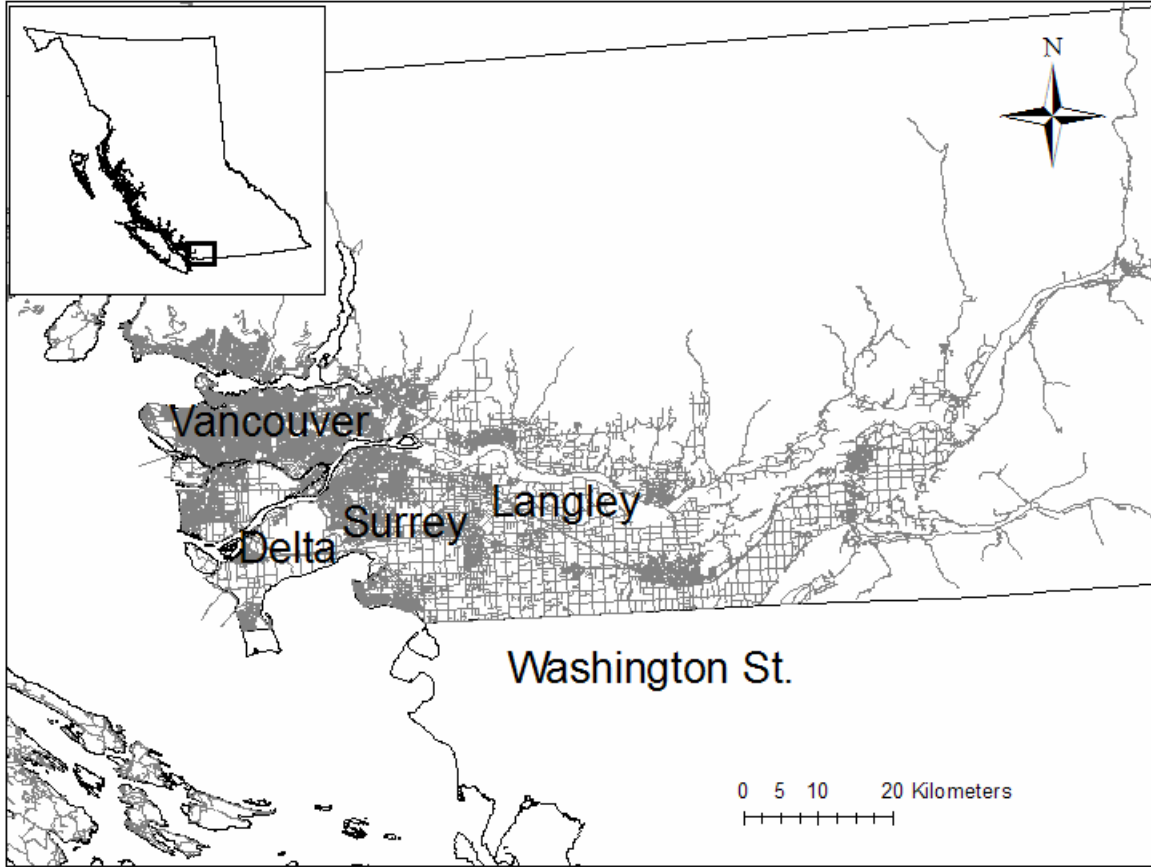


Figure 1 Study area: municipalities of Delta and Surrey, within the Fraser Valley, British Columbia.

Survey Methodology

I surveyed all likely roosting and nesting sites within the study area (Figure 1). This included all sites documented as being occupied in 1990 -1992 (Andrusiak 1994) and all old wooden barns or other tall structures with suitable openings near the roof and old single-standing trees on farm properties (Bunn et al. 1982; Taylor 1994). Structures were not surveyed without permission from the owner; consequently, 13 of the 129 sites occupied in the early 1990's were not visited.

Sites were monitored from March to September in 2007 and 2008. To ensure that occupancy was not underestimated, I surveyed all potential sites at least three times. During a survey I searched the inside and perimeter of the structure for barn owls or indications of their presence (such as fresh pellets, feathers and/or carcasses). I also climbed up the side of the structure to check beams/platforms for any nesting activity. If the beams/platforms could not be accessed at a site, a 30 min. observation was conducted at dusk during each survey, to determine if any barn owls exited or entered the structure. A structure was considered occupied if a barn owl was sighted or if I found fresh pellets or feathers during any of the three surveys. I also spoke with the owner to confirm a site's status. I conducted additional surveys of occupied sites every 1-2 months to determine if they were used for breeding. Visits of this frequency enable evaluation of whether breeding occurred, as incubation and rearing takes approx. 2.5 months, and females and chicks beg loudly during the incubation and nestling periods. In addition to surveying, I checked the records at the local raptor shelter (OWL) in Delta to determine if they had received barn owls chicks from breeding attempts outside of the main breeding season or from less obvious sites. This source identified two additional nest sites in industrial areas, which I had not previously inspected.

Land Use Characteristics and Spatial Analysis

I quantified land use within a 1 km radius (3 km²) of each potential site from digitized data layers using a Geographic Information System (GIS) software (ArcGIS 9.2). I used a 1 km radius circle, which is consistent with previous

studies (Taylor 1994; Shawyer and Shawyer 1995; Bond et al. 2005), since the average home range of a breeding barn owl is estimated to be 3 km² (Taylor 1994). A layer of current land use data was created using several data sources. Grassland and crop cover in Delta was obtained from an individual field layer from 2007 that contained information on crop types (Ducks Unlimited, unpublished data). A similar data layer was not available for Surrey, so I created an equivalent data layer by visually inspecting individual fields for land use or crop type and digitizing these data (n=1747 fields). Data on housing, commercial and industrial land use were obtained from a 2006 Vancouver Regional District land use layer map for the entire study area (Metro Vancouver 2008). Finally, data on highways and connecting ramps within the study area were obtained from BC road layer map (Terrestrial Resource Inventory Mapping, TRIM BC 2007).

To reconstruct land use in the study area during the 1990's I integrated data from several sources. Grassland, crop cover and greenhouse data were obtained from high-resolution ortho photos taken in May 1995 (1m pixel) (CWS 1995). Grass cover can be distinguished easily from other crops in these photos. Pasture and hayfields are greener than the surrounding fields. Pasture is distinguishable from hayfields by its more uneven shade of green and visible animal tracks, while hayfields have straight-lined tractor tracks. Fields that were overgrown with grass, and had more shades of brown with no tractor or animal tracks were categorized as set asides. Fields which were green/brown and had visible rows were classified as berries. Fields that were bare soil were identified

as vegetable fields and minor growth in early May were classified as grain. Since field types are typically consistent between years, I was able to reconfirm vegetable and grain fields using a high-resolution ortho photo from later in the growing season in September 1999. Finally, interviews with farmers were also used to confirm the kind of crops that had been growing on their properties over the last 15-18 years. Based on those information sources, I classified each field as hay, pasture, fallow field, berry, vegetable or grain (n=1801).

Data on housing, commercial and industrial areas in the 1990's were obtained from the Vancouver Regional District 1996 land use map (Metro Vancouver 2008). There have been no new highways built in Delta and Surrey between 1990 and 2008 (MOT 2008). I therefore used the data set on highways from 2008 (TRIM BC 2008), and calculated the change in traffic volume on each highway between 1990 and 2008. Data on traffic volume from 1990 to 2007 were obtained from the BC Ministry of Transportation (MOT 2008). Traffic volume was defined as the average number of vehicles passing a specific site on a specific highway/highway ramp for a 24 h period for any day of the year. Average traffic volume (ATV) was obtained for 1990-1994 and 2007. For some sections of highways and ramps no ATV data were available for the specific year of the historic barn owl survey (1990-1993), since many ATV surveys started in 1995. I therefore estimated traffic volume for the early 1990's by extrapolating the linear rate of traffic increase from 1995-2008. Finally, past and current traffic exposures were calculated by multiplying the length (km) of highway and connecting ramps within the potential home range of each barn owl site, by the historical (1990-

1993) and current (2007) ATV, respectively. In order to calculate the area or length of a variable, I created a barn owl home range around each site using the ArcGIS analysis tool 'buffer' with a 1 km radius and then used the analysis tool 'Intersect' to extract the information

Variable Definition and Data Analysis

I used the spatial data to create 7 landscape variables, 4 describing the current landscape and 3 describing changes to the landscape since the 1990s (Table 1). The variable describing the amount of foraging habitat within the home range of a barn owl was a composite variable with two terms, grass cover and length of grass verges (Table 1). The grass cover term included undisturbed grassland and set-asides, as well as other types of grassland. Grassland types were not considered separately as there was little or no undisturbed grassland within 3 km² of most sites and we had no information on the relative abundance of prey species in other types of grassland. The variable describing changes in the amount of foraging habitat since the 1990s assessed changes in grassland cover (Table 1). Changes in the length of grass verges along roads and between fields were not assessed as there has been minimal changes in length of these variables since the 1990s. The variable that quantified the level of urban and industrial development within the home range of a barn owl, impermeable surface (Table 1), included residential, commercial, industrial land and greenhouse developments. Greenhouses were included in this variable because they represent commercial development, even though they are considered agricultural land under the ALR (ALR 2009).

I used logistic regression models to examine how changes in land use and current land use influenced long-term occupancy, current occupancy and current nesting of barn owls. I first examined if changes in land use around a site influenced whether sites occupied in 1990-1992 remained occupied in 2007/2008. Occupancy in the early 1990's was estimated based on two criteria: the site was monitored in 1990-1992 (Andrusiak 1994) or the owner could confirm with certainty that the site had been occupied/not-occupied during those years. I compared land use changes surrounding sites that remained occupied and sites that were still available but were currently unoccupied. Next, I examined whether current land use influenced whether potential roosting/nesting sites were occupied in 2007 and 2008. Finally, I examined whether current land use influenced whether sites occupied by barn owls were used as nesting sites in 2007 and 2008. In the first analysis I evaluated the role of three landscape variables: (i) change in grass cover (pasture, hay fields, set asides, grassland), (ii) change in impermeable surface (housing, industrial, commercial and greenhouses) and (iii) change in traffic exposure. For the second and third analyses, I included the following four landscape variables: grass cover (area of grass combined with length of grass verges along fields and roads, impermeable surface, length of highways and number of grass patches (a measure of fragmentation) (see Table 1). For each analysis, I created a candidate model set consisting of logistic regression models with all possible combinations of the three or four landscape variables and a null model, a logistic regression model containing a single parameter, the constant. No interaction terms were

considered. The first candidate model set contained nine models and the second and third candidate model set contained 16 models.

For all three analyses, I used Akaike's Information Criterion (AIC) to rank and identify the best-supported models within the model set (Burnham and Anderson 2002). The log-likelihood for each model was used to calculate Akaike's Information Criterion adjusted for small sample sizes AICc (Burnham and Anderson 2002). The AICc values give a measure of the level of fit of the data to the model weighted by the number of variables in the model. $\Delta AICc$ values were calculated as the differences between the AICc of each model and the model with the highest AICc score. Models with $\Delta AICc < 2$ were considered to have strong support and models with $2 < \Delta AICc < 4$ were considered to have moderate support (Burnham and Anderson 2002). AICc weights (w_i), which indicate the likelihood of the model given the data, relative to the other models in the candidate set, were calculated from the $\Delta AICc$ values and used to assess the relative support for each of the models. Models with high w_i values were considered to be the best-supported by the data (Burnham and Anderson 2002).

Table 1 Land use variables included in statistical models examining long-term and current occupancy of roost/nest sites by barn owls and breeding at occupied sites. Land use variables were all measured within a 1 km radius of each site.

Variable	Code	Definition
Change in grass cover	Δ Grass	Current km ² of grass cover (2007/8) - historic km ² of grass cover (1990's) Grass cover includes: Pasture, hayfields, set asides, marshland
Change in impermeable surface	Δ Imp.	Current km ² of impermeable surface (2007/8) - historic km ² of impermeable land cover (1990's). Impermeable surface includes: All residential, industrial, greenhouses and commercial and land
Change in traffic exposure	Δ Traffic	Current traffic exposure (2007) - historic traffic exposure (1990's) Traffic Exposure: Length of highways and off-and on-ramps within 1 km of a barn owl site x average number of vehicles passing a specific point on the highway/highway ramp for a 24 h period over a year (ATV).
Grass cover and length of grass verges	Grass	Grass cover (km ²) includes: pasture, hayfields, set asides, grassland and highway median and verges Length (km) of grass verges along roads and between fields
Impermeable surface	Imp.	Impermeable surface includes: All residential, industrial, greenhouses and commercial land
Km of highways and highway ramps	Hwy	Length (km) of highways and connecting on-and off-ramps
Number of grass cover patches	Patches	Number of continuous patches of grass cover within 1 km of a barn owl site

Parameter likelihoods and parameter estimates and their associated unconditional standard errors of the explanatory variables were also computed. These calculations were used to assess the relative influences of the explanatory variables present in the best-supported models on the dependent variable(s).

AIC parameter likelihood is the sum of the w_i of all models in which the parameter was included. An AIC parameter estimate is defined as the mean estimate (across all models in the candidate set) of each parameter weighted by the w_i of each model in which the parameter was included. An AIC unconditional standard error is defined as the standard error of each parameter weighted by the AICc weight of each model in which the parameter was included (Burnham and Anderson 2002). I calculated Nagelkerke's r-square for all the models to assess variation in the dependent variable explained by each model contained in the model set (Nagelkerke 1991). I conducted a priori Pearson's correlation analysis to ensure no pairs of variables were highly correlated; all variables were intercorrelated with $r < 0.5$. All my data were analyzed using SPSS version 16.0 (SPSS Inc., Chicago, Illinois).

