University of Alberta

Road effects on Banff National Park bird community composition and on the age distribution and health of male Ruby-crowned Kinglets and Red-breasted Nuthatches

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Ecology

Biological Sciences

Edmonton, Alberta
Fall 2008

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Your file Votre référence
ISBN: 978-0-494-47207-1
Our file Notre référence
ISBN: 978-0-494-47207-1

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Abstract

Roads affect bird populations in a variety of direct and indirect ways. I assessed these potential effects by comparing community diversity and attributes of individual health at sites near to (50 m) and far from (400 m) a highway and a secondary road near Banff, Canada. The health measures targeted two species – red-breasted nuthatches and ruby-crowned kinglets – for which I recorded age, body mass, fluctuating asymmetry and four hematological measures. Community composition differed by habitat (aspen was more diverse than pine and spruce habitats) whereas road type and road proximity had lesser and interacting effects. Proportionately more young red-breasted nuthatches lived near the highway, but no health parameter varied with road proximity for either species. Overall, the road effects I detected were slight, suggesting either that birds are not much affected by roads at this site, or that my near and far sites were equally affected by road presence.

Acknowledgements

First, I would like to thank Colleen Cassady St. Clair for giving me the chance to work in her lab and for helping me along this endeavour. Thank you also for graciously offering me your own data to work on for the first part of this thesis. I would also like to thank my committee members, Erin Bayne and Glen Hvenegaard, for offering their advice during the course of this thesis.

This study was funded by the grant from the Alberta Sport, Recreation, Parks and Wildlife Foundation to M. Dubé and the grants from the Canadian Foundation for Innovation together with a Natural Science and Engineering Council (NSERC) Discovery Grant to C. C. St. Clair. M. Dubé was funded in part by a Canada Graduate Scholarship.

I am indebted to Parks Canada for allowing me to conduct field work in Banff National Park and for generously providing housing. Thank you also to Chris Sturdy for letting me use his lab facilities and microscope.

Thank you to Samantha Fischer for being such a wonderful field assistant. Your continuous enthusiasm and hard work carried me through these long hours in the field and through the ferocious mosquito attacks. Thank you to all my lab members for their expertise, support and friendship. A special thank you to Darren Proppe for learning with me the intricacies of leukocytes identification and for spending countless hours looking at slides in my company.

Lastly, thanks to Steven Dedesko who has been my better half since the start. Thank you for sitting through hours of tedious talks simply to make me feel better; without your continuous support and encouragement, this thesis would not be. Thank you to all my friends for always being there when I needed you and *un merci tout spécial à mes parents pour avoir laissé leur fille unique déménager en Alberta en poursuite de ses études et*

pour, comme dans tout ce que j'ai entrepris au cours de ma vie, m'avoir offert votre éternel amour et soutien.

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Chapter 1 – Introduction to the Thesis

Habitat loss and fragmentation transform unbroken habitats into a mosaic of small parcels that are isolated from one another (Hunter 2002). These changes are typified by a decrease in patch size and an increase in patch isolation (Andrén 1994), which can eventually lead to population declines and local extinctions (Wettstein and Schmid 1999, Reed 2004). An important source of habitat fragmentation is anthropogenic causes (Hunter 2002) and the associated ecological processes that have been altered by fragmentation have been studied extensively in agricultural and forestry related contexts (see Andrén 1994, Fahrig 2003, Cushman 2006, Ewers and Didham 2006 for reviews).