2.4 Results

Land use within a 1 km radius of each potential nest/roost site changed considerably between the 1990's and 2008. Grass cover decreased by 53%, the area of impermeable surface doubled and traffic exposure increased by 31% over the 15 years examined (Table 2).

Table 2 Summary of changes in land use within a 1 km radius of barn owls ($n=80$) in the Fraser Valley, British Columbia, between the 1990's and 2007 and 2008. Means are presented \pm 1SD. Traffic exposure is estimated using ATV*km of the highway, including on-off ramps connecting to highways. ATV is the average number of vehicles passing a specific point on the highway/highway ramp for a 24 h period over a year.

Variable	Mean 1990's	Mean 2007/8	t-statistic	P-value
Grass cover (km ²)	0.74 \pm 0.38	0.40 \pm 0.36	-7.52	0.00
Impermeable surface (km ²)	0.18 \pm 0.40	0.42 \pm 0.55	5.85	0.00
Traffic exposure (ATV*km)	6450 \pm 5403	8443 \pm 6672	7.40	0.00

Barn owls continued to occupy 68 of the 115 sites (59.1%) that were occupied in the Fraser Valley in the early 1990's. However, many of the previously occupied sites were no longer available to owls because they had been removed or fallen down (n=22) and been replaced with an inaccessible steel barn, sealed up (n= 10) or burned (n=3). Overall, nearly one-third of sites occupied 15 years ago were no longer available to barn owls. After excluding unavailable sites, 85% (68 of 80) of the sites used in the 1990's remained occupied.

Long-term occupancy

Four of the eight models examining how changes in land use impact long-term use of barn owl roost/nest sites received strong support ($\Delta AIC_C < 2$) and had a combined $w_i = 0.97$ (Table 3). Increase in traffic exposure was included in all four models, and had by far the highest parameter likelihood (Table 4). Sites that had experienced a larger increase in traffic exposure were less likely to be occupied (Figure 2). The probability that a nesting or roosting site occupied in the 1990's was still occupied in 2007 and 2008 was 30% higher for sites with a moderate increase in traffic exposure (1000-3000 vehicles) compared to sites which had experienced a high increase in traffic exposure (4000-6000 vehicles; Figure 2).

Change in grass cover was included in two of the strongly supported models, including the best model in the candidate set (Table 3). However, the parameter likelihood for this variable was much lower and the weighted parameter estimate had a standard error that bounded zero (Table 4). Change in

the amount of impermeable surface was also included in two of the strongly supported models, but the weighted parameter estimate was positive, which is opposite to the predicted negative effect of urban development on nest/roosting site use. In addition, the parameter likelihood was not high and the weighted parameter estimate had a standard error that bounded zero (Table 4). There was consequently little evidence that changes in grass cover or amount of impermeable surface had any effect on the long-term use of nesting/roosting sites.

Table 3 AIC ranking (by w_i) of candidate models examining how landscape variables influence long-term occupancy of sites by barn owls in the Fraser Valley, British Columbia, in 2007 and 2008. (K: number of parameters estimated in each model (includes intercept and model variance), N: Sample size, AICc: measure of the level of fit of the data to the model weighted by the number of parameters in the model, $\Delta AICc$: calculated as the differences between the AICc of each model and the model with the highest AICc score., w_i : likelihood of each model given the data, and relative to the other models in the candidate set.

Model	K	N	AICc	$\Delta AICc$	w_i	Pseudo r^{2a}
Δ Traffic + Δ Grass	3	80	69.02	0.00	0.34	0.17
Δ Traffic	2	80	69.44	0.43	0.28	0.12
Δ Traffic + Δ Imp.	3	80	70.17	1.15	0.19	0.15
Δ Traffic + Δ Grass + Δ Imp.	4	80	70.52	1.51	0.16	0.19
Null	1	80	73.41	4.40	0.04	0.00
Δ Imp.	2	80	74.90	5.89	0.02	0.01
Δ Grass + Δ Imp.	3	80	76.31	7.30	0.01	0.03
Δ Grass	3	80	76.72	7.71	0.01	0.02

^aNagelkerke's pseudo r^2

Table 4 Parameter likelihoods, weighted estimates and unconditional standard errors of variables included in the candidate models examining how landscape variables influence long-term occupancy of sites by barn owls in the Fraser Valley, British Columbia, in 2007 and 2008.

Variable	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1.00	3.70	1.92
Δ Traffic	0.97	-0.05	0.02
Δ Grass	0.52	-0.72	0.97
Δ Imp.	0.38	0.61	1.26

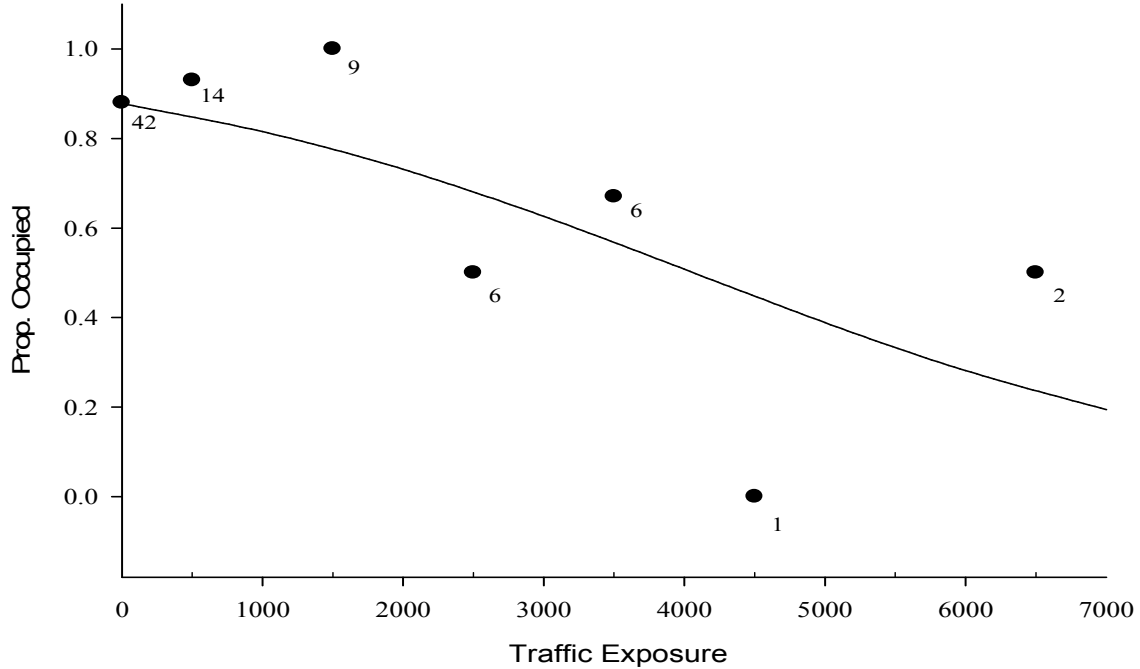


Figure 2 The relationship between the change in traffic exposure and the probability sites occupied by barn owls in the 1990's remain occupied in 2007 and 2008. Change in traffic exposure is calculated on highways within 1 km of each site (n=80). The line represents the predicted values from the best-supported AIC model (Logistic regression, $\text{Prob. Occupied} = 1 / (1 + e^{-(3.7 - 0.05 * \text{Traffic Exposure})})$). Parameters in this equation are weighted parameter estimates from an AIC analysis (Table 4). The points show raw data binned into categories of 1000 vehicles pr. 24h increases, with the midpoints presented on the X axis. The number of sites within each category is indicated next to each point.

Current distribution

Barn owls occupied 115 of the 143 (80.4%), potentially suitable sites surveyed in the Fraser Valley in 2007 and 2008, and there were differences in the amount of land use features between occupied and unoccupied sites (Table 5). Based on the AIC analysis, four of the 16 models examining how current land use influences barn owl occupancy received strong support ($\Delta\text{AIC}_C < 2$), with a combined $w_i = 0.73$ (Table 6). All of the models with strong support, including the best supported model, included the length of highway as an explanatory variable.

Models without highway as a variable received little support and all of them ranked below the null model. The parameter likelihood for the highway variable was consequently high (Table 7). Sites that had more highways within a 1 km radius had a lower chance of being occupied. The proportion of sites occupied declines gradually from 80%, when there is no highway, to 40% occupancy, when there is 7-8 km of highways within a 1 km radius (Figure 3).

The amount of impermeable cover within a 1 km radius of potential nest/roosting sites was included in two of the four strongly supported models ($\Delta AIC_C < 2$) (Table 6). However, this variable did not have a high parameter likelihood and the weighted parameter estimate was both positive (i.e. counter to what would be expected) and had an unconditional standard error that encompassed zero (Table 7). My data therefore provide limited evidence that the amount of impermeable cover within a 1 km radius of a site influences occupancy.

None of the models with strong support ($\Delta AIC_C < 2$), included grass cover, consequently the variable did not have a high parameter likelihood. However, two of the four strongly supported models included number of patches of grass cover (Table 6). But again, the parameter likelihood did not receive strong support, and the parameter estimate was both positive (i.e. counter to what would be expected) and had unconditional standard errors that bounded zero (Table 7). The data therefore provide little support that the amount of grass cover or the number of grass patches within a 1 km radius of a site influences occupancy by barn owls.

Table 5 Summary of the amounts of different land use features between occupied and unoccupied sites (n=143), in the Fraser Valley, British Columbia, in 2007 and 2008. Means are presented \pm 1SD.

Variable	Occupied (115)	Unoccupied (28)	t-statistic	p-value
Grass cover (km ²)	0.44 \pm 0.39	0.33 \pm 0.27	1.40	0.17
Grass verges (Km)	18.60 \pm 4.52	17.40 \pm 5.91	1.35	0.18
Impermeable surface (km ²)	0.38 \pm 0.48	0.39 \pm 0.46	-0.09	0.93
Highways (Km)	1.10 \pm 1.86	2.40 \pm 2.70	-3.09	0.00
# Patches	5.20 \pm 2.40	4.80 \pm 1.60	0.90	0.37

Table 6 AIC ranking (by wi) of candidate models examining how landscape variables influence the current distribution of barn owls in the Fraser Valley, British Columbia, in 2007 and 2008. Variables in the models are abbreviated as follows: Imp: amount of impermeable surface (km²), Patches: number of grass patches, Hwy: length of highways (km), Grass: areas of grass cover (km²) and length (km) of grass verges combined. Models are described using the same abbreviations as used in table 1. All habitat variables are measured within 1 km radius of each nest site.

Model	K	N	AICc	Δ AICc	wi	Pseudo r^{2a}
Hwy	2	143	137.56	0.00	0.28	0.09
Hwy + Imp.	3	143	138.42	0.86	0.18	0.10
Hwy + Patches	3	143	138.63	1.03	0.16	0.10
Hwy + Imp + Patches	4	143	139.36	1.80	0.11	0.09
Hwy + Imp. + Grass	5	143	139.97	2.42	0.08	0.13
Hwy + Grass	4	143	140.17	2.61	0.08	0.10
Hwy + Imp. + Grass + Patches	6	143	142.12	4.56	0.03	0.04
Hwy + Grass + Patches	5	143	142.12	4.56	0.03	0.11
Null	1	143	143.46	5.91	0.01	0.10
Grass	3	143	144.60	7.04	0.01	0.00
Imp.	2	143	144.62	7.06	0.01	0.06
Patches	2	143	144.66	7.11	0.01	0.03
Imp. + Grass	4	143	144.88	7.32	0.01	0.01
Imp. + Patches	3	143	145.73	8.18	0.01	0.05
Grass + Patches	4	143	146.68	9.13	0.00	0.03
Imp. + Grass + Patches	5	143	147.03	9.47	0.00	0.05

^aNagelkerke's pseudo r^2

Table 7 Parameter likelihoods, weighted estimates and unconditional standard errors for each variable included in the candidate models examining how landscape variables influence the current occupancy of barn owls in the Fraser Valley, British Columbia, in 2007 and 2008.

Variable	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1	1.30	0.78
Hwy	0.93	-0.24	0.10
Grass	0.24	0.12	0.28
Grass verge	0.24	0.01	0.01
Imp.	0.43	0.28	0.47
Patches	0.35	0.03	0.07

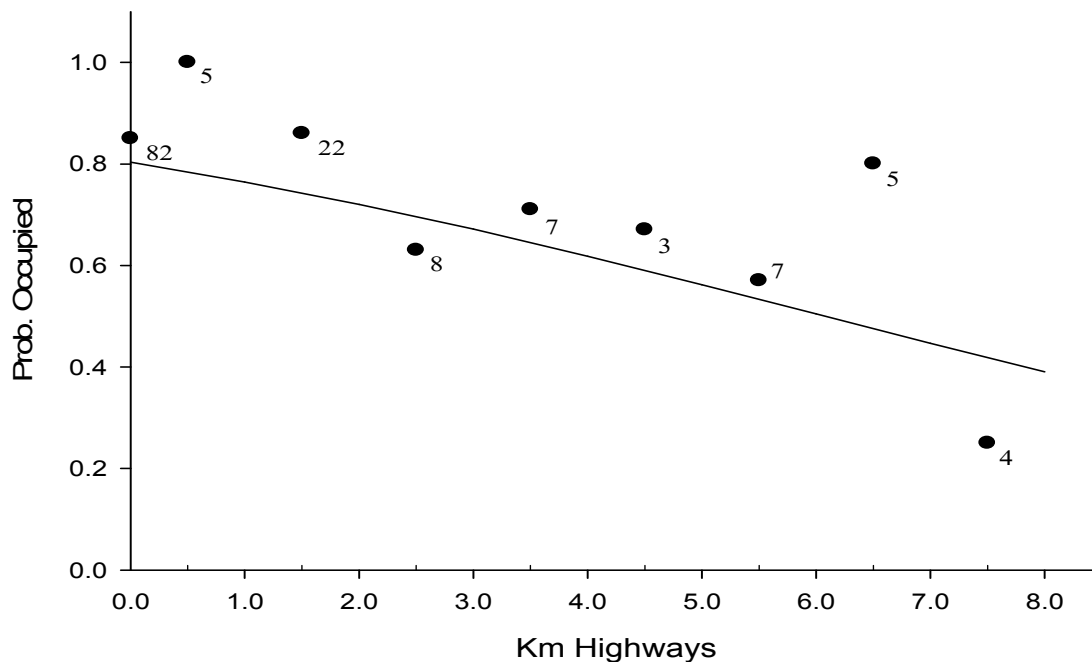


Figure 3 The relationship between the length of highways within a 1 km radius of each potential nest/roost site (n=143) and the probability that the site is occupied by a barn owl. The line represents the predicted values from the best-supported AIC model (Logistic regression, $\text{Prob. Occupied} = 1 / (1 + e^{-(1.3 - 0.24 * \text{Km Hwy})})$). Parameters in this equation are weighted parameter estimates from an AIC analysis (Table 7). The points show raw data binned into categories of 1km increases, with the midpoints presented on the X axis. The number of sites within each category is indicated next to each point.

Breeding status

Barn owls bred in 78 of the 115 (68%) occupied sites. However, I found little evidence that the landscape variables measured were able to discriminate between sites that were, or were not used for breeding. Five of the 16 models received strong AIC support ($\Delta AICc < 2$); however, the null model ranked highest with $w_i = 0.20$ (Table 8). None of the variables included in the top models had high parameter likelihoods and in all cases the weighted parameter estimates for these variables had standard errors that bounded zero (Table 9).

Table 8 AIC ranking (by w_i) of candidate models examining how landscape variables influence whether sites occupied by barn owl sites were used as nesting sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Model	K	N	AICc	$\Delta AICc$	w_i	Pseudo r^{2a}
Null	1	106	138.10	0	0.20	0.00
Imp.	2	106	138.23	0.13	0.19	0.03
Hwy + Imp.	3	106	139.43	1.34	0.11	0.10
Hwy	2	106	139.51	1.41	0.10	0.08
Patches	2	106	139.88	1.78	0.08	0.05
Imp. + Patches	3	106	140.17	2.08	0.07	0.07
Grass	3	106	140.95	2.85	0.05	0.01
Highway + Patches	3	106	141.37	3.27	0.04	0.09
Highway + Imp. + Patches	4	106	141.47	3.37	0.04	0.11
Imp. + Grass	4	106	141.81	3.72	0.03	0.04
Hwy + Grass	4	106	142.30	4.20	0.03	0.09
Grass + Patches	4	106	142.86	4.76	0.03	0.07
Hwy + Imp. + Grass	5	106	143.02	4.92	0.02	0.10
Imp + Grass + Patches	5	106	144.01	5.92	0.01	0.08
Hwy + Patches + Grass	5	106	144.45	6.36	0.03	0.07
Hwy + Imp. + Grass + Patches	6	106	145.26	7.16	0.01	0.09

^aNagelkerke's pseudo r^2

Table 9 Parameter likelihoods, weighted estimates and unconditional standard errors for each variable included in the candidate models examining how landscape variables influence whether sites occupied by barn owl sites were used as nesting sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Variable	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1	1.11	0.54
Hwy	0.34	-0.03	0.07
Grass	0.17	0.11	0.25
Grass verge	0.17	0.00	0.01
Imp.	0.47	0.40	0.60
Patches	0.28	-0.01	0.03

2.5 Discussion

Previous research suggests that population declines of barn owls can be attributed to two major factors: loss of suitable nesting sites and the decline of grassland associated agriculture, overall reducing the quality of land as habitat (Colvin 1985; Taylor 1994). My study confirms that the former, loss of suitable nesting sites is likely to be impacting barn owl populations in the Fraser Valley of British Columbia. As there has been a gradual loss of potential nest/roost sites for barn owls in the valley as old wooden barns are replaced or large old trees removed. Surprisingly, despite the considerable loss of grassland habitat over the last 15 years, I found little evidence that the amount of this key foraging habitat influenced the use of potential nesting or roosting sites in the Fraser Valley. Rather, habitat configuration, specifically the length of highways within a 1 km radius of a potential roosting or nesting site influences the distribution of barn owls in the Fraser Valley.

The population declines of barn owls in Western Europe and North America are correlated with loss of suitable nests sites (Bunn et al 1982; Percival

1991; Taylor 1994). For example, over a 13-year period in southern Scotland, Taylor (1994) estimated that 4-6% of nest sites were lost per annum. Within my study area, the loss of nest/roosting sites was somewhat lower at ~2.2% per annum over the last 15 years. Changes in barn design (i.e. made inaccessible for barn owls) as well as development (i.e. barns demolished or left to fall down) have led to the loss of many potential roosting/nesting sites in the Fraser Valley. The availability of natural nesting sites is also likely to be decreasing. All the large old trees that were used as nesting sites in the 1990's (Andrusiak 1994) had fallen down or been removed at the time of my 2007 censuses (n=5). The number of large single-standing trees has been declining in many agricultural landscapes over the last 50 years due to field enlargement programs associated with agricultural intensification (Taylor 1994).

Evidence suggests that there is a shortage of suitable nest sites, and that this may limit some barn owl populations. For example, in southern Scotland the density of breeding barn owls was higher on plots containing nest boxes compared to control plots (Shawyer 1998). Nest boxes were also quickly occupied in Northern Utah: 80% of boxes were found to contain breeding pairs of barn owls after two years (Marti 1979). These studies are consistent with the high levels of occupancy I observed in the Fraser Valley where more than 80% of apparently suitable sites were occupied. In addition, farmers in the area report that barn owls rapidly occupy and breed in newly installed nest boxes. Overall, the loss of nest/roost sites coupled with the high occupancy of the remaining

suitable sites, suggest that nesting sites for barn owls are limited in the Fraser Valley.

Changes in the configuration of the agricultural landscape, especially increased fragmentation owing to road development, have a negative effect on many wild populations (Forman et al. 2003; Jaeger et al. 2005; Fahrig and Rytwinski 2009). This pattern was observed in my study where the presence of highways and changes in traffic exposure were the major factors influencing site occupancy by barn owls. This pattern may occur because barn owls actively avoid sites located close to highways or because they are more vulnerable to mortality at such sites. It does not appear that owls or other raptors avoid foraging near highways due to pollution or noise, as they are frequently observed hunting in these areas (pers. obs.). However, there is clear evidence that vehicle collisions are a major cause of barn owl mortality in Europe and North America (De Bruijn 1994; Baudwin 1997; Newton et al. 1997; Lodé 2000; Fajardo 2001; Ramsden 2003; Boves 2006; Preston and Powers 2006) and mortality rates are particularly high on roads that are elevated compared to the rest of the surrounding landscape, such as highways (Baudwin 1997; Lodé 2000). There are studies that point out the potential risk of over-representing the importance of barn owl highway mortality, due to the higher likelihood of finding carcasses along the highway compared to other causes of death (i.e. starvation in fields, electrocution, predation) (Percival 1991; Illner 1992). However, long-term statistics from the UK, shows that the increase in the proportion of barn owls carcasses found dead on roads has risen from 12% in 1910 to 44.7% in 1996

(Glue 1971; Newton et al. 1997). This is almost a fourfold increase over 86 years, affecting predominantly dispersing juveniles and females in good condition (De Bruijn 1994; Massemin et al. 1998; Ramsden 2003; Boves 2006). Vehicle collisions are also known to kill and injure a large number of owls each year in the Fraser Valley (Preston and Powers 2006). Andrusiak (1994) reported that 63% (n=341) of the barn owls found dead in the Fraser Valley were killed by collisions with vehicles. This suggests that the lower rates of occupancy at sites close to highways may be because these birds suffer higher mortality, and predicts that these sites should have higher turnover.

Several studies in Europe and North America have also linked long-term declines in barn owl populations with the loss of grassland habitat, which is linked to the abundance of their main prey item, voles (*Microtus sp.*) (Colvin 1985; Taylor 1994). There is often a strong relationship between the area of non-intensively used grassland (i.e. cut once every two years) and the density of voles (Gorman and Reynolds 1993; Nagorsen 2005; Aschwanden et al. 2007), and the loss of such grasslands has been linked to an overall decline of vole populations in agricultural landscapes (Butet and Leroux 2001). Given that the typical barn owl diet in Europe and North America consists of 50-70% voles (Marti 1988; Taylor 1994), it was surprising that in my study I detected little effect of the loss of grass cover on the occupancy of sites. I found little evidence that either the long-term or current occupancy of a site was predicted by the area of grass cover. A potential reason I did not detect any differences in the relationship between site occupancy and the amount of grass cover is because prey

communities within grasslands might not only be influenced by the amount of grass cover but also the overall configuration of the landscape. For example, previous studies have shown proximity to urbanization has a negative impact on vole populations in grasslands (Delattre et al. 1996; Bock et al. 2002). Detailed information on vole abundance in grasslands across the Fraser Valley is needed to clarify how the type and configuration of grassland habitat, in relation to other land uses, influence vole populations.

If proximity to foraging habitat is most important during breeding, when owls must repeatedly return to the same nest site, the amount of grass cover may only influence whether breeding can occur at a site. This relationship has been demonstrated in barn owls in England, where successful breeding is associated with sites with less habitat heterogeneity and higher-quality small mammal habitat (Bond et al. 2005). In contrast, I could find no evidence that the surrounding landscape influenced whether a site was used for breeding. However, barn owls in this study often used multiple barns/trees for roosting and the roosting and nest sites were often less than 50 m apart. This spatial correlation may have obscured the importance of landscape attributes that play a role in breeding alone.

Despite losses in the area of grasslands in the Fraser Valley over the past 15 years, the current availability of suitable foraging habitat may be sufficient for breeding and therefore not a limiting factor for barn owl populations in this area. Shawyer and Shawyer (1995) estimated that 0.40 km² of unimproved grassland, or more than 13 km of grassland edge (of ca. 6 m width) are needed within a

barn owl's home range for successful breeding in southern England. If these results can be extrapolated to the Fraser Valley, which has similar climatic conditions and geographic features as southern England, it suggests that both occupied and unoccupied sites within my study area have adequate amounts of grassland edge habitat for successful breeding (Table 5). This grass edge habitat compensates for the more intensively utilized grass habitat, as previous studies have shown that grass edges along fields (Taylor 1994) and roads (Bolger et al. 2001) have the highest abundance of voles in agricultural landscapes where there is little non-utilized and semi-utilized grassland left, such as the Fraser Valley. This would suggest that grass verges along roads and fields are important foraging habitats for barn owls, predicting barn owls would be sensitive to their removal or loss.

The ability of barn owls to use alternate prey may also explain why they were not impacted by changes in the amount of grass habitats. Although barn owls are considered vole specialists (Fast and Ambrose 1976; Derting and Cranford 1989), the proportion of their diet consisting of voles can vary widely. For example, many previous studies have shown prey shifting by barn owls in response to temporal changes in vole abundance (Wallace 1948; Webster 1973). Colvin (1984) documented barn owl diets in south western New Jersey declining from 91% meadow voles in the summer, to 58% voles in the winter. Barn owls residing in urban areas tend to have a diet that consists of a higher proportion (13-55%) of rats and birds (Fairley 1966; Buckley and Goldsmith 1975; Campbell et al. 1987; Salvati et al. 2002). These patterns were also apparent within my

study. Pellet analysis showed that barn owls at different nest sites varied considerably in their dependence on species such as Shrews (*Sorex spp.*), Norway rats (*Rattus norvegicus*) and/or starlings (*Sturnus vulgaris*) (Chapter 3).

This study is the first to assess how long-term patterns of site occupancy by barn owls are impacted by agricultural landscape configuration. Although barn owls have shown considerable resilience to changes in the amount and structure of the landscape, I found that they were less likely to occupy and persist at sites with highways and high traffic exposure within their home range. This study adds to the growing evidence that the urbanization of agricultural landscapes negatively impacts the associated wildlife (Fahrig and Rytwinski 2009) and highlights the importance of managing landscape structure, rather than simply habitat availability.

Management implications

Grassland habitats continue to be lost and fragmented in the Fraser Valley and many other agricultural landscapes, as urbanization and associated infrastructure expands into these areas. Such, factors will combine to further decrease the availability of nest sites for barn owls and to decrease the suitability of the remaining sites. Further research is required to better understand how roads impact both behavioural responses and road mortality of barn owls, in order to develop mitigation measures during road construction and maintenance projects.