One type of anthropogenic fragmentation that is less well understood is the effects created by roads. Because roads form "lines of penetration" that initiate fragmentation in pristine habitat (Taaffe et al. 1963), their effects have attracted considerable study. In some cases, roads can provide tremendous net benefits for humans and for some wildlife species. For example, wolves travel along low-use corridors (Jalkotzy et al. 1997). Road edges are also beneficial for certain bird species. Usually, birds considered to be habitat generalists benefit from edges along corridors (Jalkotzy et al. 1997). Moreover, in South Dakota, grey partridges nest by the road side (Carroll and Crawford 1991). However, roads can also negatively impact wildlife both directly and indirectly (see Forman and Alexander 1998; Spellberg 1998; Trombulak and Frissell 2000; Coffin 2007 for reviews). Direct effects of roads on wildlife include habitat loss and collisions with vehicles. The effect of habitat loss is greater in small animals that have high site fidelity (Coffin 2007) and vehicle collision impacts are most important for slow moving species and ones that cross roads regularly (Coffin 2007). In Ontario, Canada, more than 32 000 vertebrates were killed by vehicles over a two-year period (Ashley and Robinson 1996). This included seven species of amphibians, 10 of reptiles, 21 of mammals and 62 of birds (Ashley and Robinson 1996).

Indirect effects of roads on wildlife are varied. An important indirect effect is fragmentation (Forman and Alexander 1998), which impedes movement in species such as the white-footed mouse (Merriam et al. 1989), creates metapopulations and alters genetic structure of the smaller populations (Andrews 1990, Reh and Seitz 1990). Other indirect effects comprise modified microclimates, which affect species richness (e.g. Haskell 2000, Godefroid and Koedam 2004), and dust deposition that can alter plant communities by disrupting photosynthesis, respiration and transpiration (Farmer 1993). Indirect effects of roads also include an increased spread of invasive species (Pauchard and Alaback 2004), changes in hydrology (Jones et al. 2000) as well as water and noise pollution (Forman and Alexander 1998).

Analogous to other wildlife, birds are affected both directly and indirectly by roads. Birds are directly impacted by collisions with vehicles (Dhindsa et al. 1988) which, for some bird species, cause territories near the road to become population sinks (Mumme et al. 2000). Birds may also suffer from indirect impacts of roads. These indirect effects can affect bird behaviours such as increased dispersal rates in young birds at road edges (Foppen and Reijnen 1994), modified territories when edges are considered boundaries (King et al. 1997), and barrier effects to movement (e.g. Laurance et al. 2004). Other indirect effects impacting birds include changes in vegetation structure along road edges (e.g. Male and Nol 2005) and noise pollution (e.g. Kuitunen et al. 1998). Of these effects, noise is thought to have significant impacts on birds (Leedy and Adams 1982; Illner 1992; Kuitunen et al. 1998) because most species rely on acoustic communication (Coffin 2007). Those species that produce songs that overlap with the low frequencies caused by traffic noise appear to be disproportionately affected by road noise (Rheindt 2003).

These direct and indirect impacts of roads on birds have been studied most extensively in the Netherlands. There, it appears that breeding bird densities decline with road proximity for some species (van der Zander et al. 1980; Reijnen and Foppen 1994; Reijnen et al. 1995; Reijnen et al. 1996). Moreover, the proportion of young male birds was higher near the road in Willow Warblers (*Phylloscopus trochilus*), which was associated with declines in both pairing success and productivity (Reijnen and Foppen 1994).

Two aspects of road ecology that are relatively understudied in birds are community composition and physiological health. The community data that have been collected so far suggests that bird richness and diversity decline near high-traffic roads in southern Germany (Rheindt 2003) and, possibly in French Guiana (Thiollay 1999) and Brazil (Laurance 2004) but associated habitat modification made it difficult to identify the effects attributable to road proximity. In eastern Australia, habitat rather than road presence predicted the bird community composition (Maron and Kennedy 2007). Due to habitat modifications at road edges, I would predict increased abundance of ground foraging and ground nesting birds in close proximity to roads. Modified vegetation at edges decreases tree density and increases understory cover (Murcia 1995), which would be favoured by these groups of birds. On the other hand, at a community level, road effects could influence population sizes if birds cannot modulate their song frequencies to accommodate road noise (Slabbekoorn and Peet 2003) or if birds avoid roads (Bayne et al. 2005). However, the changes in population sizes that may result from these effects would be hard to detect in community studies due to large variation in species preferences and coping abilities.