This study has documented a gradual loss of suitable nest sites in the Fraser Valley. This could be mitigated by providing nest boxes that are readily occupied by barn owls (Marti 1979). This study would suggest that managers should consider where nest boxes are located. Prime candidate sites, would have minimal length of highways within a 1km radius, and large amounts of available grass habitat. Managers may also want to consider actions that could reduce barn owl mortality on highways. One option is to discourage barn owls from crossing highways at a low flight height (i.e. 1-2 m above ground-level) by separating existing grass verges or grassland close to highways by low-flight preventive measures such as hedges or a dense row of trees planted next to the highway.

3: The Effects of Land Use on Diet and Productivity of Barn Owls *Tyto alba* in the Fraser Valley, British Columbia, Canada

3.1 Abstract

Changes in agricultural practices and increased urbanization have led to the loss of habitat, and a more uniform, homogeneous landscape, shown to negatively affect populations of farmland birds. In this study I used an AIC-based approach to investigate (i) how current land use impacts diet composition, and (ii) whether diet composition and agricultural land use influence the productivity of barn owls in the Fraser Valley, British Columbia, Canada. I assessed the diet and productivity during weekly monitoring of nest sites. I quantified diet composition by identifying prey items found in the pellets and used the proportion of voles by biomass as an index of diet quality. I quantified the composition and configuration of the agricultural landscape within a 1 km radius of each nest site from digitized data layers. Variables extracted included grass cover, area of impermeable surface, length of highways and the number of grass patches within a 1 km radius of the nest site. Barn owl pellets contained 17 different prey species. Voles were the major prey, contributing on average 67% by number and 70% by biomass. I found some evidence that diet quality is influenced by the amount of impermeable surface within 1 km of a nest site, and compelling evidence that diet quality has a positive effect on fledging success. I also found that fledging success declines as the amount of impermeable surface within 1 km of the nest

site increases. I argue these results suggest that landscape effects on productivity are mediated via impacts on diet quality.

3.2 Introduction

Over the last 35 years, birds associated with agricultural landscapes have experienced strong population declines and range contractions across both Western Europe and North America (Fuller et al. 1995; Krebs et al. 1999; Murphy 2003; Peterjohn 2003; Brennan and Kuvlesky 2005; Donald et al. 2006).

Declines have been attributed to the loss of agricultural land to urbanization (Filippi-Codaccioni et al. 2008; Ludwig et al. 2009) and the degradation of habitat quality (Fuller et al. 1995; Krebs et al. 1999; Donald et al. 2006). Habitat is degraded as small fields with rotational crop practices are converted to large, intensively utilized mono-culture fields, and/or subjected to modern agricultural practices (i.e. use of agrochemicals, modernized machinery; Fuller et al. 1995; Krebs et al. 1999; Wilson et al. 2005). These changes in landscape composition have been linked to the reduced productivity and survival of many farmland birds (Fuller et al. 1995). Newton (2004) argued that most farmland bird population declines (~70%) are associated with lower productivity rather than reduced survival.

Changes in agricultural practices can reduce the productivity of farmland birds in a variety of ways. Breeding habitat can be lost due to the drainage and conversion of grasslands for cultivation (Vickery et al. 2001; Wilson et al. 2005). Habitat quality can also be degraded due to the increased use of herbicides and pesticides, which reduces food availability (Rands 1985; Taylor et al. 2006). For

example in Britain, herbicides were found to reduce food availability for turtle doves (*Streptopelia turtur*) reducing both the number of breeding attempts and chick survival (Browne and Aebischer 2004; 2005). In addition, changes in agricultural practices can reduce the suitability of nesting habitat for many species. For example, increased use of fertilizers allows earlier and more frequent haying, reducing the nesting success of ground-nesting birds (Green and Stove 1993; Schekkerman et al. 2008). Intense grazing regimes can also degrade nesting habitat by reducing nest cover and increasing nest predation rates (Chamberlain and Crick 2003).

The range contraction and population declines observed in barn owls (*Tyto alba*) across Europe and North America can be attributed to changes in agricultural landscape that reduce both survival and productivity (Bunn et al. 1982; Colvin 1985; Taylor 1994; Toms et al. 2001; Ramsden 2003). Barn owls forage on grassy verges along roads, which makes them vulnerable to collisions with motorized vehicles, and increased traffic and road networks have been associated with reduced survival (Ramsden 2003; Boves 2006; Preston and Powers 2006). The productivity of barn owls can be reduced directly because of loss of suitable nesting sites, particularly wooden barns and old trees (Taylor; 1994; Ramsden 1998), or reductions in the abundance of their primary prey (*Microtus spp.*) due to loss of grasslands (Colvin 1985; Butet and Leroux 2001). Since survival and productivity can be influenced by different aspects of the agricultural landscape, many features of the landscape may need to be considered in order to halt population declines.

The Fraser Valley in south western British Columbia has experienced extensive urbanization and loss of grasslands over the last five decades (Moore 1990; Boyle 1997). Previous work (Chapter 2), suggests that highways increase mortality and can influence distribution. However, the extent to which landscape composition and configuration influence the productivity of barn owls in this area is poorly understood.

Previous work has shown that voles are the preferred prey of barn owls and that breeding success increases with the proportion of voles in the diet (Gubanyi 1992; Taylor 1994). If landscape composition and configuration within the home range of a barn owl determines the distribution and abundance of prey, increasing amounts of grasslands and decreasing amounts of developed areas should be associated with higher densities of voles, and influence the proportion of voles in the diet of barn owls. Furthermore, landscape features impacting the abundance of voles should also be directly linked to fledging success and condition of barn owl broods. Landscape configuration could also impact the productivity of barn owls via impacts on foraging efficiency or survival. For example, fragmentation of grassland habitat that increases the number of grass patches could increase travel time reducing foraging efficiency and negatively affect productivity. The amount of highway within a home range could increase the risk that one parent is killed during the breeding season and reduce the number of young produced (Figure 4).

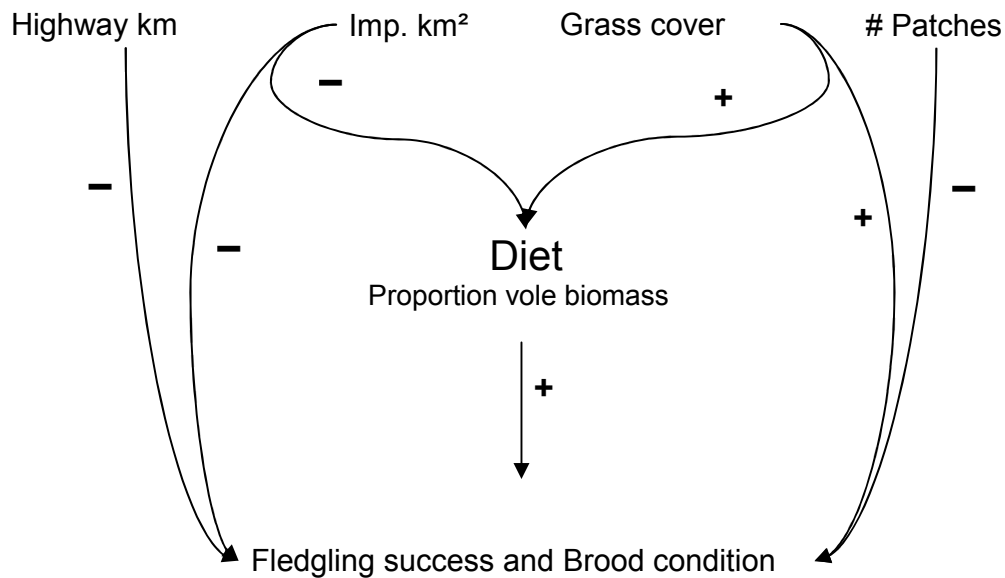


Figure 4 The predicted interrelationships between landscape features, barn owl diet and productivity.

In this chapter, I examine how landscape composition and configuration influences diet, fledging success and/or brood condition of barn owl broods in the Fraser Valley, British Columbia. I test the following three hypotheses: (i) landscape composition and configuration will influence barn owl diet, (ii) the diet of barn owls will influence productivity and brood condition, and finally (iii) landscape composition and configuration will influence barn owl productivity and brood condition.

3.3 Methods

Study Species

The barn owl is widely distributed in temperate and tropical regions across the globe. In North America the barn owl is widespread in the US, but in Canada its range is restricted by climate to south western British Columbia and southern

Ontario (Cramp 1985; Snow and Perrins 1998). In British Columbia, the highest densities are found in the Fraser Valley, but barn owls also occur on southeastern Vancouver Island, in the southern Okanagan valley and the Creston valley (Campbell et al. 1990).

Barn owls can initiate clutches in every month of the year, although breeding activity peaks in the spring and second broods are uncommon in temperate regions (Keith 1964; Witmer and Patrick 1987). Previous monitoring in British Columbia showed that 74% of clutches were laid between early March and the beginning of May ($n = 84$; Campbell et al. 1990). Clutch sizes range from 1 to 12 eggs (mean \pm SD= 4.8 ± 2.3 eggs, $n=84$, Campbell et al. 1990), and eggs are typically laid at 2-3 day intervals (Smith et al. 1974). Incubation starts with the first egg laid, and females incubate the eggs for between 29–34 days (30.8 ± 0.9 days; Smith et al. 1974). Chicks hatch asynchronously over approximately 1-2 weeks creating large size asymmetries within the brood. Males provide all the food consumed by females and chicks during incubation and the first two weeks of the nestling period. After this period, females will leave the nest to forage for themselves and to help provision young (Marti et al. 2005). Barn owl chicks fledge after 62-67 days (4.3 ± 0.5 days, $n=11$; Smith et al. 1974). However, fledglings will roost at, or in close proximity to, the nest site for 7-8 weeks after fledging (Smith et al. 1974; Lenton 1984).

Barn owls feed principally on small mammals, but will also consume birds, bats and frogs (Marti et al. 2005). Pellet studies across North America suggest they specialize on voles, as voles make up ~ 60-90% of the remains (Colvin and

McLean 1986; Campbell et al. 1987; Marti 1988). Fledging success has been found to increase with the amount of voles found in the diet of barn owls (Gubanyi 1992; Taylor 1994).

Study Site

I monitored the breeding and diet of barn owls within the municipalities of Delta and Surrey, an area of 681 km² within the Fraser Valley, British Columbia, Canada (49° 8' 0" North, 122° 18' 0" West). The area is bounded by the Fraser River to the North, the US border to the South, Georgia Strait to the West and the municipality of Langley to the East (Chapter 2: Figure 1). The Fraser Valley is an area of key importance for migratory and resident farmland birds. The area has traditionally been used for pasture and hay production, but over the last 35 years agricultural practices like vegetable and berry production and greenhouses have become more prevalent (Statistics Canada 2006). The human population of the Fraser Valley (Metro Vancouver and Fraser Valley Regional District) has increased by 400% since the 1960's (Boyle 1997). This has coincided with ~ 5000 ha (7.5%) of land being taken out of agricultural production since 1974 (Agricultural Land Reserve 2009).

Monitoring of breeding

Nest sites were located by surveying all likely nest sites within the study area, beginning in March, and were continuously monitored until the last chicks fledged at the end of August in 2007 and 2008. Surveys included all active nest sites documented in a previous study (Andrusiak 1994), and all old wooden

barns or other tall structures with suitable openings near the roof and old single standing trees on farm properties (Bunn et al. 1982; Taylor 1994). Sites used by barn owls were re-visited every 1-2 months to ensure that all successful breeding attempts were detected: incubation and rearing takes approx. 2.5 months in barn owls. During these surveys, I checked the nest box or platform for any nesting activity. If the building was in poor condition or the nest box or platform could not be accessed, I conducted 10-15 min. observations at dusk to determine if females were likely to be incubating or nestlings were present. Females screech and chicks beg loudly during the incubation and nesting period. To minimize disturbance, I conducted nest inspections after dusk. Previous research in Europe suggests that this timing minimizes disturbance to the incubating female and the chicks (Bettina Almasi, pers. comm.).

Data collected at nest sites

I obtained data on fledging success at 63 nest sites (2007, n=29; 2008, n=34). Forty-six of these nest sites were monitored throughout the breeding season (2007: n=18, 2008: n=28). Some sites (n=17) were monitored less extensively because the owners or condition of the building did not allow nest sites to be accessed or breeding was first documented mid-way through the nestling period. Once clutches were initiated, sites were visited every 10-15 days until hatching, and then every 6-10 days until chicks were 45-55 days old. To minimize disturbance I conducted all nest visits at night until chicks were 21-28 days old. Subsequent nest visits could be conducted during the day because the female no longer roosts with the chicks. Nests were not visited after chicks were

45-55 days old because chicks are vulnerable to premature fledging if handled after this point (Smith et al 1974; Bunn et al 1982). Fledging success was estimated as the number of surviving chicks present on the final visit.

During each nest visit, I removed chicks from the nest, and obtained the following measures: mass (g), tarsus length (mm), wing length (mm) and the length of the 10th primary (mm). I identified individual chicks within a brood by dabbing different colours of non-toxic temporary paint on the back of their heads. I aged nestlings based on their mass (g) when they were first weighed, in most cases when they were younger than 7 days, using a growth curve constructed from a sub-sample of nestlings monitored from the day they hatched onwards (n=11). I considered nestlings that weighed 20 g or less to have hatched within the last 24 hours (Howell 1964; Rich and Carr 1999). Chicks were banded with a stainless steel Canadian Wildlife Service numbered band (7A) when they were 35-55 days old. At this time I also took a 100 μ L blood sample from the brachial vein of each chick to allow for molecular sexing. This research was carried out under all the appropriate wildlife and animal ethics permits: Provincial wildlife permit (SU07-30650), Animal care permit (810B/06), Environment Canada permit (59-08-0352) and Sub Banding Permit (10759V).