A way to countervail the difficulty of identifying variations in populations through demography would be to use health parameters as proxies for these changes. Physiological health parameters in the context of roads are also understudied, despite speculation that birds compensate for road effects – in particular road noise – with a stress response that impacts bodily functions (Illner 1992; Reijnen and Foppen 1994; Reijnen et al. 1997). I would predict that roads would inflict stress on birds living close to them that would decrease birds' health, potentially impact survival (e.g. Haramis et al. 1986) and even reduce population sizes.

It is important to know the extent to which roads impact community composition and health parameters because birds represent a large component of terrestrial diversity

(Hickman et al. 2003), and they also portray changes in habitat quality (Savard et al. 2000). Birds can be negatively impacted by reduced health due to chronic stress, which can lead to immunosuppression (Hõrak et al. 1998, Clinchy et al. 2002), which in turn can decrease body condition (Perez-Tris et al. 2004). Chronic stress in birds can reduce offspring survival (Saino et al. 1997) and reproductive success (Hanssen et al. 2003, Boonstra 2004) and lower body condition can negatively affect fecundity and survival (Haramis et al. 1986; Brittas 1988; Smith and Moore 2003) as well as brood care investment (Hanssen et al. 2003); all of these negatively influencing fitness.

The objective of this thesis was to examine the effects of road proximity on the community composition and physiological parameters of birds in Banff National Park, Canada. Banff National Park is an ideal study area because the impacts of roads are most important where both traffic volume and species diversity are high (Forman et al. 2002). Such a situation occurs in Banff National Park where both the TransCanada Highway, with up to 28 000 vehicles daily (Parks Canada unpublished data) and the Bow Valley Parkway, with up to 3 500 vehicles daily (Parks Canada unpublished data) dissect the National Park. Despite the high traffic volume, the valley supports a diverse vertebrate community that includes at least 260 species of birds (Parks Canada 2007).

In chapter two, I compared the community composition near to and far from the road with measures of species richness, abundance, diversity and dissimilarity. I also evaluated how the different compositions of various foraging, nesting and song guilds varied with road proximity. By exploring the differences in community composition rather than individual species, I hoped to gain a holistic view on the birds' community reaction to road proximity. In chapter three, I assessed how physiological indicators of health as well as one demographic parameter (age) differed with road proximity in males of two territorial songbird species. By further exploring age and measures of physiological condition at a population level, I set out to explore the mechanisms that may cause these changes in community composition or that could otherwise create differences in community composition in the long term. In the final chapter, I summarize my findings and synthesize them in relation to fragmentation. With this thesis, I aimed to provide a better understanding of the effects of roads on North American birds.

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Chapter 2 – Effects of highway proximity on the composition of a montane bird community in Banff National Park, Canada*

Introduction

Roads are increasingly abundant throughout the world and cause substantial habitat loss and fragmentation (Forman et al. 2003). In the United States alone, the direct and indirect effects of roads already extend to over 20% of the land area (Forman 2000). Direct effects of roads on wildlife include habitat loss as well as collisions with vehicles. Indirect effects include modified microclimates and plant communities, increased spread of invasive species, altered hydrological regimes, and air, noise and water pollution (see Forman & Alexander 1998; Spellberg 1998; Trombulak & Frissell 2000; Coffin 2007 for reviews). Roads may also facilitate secondary effects on wildlife such as altering the distribution and abundance of predators (James & Stuart-Smith 2000) or poachers (Blake et al. 2007), and promoting urban development (Aguayo et al. 2007) and resource extraction (Chomitz & Gray 1996). A combination of these effects degrades habitat wherever roads occur, but these effects may be most important in seemingly pristine habitat in areas that are otherwise relatively free of anthropogenic disturbances.

Such pristine land is often found in parks and protected areas, which are intended to protect biodiversity (IUCN 2008). Because road impacts are generally greatest where both species diversity and traffic volume are high (Forman, Reineking & Hersperger 2002), it is especially important to understand and mitigate road effects in protected areas that are also dissected by major transportation corridors. Such a situation occurs in Banff National Park, Canada, where the TransCanada Highway conveys up to 28 000 vehicles a day in peak seasons (Parks Canada unpublished data). Parallel to the TransCanada Highway is the Bow Valley Parkway, which carries an additional 3 500 vehicles a day (Parks Canada unpublished data). Despite the high traffic volume

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* I used "we" throughout this chapter to reflect all contributors.

in the valley bottom, much of the habitat on either side of it is relatively unaffected by human development and supports diverse vertebrate communities. Although the road infrastructure in Banff has attracted considerable research (Clevenger & Waltho 2000; Clevenger, Chruszcz & Gunson 2001; Clevenger & Waltho 2005), none has addressed the effects of the road on the bird community composition in Banff, which includes at least 260 species (Parks Canada 2007).

In other locations, birds have received considerable study in the context of roads and are known to suffer direct effects of road-kill (Dhindsa et al. 1988, Mumme et al. 2000) and habitat loss (Forman, Reineking & Hersperger 2002). However, habitat loss from roads is unlikely to have a significant impact on bird populations. Birds can have three main behaviours in response to linear features such as roads: (1) perceive them as natural gaps and incorporate them in their territories (Rail et al. 1997); (2) perceive them as territorial boundaries which cause "passive displacement" (King, Griffin & DeGraaf 1997; Rail et al. 1997); or (3) avoid them (Chasko & Gates 1982). For habitat loss to have the greatest impact on bird populations, birds would need to avoid roads, although it would also be possible to see an impact if populations are near to or at carrying capacity (Bayne et al. 2005). This way, no passive displacement is possible for lack of available habitat to displace to.

Indirect effects of roads on birds include changes in microclimate and vegetation structure on road edges (Forman, Reineking & Hersperger 2002; Male & Nol 2005), barrier effects on movement (Bélisle & St. Clair 2001; St. Clair 2003; Laurance, Stouffer & Laurance 2004) and noise pollution (Leedy & Adams 1982; Illner 1992; Kuitunen, Rossi & Stenroos 1998). One or several of these direct and indirect effects may provide the mechanism by which the population density of breeding birds typically decreases near roads (Räty 1979; van der Zander, ter Keurs & van der Weijden 1980; Illner 1992; Reijnen & Foppen 1994, Reijnen, Foppen & Meeuwsen 1996). In a few other cases, bird density increased near roads, but this difference was attributed to habitat rather than road effects (e.g. Ferris 1979; Clark & Karr 1979). Reduced population densities near roads may ultimately result in lower species richness (Rheindt 2003) in the areas near roads.

One particularly problematic effect of roads on birds is believed to be noise pollution (Leedy & Adams 1982; Illner 1992; Kuitunen, Rossi & Stenroos 1998), which is assumed to afflict birds because they communicate primarily with auditory signals (Catchpole & Slater 1995). Over a decade ago, Reijnen et al. (1995) predicted that bird responses to roads may differ in relation to how much their song frequency overlaps with traffic noises. More recently, Slabbekoorn and Peet (2003) showed that great tits (*Parus major*) living in the vicinity of roads sing with higher minimum frequencies. They further suggested that birds that could not modulate song frequencies might cease to occur near roads. In support of this idea, Rheindt (2003) demonstrated that densities of bird species with high song frequencies were less affected by road noise than those with low song frequencies. Because traffic volume is correlated with road noise (Ma et al. 2006) and is generally an important predictor of road effects (Jaeger et al. 2005), the effects of noise would presumably be greater near high volume roads.