Nestling growth, sex and condition

Chick growth in barn owls is impacted by provisioning rates. Previous work on European barn owls has shown that the asymptotic mass of nestlings varies considerably and is strongly influenced by the amount of food delivered

over the nestling period (Durant and Handrich 1998). I therefore used the deviation in asymptotic mass from the sex-specific mean as a measure of nestling condition. I estimated the asymptotic mass for each chick by fitting a logistic growth curve. Barn owl growth can be approximated using a logistic growth curve (Ricklefs 1968) because peak mass is achieved by nestlings at about 40 days (Sumner 1929; Taylor 1994; Durant and Handrich 1998), and mass recession prior to fledging takes place after measurements ceased. Individual growth curves were only fitted if chicks were measured at least four times (mean=6 times) and survived to at least 35 days (n=128). For each chick in a brood, I calculated a standardized condition score measured as the deviation from the mean sex-specific asymptotic mass during the nestling period divided by the sex-specific standard deviation. The mean score for all the chicks within each brood was used to determine the condition of a brood.

I sexed chicks using either a PCR-based molecular technique (n=23) or morphological data (n=106). Molecular sexing was conducted using the primers P2 and P8, which bind to the Z and W chromosome (Griffith et al. 1998). The PCR amplification was carried out in a total volume of 20 μ l, which included: 10X (15mM MgCl₂), dNTPs (2mM), MgCl₂ (25mM), P2 (2 μ M), P8 (2 μ M), Taq polymerase (5U/ μ l) and H₂O. PCR was performed in an Eppendorf thermal cycler, with an initial denaturing step at 94°C for 3 min, followed by 21 cycles of denaturing at 94°C for 30 sec, annealing at 63°C for 30 sec and extension at 72°C for 45 sec and than a final run of 72°C for 5 min. The PCR products were separated by gel-electrophoresis for 90 min, at 120V, in a 3% agarose gel,

stained with ethidium bromide. Chicks that could not be sexed using the molecular technique because blood samples were not obtained, or the molecular technique failed to yield results, were sexed based on their asymptotic mass. Adult females are ~ 20% heavier than adult males, and the asymptotic mass of molecularly sexed chicks was greater in female nestlings (mean=539.3g, 95% CI: 503.7g - 575.0g, n=12) than the male asymptotic mass (mean=474.8g, 95% CI: 443.0g - 506.7g, n=11). One chick had an asymptotic mass that fell between 503.7 and 506.7 g, and was sexed based on its relative size within the brood.

Assessing the diet of females and their brood

Diet was examined by collecting regurgitated pellets at nest sites on visits conducted every 6-10 days during the late incubation and nestling period (March – August). Female's brood nestlings until they are ~ 2 weeks old so pellets collected within that period may be produced by either the female or the nestlings. Prior to collecting any pellets, all old pellets were removed from the nest site and discarded. In total 886 pellets were collected from 23 nest sites in 2007 and 638 pellets from 28 nest sites in 2008. Pellets were frozen until they could be processed.

Pellets were processed by carefully taking them apart so that prey items could be identified based on the bone remnants, fur and other body parts. The number of individuals of any species within each pellet was determined by pairing each skull with the correct number of ischia, left and right mandibles, tibiae/fibulae, or in the case of birds each skull with sternum, gizzard sac and feet. The remaining bones contained within the pellet, were assembled to

determine the minimum number of additional individuals whose skull may have been crushed. The remains of each prey item were assumed to be contained within a single pellet as it is very rare that bones from one prey item to be mixed into two successive pellets (Raczynski and Ruprecht 1974).

I considered three descriptors of the composition of the diet for each nest site where I had collected at least 16 pellets during a minimum of 4 visits. These diet variables were: (i) the Shannon-Wiener diversity index: $H' = -\sum p_j \log p_j$ (Colwell and Futuyama 1971), (ii) the proportion of voles (# voles/total # prey items), and (iii) the proportion of biomass composed of voles (biomass of voles (g)/total biomass of all prey items (g)). Information on body mass for the different species of prey was obtained from BC field guides on rodents, shrews, lagomorphs and birds (Nagorsen 1996; Sibley 2003; Nagorsen 2005). All three diet variables were highly intercorrelated ($r > 0.66$). Since the proportion of vole biomass controls for differences in prey biomass (6-160g), and has been used as an index of diet quality in other studies (Ottens et al. 1972; Meek 2009), I used only this diet variable in subsequent analyses.

Current land use and spatial analysis

I quantified land use within a 1 km radius (3 km²) of each potential site from digitized data layers using Geographic Information System (GIS) software (ArcGIS 9.2). I used a 1 km radius as other studies have estimated the home range of a barn owl during the breeding season to be approximately 3 km² (Taylor 1994; Shawyer and Shawyer 1995).

A layer of current land use data was created using several data sources. Grassland and crop cover in Delta was obtained from an individual field layer from 2007 that contained information on crop types (Ducks Unlimited, unpublished data). A similar data layer was not available for Surrey, so I created an equivalent data layer by visually inspecting individual fields for land use or crop type and digitizing these data (n=1747 fields). Data on housing, commercial and industrial land use were obtained from a 2006 Vancouver Regional District land use layer map for the entire study area (Metro Vancouver 2008). Finally, data on highways and connecting ramps within the study area were obtained from BC road layer map (Terrestrial Resource Inventory Mapping, TRIM BC 2007). I extracted four landscape variables from the GIS data layers: 1) amount of grass cover [grass cover of fields and uncultivated land (km²) and length of grass verges (width<3 m) along fields and minor roads (km)], 2) amount of impermeable surface (km², including urban development and greenhouses), 3) length of highway (km), and 4) number of grass patches (field or uncultivated grassland >0.025 km²) (see Chapter 2: Table 1). These variables were somewhat inter-correlated (landscape data set: mean $r_p \pm SD = 0.25 \pm 0.19$; range: 0.00-0.53; n=63; diet dataset: mean $r_p = 0.20 \pm 0.19$; range: 0.02-0.58; n=39), but all variables were never the less included in all analyses.

Data analysis

I used general linear models, fitted assuming a normal error distribution, to examine seasonal and inter-annual variation in breeding performance and evaluate the relationships between current land use, diet composition and the

fledging success and condition of barn owl broods in Delta and Surrey. I first evaluated whether year and/or hatch date (of the first egg that hatched) influenced clutch size, fledging success or brood condition. To evaluate the relationship between the landscape composition, diet and barn owl breeding performance I conducted six related analyses. In the first analysis, I investigated whether the landscape composition within the home range of a barn owl nest influenced the quality of the brood's diet. The second and third analyses assessed whether diet quality predicted fledging success and/or chick condition. The fourth and fifth analyses evaluated whether landscape composition influenced fledging success and/or brood condition. Finally, I assessed whether variation in fledging success was best explained by diet composition or any landscape metrics included in strongly supported models in the fourth analysis. For all six analyses, I created candidate model sets that included general linear models with all combinations of the explanatory variables being considered and a null model, a general linear model with a single parameter, the constant. No interaction terms were considered. I did not include date and year in any of these analyses as I found no evidence of seasonal or inter-annual variation in fledging success or brood condition (see Table 10). I also did not include brood size in the fifth analysis because that there was no relationship between brood size and the mean condition of nestlings within a brood (Univariate Analysis of Variance; $F_{6,26}=0.89$; $p=0.51$).

For all analyses, I used Akaike's Information Criterion (AIC) to rank models within the model set (Burnham and Anderson 2002). The log-likelihood

for each model was used to calculate Akaike's Information Criterion adjusted for small sample sizes AICc (Burnham and Anderson 2002). The AICc values give a measure of the level of fit of the data to the model weighted by the number of variables in the model. Δ AICc values were calculated as the differences between the AICc of each model and that of the most parsimonious model. Models where the Δ AICc <2 were considered to have strong support and models where Δ AICc <4 were considered to have moderate support (Burnham and Anderson 2002). AICc weights (w_i), which indicate the likelihood of the model given the data, relative to the other models in the candidate set, were calculated from the Δ AICc values and used to assess the relative support for each of the models. Models with high w_i values were the best-supported by the data (Burnham and Anderson 2002). Parameter likelihoods and parameter estimates and their associated unconditional standard errors were also computed to assess the relative influences of the parameters present in the best-supported models. AIC parameter likelihood is the sum of the w_i of all models in which the parameter was included. An AIC parameter estimate is defined as the mean estimate (across all models in the candidate set) of each parameter weighted by the w_i of each model in which the parameter was included. An AIC unconditional standard error is defined as the standard error of each parameter weighted by the AICc weight of each model in which the parameter was included (Burnham and Anderson 2002). Pearson's r^2 was included as a measure of model fit. Models were tested for residuals and outliers, using Studentized residuals and Cook's

distance; all models were found to be within the acceptable limits. All analyses were done using SPSS version 16.0 (SPSS Inc., Chicago, Illinois).

3.4 Results

Seasonal and inter-annual variation in breeding performance

Barn owls began breeding earlier and young hatched almost 2 months earlier in 2008 than 2007. Clutch sizes were also larger in 2008 than 2007 (Table 10). Inter-annual variation in clutch size was due to the earlier onset of reproduction combined with seasonal declines in clutch size (Figure 5). The only strongly supported model ($\Delta AIC_C < 2$) in the candidate set examining date and year effects on clutch size included date (Table 11). Year was included in the second best model but its parameter likelihood was relatively low.

Despite inter-annual variation in the timing of breeding and seasonal declines in clutch size, neither year nor date influenced the number of chicks fledged, or the mean condition of the brood (Table 11). The null model ranked highest in both candidate sets, and the parameter likelihoods for year and date did not receive strong support in either analyses (<0.3).

Table 10 Inter-annual variation in breeding performance and diet quality of barn owls in the Fraser Valley between March and August 2007 and 2008. Means are presented \pm 1SD. Diet quality calculated as the proportion of prey biomass consisting of voles in the diet of active nest sites. Brood condition score was based on the measurement for each chick in the brood and its deviation from the mean sex-specific asymptotic mass during the nestling period divided by the sex-specific standard deviation. The mean score for all the chicks within each brood was used to determine the condition of a brood. Proportion of voles in the diet was measured as the biomass composed of voles (biomass of voles (g)/total biomass of all prey items (g)).

Variable	2007	2008	t-statistic	P-value
Clutch size	4.61 \pm 1.24 (n=18)	6.05 \pm 1.62 (n=19)	-3.03	0.01
# Hatched	3.85 \pm 1.31 (n=20)	5.38 \pm 1.53 (n=21)	-3.43	0.00
# Fledged	2.66 \pm 0.94 (n=29)	2.79 \pm 1.37 (n=34)	-0.46	0.65
Brood condition	0.06 \pm 0.87 (n=18)	-0.02 \pm 0.65 (n=28)	0.38	0.71
Diet quality	0.68 \pm 0.17 (n=18)	0.73 \pm 0.17 (n=21)	-0.91	0.37

Table 11 AIC ranking (by w_i) of candidate models examining how hatching date and year influence clutch size, fledging success and brood condition in barn owl nests in the Fraser Valley, British Columbia, in 2007 and 2008.

Model	K	N	AICc	Δ AICc	w_i	R ²
Clutch Size						
Date	3	37	20.11	0.00	0.72	0.43
Date + Year	4	37	22.54	2.43	0.28	0.44
Year	3	37	31.98	11.88	0.00	0.03
Null	2	37	38.23	18.12	0.00	0.00
Fledging Success						
Null	2	63	24.11	0.00	0.54	0
Date	3	63	26.09	1.98	0.20	0.00
Year	3	63	26.09	1.99	0.20	0.00
Date + Year	4	63	28.32	4.21	0.07	0.00
Brood Condition						
Null	2	46	-25.42	0.00	0.56	0.00
Date	3	46	-23.33	2.09	0.20	0.05
Year	3	46	-23.28	2.15	0.19	0.04
Date + Year	4	46	-20.94	4.48	0.06	0.06

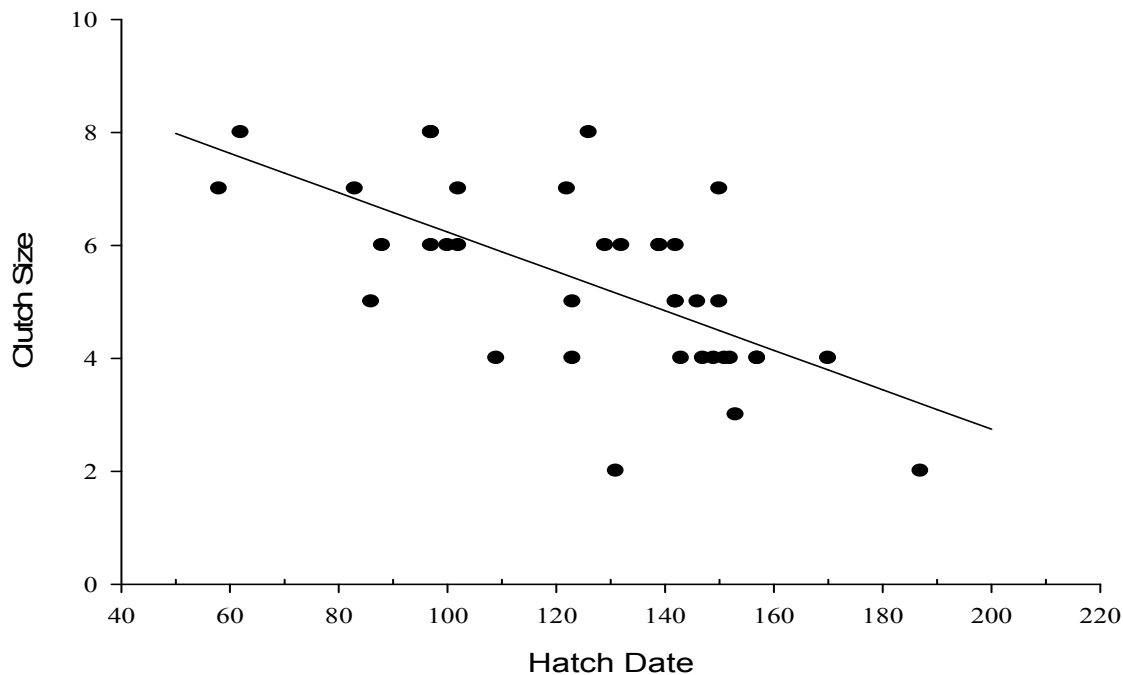


Figure 5 The relationship between clutch size and hatch date of the first chick in each brood of nesting barn owls in the Fraser Valley. The points include data from both 2007 and 2008. The line represents the predicted values from the best-supported AIC model (Multiple regression, Clutch Size = $10 - 0.04 \times \text{Hatch Date}$). The points represent individual nest sites ($n=37$; $R^2=0.11$).

Variation in diet

Barn owls ate a variety of prey, with a total of 17 different species found in the pellets collected during this study (Figure 6). Voles (primarily field voles, *Microtus townsendi*) were the main prey item, although shrews (*Sorex spp.*) were relatively common prey items, particularly in 2007. The proportion of biomass composed of voles did not vary between years (Table 9; $t = -0.91$, $df = 37$, $p = 0.37$) or across the season (data not shown). However, there was considerable variation among nest sites in the proportion of biomass composed of voles (range: 0.36-0.95; Table 10).

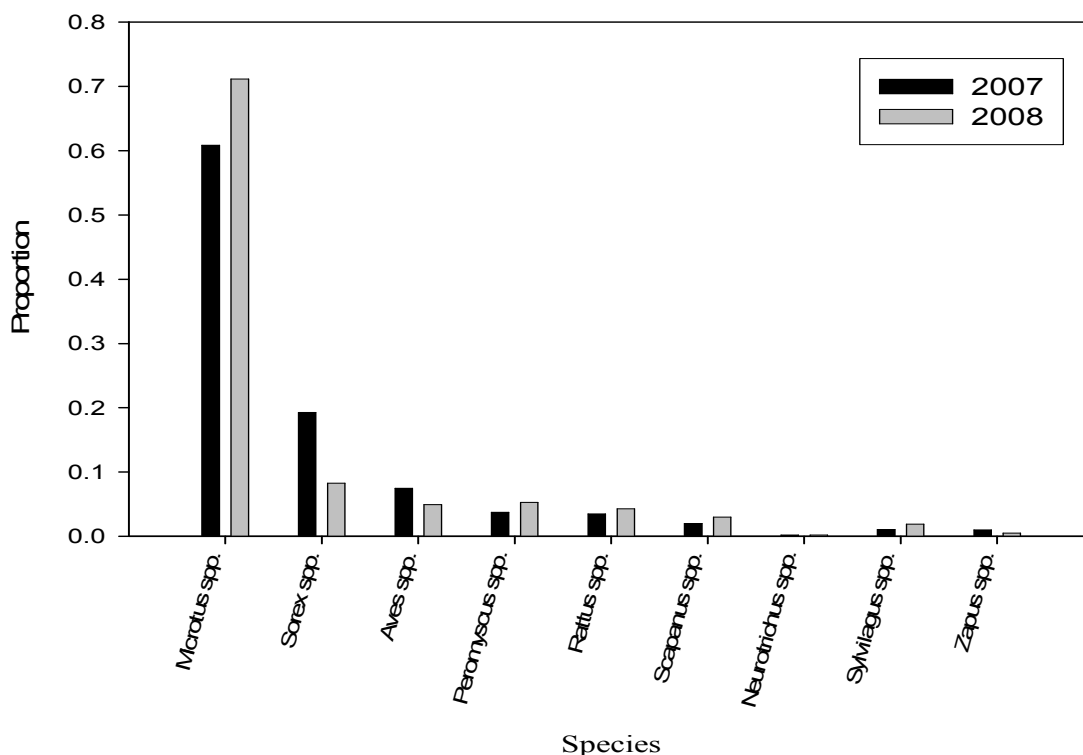


Figure 6 The proportion of total biomass contributed by each prey taxon found in barn owl pellets collected in 2007 (n=886) and 2008 (n=638). Prey were classified as *Microtus* spp.: townsendii and oregoni, *Sorex* spp.: cinereus, monticolus, and vagrans, Aves: *Sturnus vulgaris*, *Colaptes auratus*, *Columba livia*, Passeriformes, *Calidris mauri*, *Peromyscus maniculatus*, *Rattus* spp.: rattus and norvegicus, *Scapanus orarius*, *Neurotrichus gibbsii*, *Sylvilagus floridanus*, *Zapus trinotatus*. For the common names of prey species see appendix 1.

Does landscape composition and configuration explain variation in diet quality?

I found some evidence that the landscape composition at a nest site influenced the diet of the female barn owl and the brood during the breeding season. Barn owls with more impermeable surface within 1 km of the nest site had a lower proportion of vole biomass in their diet. In the AIC analysis, the amount of impermeable surface was in two of the six strongly supported models ($\Delta AIC_C < 2$) including the best model (Table 12). However, the parameter

likelihood was not high and the weighted parameter estimate had an unconditional standard error that bounded zero (Table 13). The degree of habitat fragmentation, estimated using the number of grass patches within 1 km of the nest site, also had a weak negative impact on the proportion of voles in the diet. The variable number of grass patches, was in three of the six strongly supported models ($\Delta AIC_C < 2$; Table 12), but again the parameter likelihood was not high and the weighted parameter estimate had an unconditional standard error that bounded zero (Table 13). Length of highways was in two of the six strongly supported models ($\Delta AIC_C < 2$; Table 12). However, this variable received even less support than the two other variables, and the weighted parameter estimate had an unconditional standard error that bounded zero (Table 13).

Table 12 AIC ranking (by w_i) of candidate models examining how land use influences diet quality (proportion vole biomass) of barn owl nest sites in the Fraser Valley, British Columbia, in 2007 and 2008. Landscape variables are defined in Chapter 2: Table 1.

Model	N	K	AICc	$\Delta AICc$	W_i	R^2
Imp.	3	39	-135.81	0.00	0.18	0.06
Null	2	39	-135.80	0.01	0.18	0.00
Patches	3	39	-135.57	0.23	0.16	0.05
Imp. + Patches	4	39	-135.38	0.43	0.14	0.11
Hwy	3	39	-134.40	1.40	0.09	0.03
Hwy + Patches	4	39	-134.17	1.63	0.08	0.08
Hwy + Imp.	4	39	-133.35	2.45	0.05	0.06
Hwy + Imp. + Patches	5	39	-132.77	3.03	0.04	0.11
Imp. + Grass	5	39	-131.22	4.59	0.02	0.07
Grass + Patches	5	39	-131.18	4.63	0.02	0.07
Grass	4	39	-131.06	4.74	0.02	0.00
Imp. + Grass + Patches	6	39	-130.09	5.71	0.01	0.11
Hwy + Grass	5	39	-129.49	6.31	0.01	0.03
Hwy + Patches + Grass	6	39	-129.20	6.60	0.01	0.09
Hwy + Imp. + Grass	6	39	-128.45	7.36	0.00	0.07
Hwy + Imp. + Grass + Patches	7	39	-127.14	8.66	0.00	0.11

Table 13 Parameter likelihoods, weighted estimates and unconditional standard errors of every variable included in the candidate model set predicting how land use influences diet quality (proportion vole biomass) of barn owl nest sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1	0.75	0.06
Imp.	0.45	-0.06	0.09
Patches	0.46	-0.01	0.01
Hwy	0.28	-0.01	0.01
Grass	0.08	0.001	0.01
Grass verge	0.08	0.000	0.00

Does diet quality increase fledging success or chick condition in broods?

I found strong support for the hypothesis that diet quality, calculated as the proportion of vole biomass in the diet, influenced fledging success (Figure 7).

The model that included diet quality effects on fledging success received three times more support than the null model (Table 14), and had a positive impact on fledging success (Table 15). In contrast, I found no evidence that diet quality influenced mean brood condition. The model that included diet quality received minimal support; consequently it was ranked below the null model (Table 14) and the weighted parameter estimate had an unconditional standard error that bounded zero (Table 15).

Table 14 AIC ranking (by w_i) of candidate models examining how diet quality (i.e. proportion of vole biomass in diet) influences fledging success and brood condition at barn owl nest sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Model	K	N	AICc	ΔAICc	w_i	R²
Fledging success						
Diet	3	39	-1.21	0.00	0.76	0.11
Null	2	39	1.10	2.31	0.24	0.00
Brood condition						
Null	2	38	-14.98	0.00	0.74	0.00
Diet	3	38	-12.90	2.074	0.26	0.09

Table 15 Parameter likelihoods, weighted estimates and unconditional standard errors of every variable included in the candidate model set predicting how diet quality (i.e. proportion of vole biomass in diet) influences fledging success and brood condition at barn owl nest sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Fledging success			
Intercept	1	1.91	0.80
Diet	0.76	1.48	1.12
Brood condition			
Intercept	1	0.07	0.26
Diet	0.26	-0.11	0.29

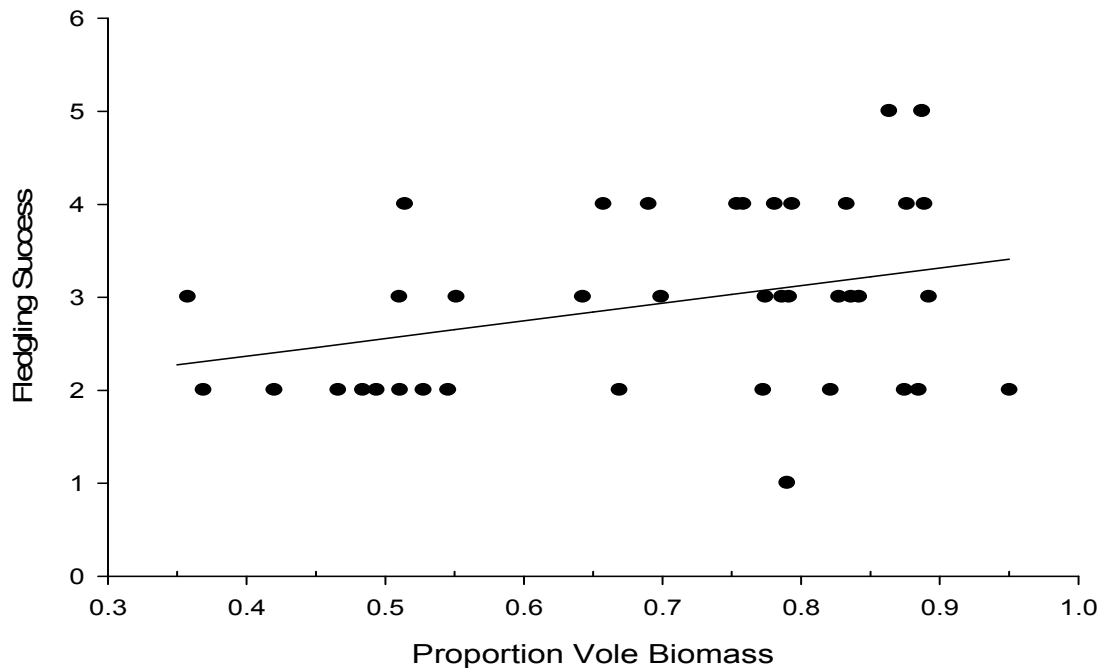


Figure 7 The relationship between fledging success, measured as the number of chicks within each brood that made it to 45-55 days, and diet quality (i.e. proportion of total biomass composed of voles) for barn owls nesting in the Fraser Valley in 2007 and 2008. The line represents the predicted values for the best-supported AIC model (Multiple regression, $Fledging\ Success = 1.9 + 1.48 * Diet\ Quality$. Parameters in this equation are weighted parameter estimates from an AIC analysis (Table 15). The points represent individual nest sites ($n=39$; $R^2=0.11$).

Does landscape composition or configuration influence fledging success or brood condition?

I found evidence that one feature of the landscape influenced fledging success; barn owls whose nests sites were surrounded by larger areas of impermeable surface fledged fewer young (Table 16; Figure 8). The area of impermeable surface was included in the two strongly supported models ($\Delta AICc < 2$), and the two models with moderate support ($2 < \Delta AICc < 4$), and consequently had a high parameter likelihood (Table 17). There was little evidence that the number of patches of grass, the amount of grass cover, or the length of highway

within 1 km of the nest site influenced fledging success. The number of grass patches was included in the second best supported model but had a lower parameter likelihood and a weighted parameter estimate with an unconditional standard error that bounded zero (Table 17). The amount of grass cover and the length of highway were not included in any of the top models, consequently these variables had even lower parameter likelihoods and weighted parameter estimates with unconditional standard errors that bounded zero (Table 17).

Table 16 AIC ranking (by w_i) of candidate models examining how land use influences fledging success of barn owl chicks in the Fraser Valley, British Columbia, in 2007 and 2008. Landscape variables are defined in Chapter 2: Table 1.

Model	K	N	AICc	ΔAICc	W_i	R²
Imp.	3	63	19.90	0.00	0.38	0.10
Imp. + Patches	4	63	21.77	1.87	0.15	0.10
Hwy + Imp.	4	63	22.10	2.21	0.13	0.10
Imp. + Grass	5	63	23.31	3.42	0.07	0.11
Hwy	3	63	23.94	4.05	0.05	0.04
Hwy + Imp. + Patches	5	63	24.05	4.15	0.05	0.10
Null	2	63	24.11	4.21	0.05	0.00
Imp. + Grass + Patches	6	63	24.69	4.80	0.03	0.13
Hwy + Patches	4	63	25.75	5.86	0.02	0.04
Hwy + Imp. + Grass	6	63	25.76	5.86	0.02	0.11
Patches	3	63	25.86	5.96	0.02	0.01
Hwy + Imp. + Grass + Patches	7	63	27.21	7.31	0.01	0.13
Grass	4	63	27.75	7.86	0.01	0.01
Grass + Patches	5	63	28.19	8.30	0.01	0.04
Hwy + Grass	5	63	28.31	8.41	0.01	0.04
Hwy + Patches + Grass	6	63	29.50	9.61	0.00	0.06

Table 17 Parameter likelihoods, weighted estimates and unconditional standard errors of every variable included in the candidate model set predicting fledging success of barn owl chicks from nest sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1	3.04	0.33
Imp.	0.84	-0.92	0.62
Patches	0.29	-0.02	0.03
Hwy	0.28	-0.01	0.05
Grass	0.14	0.08	0.17
Grass verge	0.14	0.00	0.01

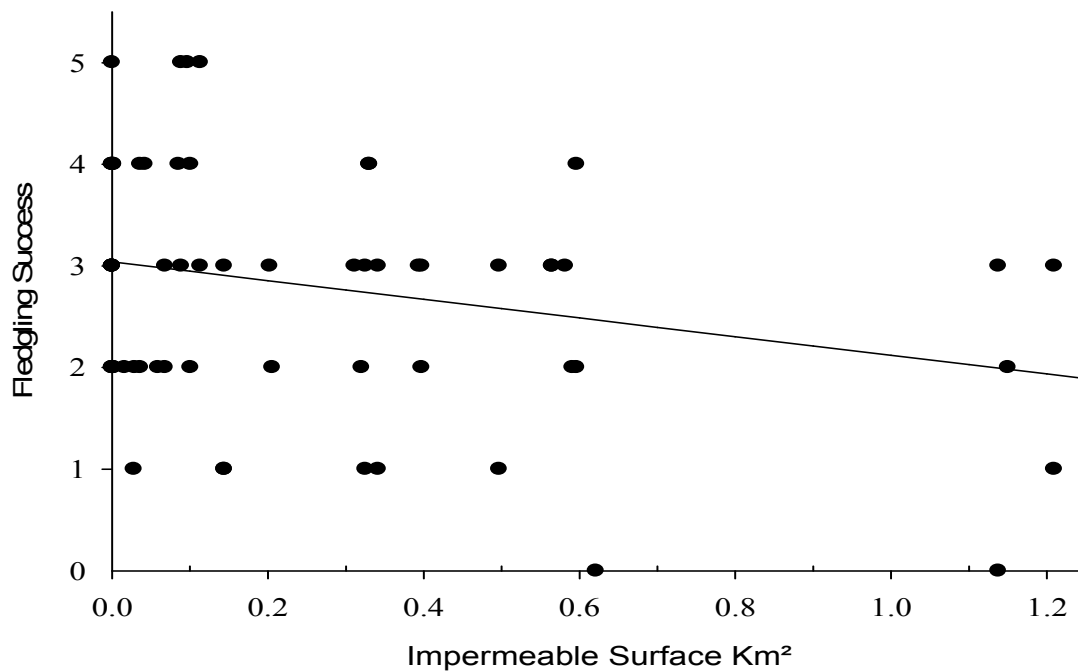


Figure 8 The relationship between fledging success, measured as the number of chicks that survive to 45-55 days, and the amount of impermeable surface (km²) within a 1 km radius of each barn owl nest site in the Fraser Valley. The line represents the values from the best-supported AIC model (Multiple regression, Fledging Success= 3.0 – 0.92*Imp. Parameters in this equation are weighted parameter estimates from an AIC analysis (Table 17). The points represent individual nest sites (n=63: R²=0.10).

I found little evidence that brood condition was influenced by landscape composition around the nest site. Three of the 16 candidate models received strong support ($\Delta AICc < 2$), but the null model ranked highest and had 1.6 and 2.4 times the support of models that included the length of highways and the amount of impermeable surface within 1 km of the nest site, respectively (Table 18). The parameter likelihoods of all variables were not high and the weighted parameter estimates had unconditional standard errors that bounded zero (Table 19).

Table 18 AIC ranking (by w_i) of candidate models examining how land use influences barn owl brood condition in nests in the Fraser Valley, British Columbia, in 2007 and 2008. Landscape variables are defined in Chapter 2: Table 1.

Model	K	N	AICc	$\Delta AICc$	W_i	R^2
Null	2	46	-25.42	0	0.24	0.00
Hwy	3	46	-24.58	0.85	0.15	0.03
Imp.	3	46	-23.75	1.67	0.10	0.01
Grass	4	46	-23.25	2.18	0.08	0.05
Patches	3	46	-23.16	2.26	0.08	0.00
Hwy + Grass	5	46	-22.43	2.99	0.05	0.02
Imp. + Grass	5	46	-22.34	3.08	0.05	0.09
Hwy + Imp.	4	46	-22.34	3.09	0.05	0.03
Hwy + Patches	4	46	-22.24	3.19	0.05	0.03
Grass + Patches	5	46	-21.53	3.90	0.03	0.03
Imp. + Patches	4	46	-21.38	4.05	0.03	0.01
Imp. + Grass + Patches	6	46	-20.80	4.62	0.02	0.02
Hwy + Patches + Grass	6	46	-20.58	4.85	0.02	0.10
Hwy + Imp. + Grass	6	46	-20.51	4.92	0.02	0.10
Hwy + Imp. + Patches	5	46	-19.87	5.55	0.01	0.04
Hwy + Imp. + Grass + Patches	7	46	-18.74	6.68	0.01	0.11

Table 19 Parameter likelihoods, weighted parameter estimates and unconditional standard errors of every variable included in the candidate model set predicting barn owl brood condition in nest sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1.00	3.33	0.61
Imp.	0.34	0.33	0.56
Patches	0.24	-0.02	0.04
Hwy	0.22	0.02	0.08
Grass	0.10	-0.04	0.10
Grass verge	0.10	-0.01	0.01

Are landscape effects on productivity mediated via impacts on diet quality?

To assess whether the amount of impermeable surface around a nest site has an effect on fledging success or brood condition that is independent of diet quality, I evaluated the relative support for models including diet quality and/or impermeable surface. There was little evidence for direct effects of the area of impermeable surface around nest sites on fledging success. The only strongly supported model ($\Delta AICc < 2$) included diet quality and this model received almost four times the support of the second ranked model that included both diet quality and impermeable surface (Table 20). The diet quality variable also had a higher parameter likelihood than the landscape variable (Table 21). There was no support for that either diet quality or the amount of impermeable surface influenced brood condition (Table 20). The null model ranked highest, and was the only strongly supported model ($\Delta AICc < 2$). In addition, the parameter estimate for both diet quality and impermeable surface were both opposite to what was predicted (Table 21).

Table 20 AIC ranking (by w_i) of candidate models examining how land use and diet quality (measured as the proportion of vole biomass in the diet) influences fledging success and brood condition at barn owl nest sites in the Fraser Valley, British Columbia, in 2007 and 2008. Landscape variables are defined in Chapter 2: Table 1.

Model	K	N	AICc	Δ AICc	W_i	R ²
Fledging success						
Diet	3	39	-1.21	0.00	0.56	0.11
Diet + Imp.	4	39	1.10	2.31	0.18	0.12
Null	2	39	1.10	2.31	0.18	0.00
Imp.	3	39	2.64	3.84	0.08	0.02
Brood condition						
Null	2	38	-14.98	0.00	0.55	0.09
Diet	3	38	-12.90	2.07	0.20	0.01
Imp	3	38	-12.90	2.08	0.19	0.01
Diet + Imp.	4	38	-10.53	4.44	0.06	0.01

Table 21 Parameter likelihoods, weighted parameter estimates and unconditional standard errors of every variable included in the candidate model set predicting how land use and diet quality (measured as the proportion of vole biomass in the diet) influences fledging success and brood condition at barn owl nest sites in the Fraser Valley, British Columbia, in 2007 and 2008.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Fledging success			
Intercept	1	1.96	0.82
Diet	0.74	1.42	1.13
Imp.	0.26	-0.08	0.21
Brood condition			
Intercept	1	0.05	0.27
Diet	0.25	-0.10	0.28
Imp.	0.25	0.06	0.19

3.5 Discussion

The composition and configuration of the agricultural landscape is expected to influence the rodent community and consequently impact the diet and productivity of barn owls. Colvin (1985) and Taylor (1994) argued that the loss of grassland will reduce vole abundance and that the reduced availability of their

preferred prey will lower barn owl breeding success. My study found that the amount of impermeable surface, and not grass cover, within the home range of a barn owl influenced fledging success. However, my study did confirm that the proportion of voles found in the diet of barn owls influences fledging success. There was little evidence of direct effects of land use on fledgling success, as the negative relationship between impermeable surface and fledgling success did not hold after controlling for diet quality. Instead, the weak relationship between the amount of impermeable surface and diet quality and the strong relationship between diet quality and fledging success suggest that landscape effects on fledging success are mediated via their impact on diet quality.

The small mammal community that comprises the prey base for barn owls is likely to be influenced by urban development and changes to the quantity and type of grassland in the agricultural landscape. Urbanization is expected to lead to an increase in the abundance of rats and house mice and reduced abundance of voles in the remaining grassland (Yalden 1980; Dickman and Doncaster 1989; Bock et al. 2002; Mahan and O'Connell 2005). Vole population declines in the remaining grassland could be due to predation by cats or rats in adjacent urban areas (Crooks and Soulé 1999). The observed decrease in the proportion of voles in the diet of barn owls as the amount of impermeable surface (urbanization) increases is consistent with the expected changes in the barn owl's prey community. However, the level of model uncertainty in my AIC based analysis indicates that the negative relationship between urbanization and the proportion of voles in the diet was relatively weak. There are two potential

explanations for the high level of model uncertainty. First, the level of model uncertainty may simply be a consequence of the relatively small sample size (n=39). Second, the foraging preference and/or foraging abilities of barn owl might to some extent mask how land composition influences prey community. Barn owls are considered vole specialists (Fast and Ambrose 1976; Derting and Cranford 1989), and as such, are expected to actively seek voles even when they are not particularly abundant. Barn owls may also be less capable of catching some alternative prey, such as adult rats (>200g), that are abundant in urban areas (Taylor 1994). Consequently, the diet of barn owls living in more urban areas may be influenced by, but not accurately reflect the prey community in urban areas. If this argument were true you might predict that owls living in more urban areas are forced to spend more time foraging or deliver prey at a reduced rate. Further work on the relationship between urbanization, diet composition and foraging behaviour of barn owls is needed.

Changes in the amount and types of grass cover are also expected to lead to changes in the prey community (Nagorsen 1996; Nagorsen 2005). In the case of voles, abundance is closely linked to non-intensively utilized grassland (i.e. grassland that is cut once every two years; Gorman and Reynolds 1993, Nagorsen 2005, Aschwanden et al. 2007) and the loss of such grasslands has been linked to an overall decline of vole populations in agricultural landscapes (Butet and Leroux 2001). One would therefore expect a direct association between non-intensively utilized grassland and the diet of owls. Romanowski and Zmihorski (2008) showed that this was the case for nesting long-eared owls (*Asio*

otus) in Poland, as they found a higher proportion of voles in the diet when there was more permanent grassland within the home-range (700 m radius).

Interestingly, I found no evidence that diet composition varied with the amount of grass cover within barn owl home ranges. There are at least two reasons for why the proportion of voles may not have been related to the amount of grass cover.

First, the metric used, grass cover within the home range might have been too coarse and consequently failed to quantify the area of high quality vole habitat, and variation in the abundance of voles. However, based on the current land use mapping, there is very little non-intensively utilized grassland left (~ 5%) within the home ranges of barn owls in the Fraser Valley and therefore one would expect more intensively utilized grassland and grass verges to be important foraging habitat for barn owls. Habitat specific information on vole abundance (e.g., by live-trapping) is unavailable but would facilitate future analyses. Second, it is possible that the prey community within a grassland is strongly influenced by its proximity to other habitat features within the landscape and that the location of grassland habitat is as important as the amount. Habitat features that might influence the prey community in adjacent grassland include impermeable surfaces and development occupied by rates or cats, roads that limit daily vole movement and dispersal, and other non-grass crops that might be more permeable to some species than others. Information on how habitat features influence vole communities in grassland habitat would allow this explanation to be evaluated.

As predicted if barn owls are vole specialists and urbanization leads to a reduction in vole abundance that reduces productivity, I found compelling evidence that the amount of impermeable surface within a barn owl's home range had a negative effect on the number of chicks fledged. Furthermore, this relationship was driven primarily by diet quality rather than being a direct effect of the amount of impermeable surface. The high level of support for the model relating the amount of impermeable surface to fledging success, and the analysis showing that diet rather than landscape composition explains variation in fledging success, suggest that the relatively weak support for landscape effects on diet composition was in part due to small sample size (see above). My results and conclusion are also consistent with previous work examining the relationship between landscape composition and nesting success of barn owls in southern England. Bond et al. (2005) found that unsuccessful sites were associated with higher levels of poor-quality small-mammal habitat, such as suburbia and improved grassland.

Landscape composition effects on diet quality were expected to influence the quality as well as the number of barn owl nestlings that fledge. However, I found no evidence that the amount of impermeable surface or diet quality influenced the condition of barn owl broods. Differences in the landscape lead to differences in productivity, which were primarily driven by variation in the level of brood reduction observed at a site (90% of nests in this study experienced brood reduction). Brood reduction may therefore be the response to variation in quantity and quality of food, and thus limit the ability to detect landscape effects on

condition. In general, brood reduction is fairly common in barn owls; last-hatched nestlings, in particular, suffer high mortality, usually within 2-10 days of hatching (See Andrusiak 1994; Taylor 1994). Previous research has also shown that breeding barn owls will not increase their feeding rate when their brood has been experimentally enlarged (Roulin et al. 1999). It is therefore plausible that parents would rather invest more energy in having a second brood later in the season, or next season, as overall reproductive output in owls has shown to be more related to the number than the size of the broods produced during a lifetime (Korpimäki 1992; Marti 1997; Brommer et al. 1998).

Changes in the configuration of the agricultural landscape, especially increased fragmentation, have been shown to have a direct negative effect on many wildlife populations (Forman et al. 2003; Jaeger 2005; Fahrig and Rytwinski 2009). Landscape configuration was expected to impact both barn owl survival and foraging efficiency, and consequently influence fledging success and brood condition. However, I found no evidence that the length of highways, which may elevate the risk of adult mortality, had any influence on productivity. Two breeding attempts monitored during this study were abandoned during the early stages of chick raising and there was some evidence that abandonment was associated with the highway related mortality of one parent. In both cases the site was close to a major highway and after the breeding attempt failed only one owl was observed at each site for 2-3 months. In one case a dead owl was found on the highway within 500 m of the nest site. Additional long-term data would give a clearer indication whether the lengths of highways within a barn owl home

range can have a significant impact barn owl productivity. I also found no evidence that fragmentation, measured using the number of grass patches within 1 km of a nest site had any effect on fledging success or brood condition. However, greater understanding barn owl foraging behaviour is needed to define fragmentation from the perspective of a barn owl and determine whether fragmentation of the agricultural landscape can influence fledging success and brood condition.

There remains considerable debate about the foraging preferences of barn owls and the importance of voles for successful reproduction. Fast and Ambrose (1976) and Derting and Cranford (1989) demonstrated that when given a choice, barn owls selectively choose to hunt voles rather than other available rodent species. In addition, numerous field studies comparing the barn owl diet with the relative abundance of different prey species showed that voles form a larger proportion of the diet than expected based on their relative abundance in the surrounding landscape (Marti 1974; Colvin 1984; Gubanyi et al. 1992). In contrast, Meek (2009) found no evidence that habitat influences barn owl diet and argued that barn owls are opportunistic foragers, which respond to temporal fluctuations in the availability of different prey species. I found that voles constituted, on average 67% of the prey biomass consumed by female barn owls and their brood during the nestling period and that reproductive success declined as the proportion of voles in the diet decreased. Despite finding considerable variation in the diet composition of barn owls, my study therefore supports the conventional wisdom that voles are a key component of their diet.

If voles are a critical component of the diet, one might expect barn owl productivity to track annual vole cycles. Vole cycles have been demonstrated to be closely linked to the fledging success of barn owls in Scotland, with fledging success being greatest during peak vole years and lowest during the crash phase of the three year vole cycle (Taylor 1994). Vole cycles have similar impacts on the fledging success and first-year survival of Tengmalm's and Ural owls (Korpimäki and Lagerström 1988; Korpimäki 1992). Field vole abundance does fluctuate annually in the Fraser Valley (Krebs 1979) and inter-annual fluctuations in vole abundance in the diet of barn owls have also been detected (Campbell et al. 1987). I might therefore have expected inter-annual variation in productivity between the two years, but detected none. Moreover, the proportion of voles consumed across all nest sites did not vary significantly between years, and in comparison to other pellets studies conducted in the Fraser Valley, the proportion of voles seems to have been in the increase phase (Dawe et al. 1978; Campbell et al. 1987). However, I did observe large inter-annual variation in the onset of breeding, with the breeding season starting almost two months later in 2007 compared to 2008. Although this appears to have been driven more by climate than inter annual variation in prey abundance: 2007 had above-normal precipitation in the three first months, with March having close to twice as much rain than normally expected (214.8 vs. 111.8 mm), in comparison 2008 had below average precipitation for the same time period (Environment Canada 2009). The increased amount in rainfall might impair the owl's hunting efficiency, as heavy rains are often associated with strong winds, which would make it

harder for the owls to detect prey using auditory cues. In addition, rainfall during winter when temperatures are close to zero has shown to reduce vole activity (Baumler 1975; Lehmann and Sommersberg 1980).

In summary, my work on barn owl diet and breeding ecology in the Fraser Valley demonstrates that increased urbanization of the agricultural landscape influences fledging success. This study also suggests that this pattern is driven by the effect of urbanization on the prey communities in grasslands. However, further work on how urbanization and other non-grassland habitat surrounding grassland influence the rodent community within remaining grassland would further our understanding of the exact mechanisms behind these trends. This may facilitate the management of the remaining grassland habitat in the Fraser Valley and contribute to the successful reproduction of barn owls in more urban environments.

4: Conclusion

Krebs et al. (1999) estimated that, “in the past 20 years, ten million breeding individuals of ten species of farmland birds have disappeared from the British countryside”. Since this time, many studies have continued to show that birds associated with agricultural landscapes have experienced strong population declines and range contractions across both Western Europe and North America (Murphy 2003; Peterjohn 2003; Brennan and Kuvlesky 2005; Donald et al. 2006). The declines have been linked to changes in agricultural practices (i.e. use of agrochemicals, modernized machinery; Fuller et al. 1995; Krebs et al. 1999; Wilson et al. 2005) and the loss of agricultural land and grassland to urbanization (Filippi-Codaccioni et al. 2008; Ludwig et al. 2009). These human-induced changes have been shown to impact both the survival and productivity of several species of birds, all with varying ecology and life history strategies. Thus, it is vital to understand how individual species respond to human-induced changes in landscape composition and configuration in order to maintain the development of land management practices that continue to support biodiversity.

In this thesis, I have examined how the distribution and productivity of the barn owl, an iconic bird strongly linked to agricultural landscapes in North America, has responded to changes in landscape composition and configuration, and how current features of the landscape influence their distribution, diet and productivity. My research was conducted on the barn owl population in the Fraser

Valley, British Columbia, Canada, an area which has undergone considerable changes in land use over the last 35 years, driven both by changes in agricultural practices and increased urbanization.

Chapter 2 focused on the landscape features predicting the distribution of barn owls in the Fraser Valley. I examined how changes in barn owl occurrence were influenced by changes in landscape composition and configuration over the last 15 years, and assessed the landscape features predicting the current distribution of owls. Based on previous work, the availability of grassland habitat for foraging was predicted to be the key feature affecting distribution (Colvin 1984; Shawyer and Shawyer 1995; Taylor 1994). However, I found that the most important landscape feature impacting the persistence of barn owls as well as their current distribution was associated with traffic volume on highways. This is consistent with accumulating evidence from Europe and North America that vehicle collisions are a major cause of barn owl mortality (De Bruijn 1994; Baudvin 1997; Newton et al. 1997; Lodé 2000; Fajardo 2001; Ramsden 2003; Boves 2007; Preston and Powers 2006). Thus the lower rates of occupancy I observed at sites close to highways are likely due to higher rates of mortality, and therefore higher rates of turnover of breeding pairs at these sites. In addition, a cause for concern also recognized by previous research (see Taylor 1994) is the rate at which old barns and trees functioning as nest/roost sites are lost due to urban development. Over the last 15 years, there has been ~2.2% annual losses of suitable nest/roosting sites within my study area.

Landscape structure and configuration may lead to reduced abundance (Chapter 2), but decline in nest/roost sites, food availability and increased mortality may also reduce successful reproduction (Lindenmayer and Fischer 2006). In order to further understand the impacts of current landscape on productivity, Chapter 3 investigated three hypotheses about how landscape features impacts the diet and productivity of barn owls. First, there is considerable evidence to suggest that voles are a key component of the barn owl's diet (Marti 1974; Fast and Ambrose 1976; Colvin 1984; Derting and Cranford 1989; Taylor 1994), and I investigated whether landscape composition and configuration explains variation in the proportion of voles in the diet, a proxy for diet quality. I found some evidence for this being the case, as barn owls with home ranges with a greater area of urbanization had a lower proportion of vole biomass in their diet. This would suggest as areas become increasingly urbanized, there is a change in the prey community, with an increase in the abundance of human-associated rodents (rats and house mice) and reduced abundance of voles in the remaining grassland (Yalden 1980; Dickman and Doncaster 1987; Bock et al. 2002; Mahan and O'Connell 2005). Therefore, vole habitat close to urban areas may become degraded due to increased predation from rats and cats (Crooks and Soulé 1999).

My second hypothesis was whether this observed variation in diet quality influenced the productivity of breeding barn owls. I assessed this by examining which landscape features influenced the number of chicks that fledged, and the overall condition of the brood. Variation in fledging success was positively

influenced by diet quality, consistent with previous work by Gubanyi et al. (1992). In contrast, there was no evidence that brood condition was influenced by either diet or landscape features. Although there is variability in the condition of young within a brood, barn owls tend to lay an optimistic number of eggs and then reduce their brood size to suit current conditions via brood reduction (see Baudvin 1980; Andrusiak 1994; Taylor 1994; Roulin et al. 1999). Thus, barn owls are able to buffer most of the brood from the impacts of varying food conditions. The final hypothesis concerned the potential direct effects of landscape composition and configuration on fledging success. Although I found evidence that the amount of urbanization reduced fledging success, this relationship was driven primarily by variation in diet quality rather than being a direct effect of urbanization.

In summary, my work on the landscape ecology of barns owls in the Fraser Valley has demonstrated that changes to the agricultural landscape can influence the distribution and demography of barn owls in three ways. First, as a result of old wooden barns being replaced and large old trees removed for urban development there has been a gradual loss of potential nest/roost sites. Second, sites with increased traffic expose and highways within their home ranges are less likely to be persistently occupied by barn owls, suggesting increased vehicle mortality (Chapter 2). Third, urbanization of the agricultural landscape decreases the abundance of voles in the diet of barn owls, which negatively impacts productivity (Chapter 3). Overall, these results show that the survival and productivity of barn owls in the Fraser Valley seem to be influenced by both

composition and configuration of the landscape and points to the importance of considering both when managing for barn owl habitat.

Future research focusing on monitoring foraging behaviour would be useful to investigate whether there are any costs associated with increased habitat fragmentation. For example, longer time spent foraging would be expected when habitats become increasingly fragmented, with potential implications for breeding success. In terms of management, a better understanding of how roads impact both behavioural responses and road mortality of barn owls would be important for developing mitigation measures during road construction and maintenance.

4.1 Management Recommendations

The Fraser Valley is under continued development pressure, and as a result of urbanization grasslands are still being lost and fragmented. The following is a list of recommendations for the management of barn owl in the Fraser Valley based on the results of this thesis.

Maintain productivity by:

- Halting the loss of roost/nest sites in the agricultural landscape.

Provide new nest boxes in favourable locations. Sites located > 1km from highways and with minimized amounts of impermeable surface are more likely to be occupied and produce more fledglings.

- Managing vole populations and hence diet quality. Managing vole populations is likely to require greater understanding of how urbanization influences rodent communities in remaining grasslands.

Reduce mortality by:

- Reducing the risk of vehicle collisions on highways. This could be accomplished by forcing barn owls to cross highways at heights above >4m by separating existing grass verges or grassland close to highways by hedges or a dense row of trees.

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Appendix: List of Prey Species Found in Pellets

Includes scientific and common names.

Prey species	
Scientific name	Common name
<i>Calidris mauri</i>	Western Sandpiper
<i>Colaptes auratus</i>	Northern flicker
<i>Columba livia</i>	Rock pigeon
<i>Microtus orgeni</i>	Creeping vole
<i>Microtus townsendii</i>	Field vole
<i>Neurotrichus gibbsii</i>	Shrew mole
<i>Passeriformes</i>	Small seed-eating birds
<i>Peromyscus maniculatus</i>	Deer mouse
<i>Rattus rattus</i>	Black rat
<i>Rattus norvegicus</i>	Norway rat
<i>Scapanus orarius</i>	Coast mole
<i>Sorex cinereus</i>	Common shrew
<i>Sorex monticolus</i>	Dusky shrew
<i>Sorex vagrans</i>	Vagrant shrew
<i>Sturnus vulgaris</i>	Starling
<i>Sylvilagus floridanus</i>	Eastern cottontail
<i>Zapus trinotatus</i>	Pacific jumping mouse