Our objective was to determine the effects of roads on bird communities in Banff National Park adjacent to both the high-traffic TransCanada Highway and the lower-traffic Bow Valley Parkway. Stemming primarily from the hypothesis that road noise may affect birds (Reijnen et al. 1995), we predicted that species richness and diversity would diminish near the roads relative to more distant sites, particularly adjacent to the highway, and that the two roads would support different bird communities. We further predicted that bird species with song frequencies overlapping the main frequencies of traffic noise would be less abundant near the TransCanada Highway. Finally, we hypothesized the greater understory vegetation that is typically associated with road edges (Murcia 1995) would support greater abundance of those species that forage or nest on the ground. The comparison of road effects in the same area for both a high- and low-use road allows us to separate edge and noise effects in a way that few others have done.

Methods

STUDY AREA

The study was conducted along the TransCanada Highway (hereafter "highway") and Bow Valley Parkway (hereafter "secondary road") in Banff National Park, Canada (51° 8', 115° 24'), between the east entrance to the park and Castle Junction. The area is characterized by forested stands dominated by lodgepole pine *Pinus contorta*, white spruce *Picea glauca*, Englemann spruce *Picea englemannii*, and trembling aspen *Populus tremuloides*. In addition to this forested habitat that characterizes the valley bottom, there are several lakes, the Bow River and its tributaries, and the town of Banff. During the study period, traffic volume on the highway averaged 17 232 cars daily for June 1999 and 2000 and averaged 1 355 cars daily for the same period on the secondary road (Parks Canada unpublished data). However, there existed a voluntary closure of the secondary road from 18:00 until 09:00 on week days during the study period.

FIELD CENSUSES

In 1999 and 2000, forest-dwelling birds (see Table 2.1 for all common and scientific names) were surveyed with point count sites that were positioned near to (mean ± *SD:* 51 ± 4 m) and far from (373 ± 63 m) the two roads in three habitat types characterized by their dominant tree species – pine, spruce, and aspen. Sites were paired by road distance within each habitat and road location and there were 6 replicate sites per distance, habitat, and road category for a total of 72 point count locations. Sites were surveyed, by one of four observers, twice early in the morning (alternating between near and far sites) between 05:00 and 09:00 from June 2 to 29 of each year, for a total of four visits per site. The repeated visits to each site over the two-year period increased our ability to detect the maximum number of species and their abundance at each site. The noise at each point count site was also measured by averaging sound readings taken with a TES-1350A sound meter (TES Electrical Electronic Corporation) every 5 seconds during a 1 minute period.

At each point count, all birds detected by sight or sound within 50 m were recorded during a cumulative 10 minute observation period (Bibby et al. 2000). Prior to each field season, observers worked together to homogenize distance estimates. The surveys were interrupted whenever the background road noise interfered with the observer's ability to hear quiet bird species. The survey resumed when the road noise abated. To avoid the bias that might stem from spending more time at the sites close to roads, we extended the duration of point counts at the paired distant sites by adding the extra minutes, at evenly spaced intervals, as non-censused time. For example, if accommodating traffic interruptions generated a point count of 50 minutes duration near the road, we censused for 2 minutes, then waited 8 minutes 5 times at the adjacent site far from the road.

STATISTICAL ANALYSES

To understand the contributions of road distance, road type, and habitat on the composition of bird communities in Banff, we conducted three types of analyses: (1) an overview of community composition using richness and diversity measures with ANOVAs; (2) an assessment of community similarity using PERMANOVA (Anderson 2001; McArdle & Anderson 2001), which was illustrated with an ordination; and (3) an indicator species analysis intended to identify species that were particularly responsive to the road distance variable. To reduce the weight of the more abundant species (McCune & Grace 2002) and to meet the ANOVA assumptions, we square root transformed bird abundance values for all analyses with the exception of calculating diversity indices.

For the first set of analyses, we examined four response variables for each combination of road type, habitat type, and road distance category with three-way ANOVAs. First, we recorded the abundance of each species at a given site as the highest count observed at one of the four site-visits. Second, we determined the maximum number of species recorded for each site with a cumulative count of species over the four visits. Because species richness and maximum abundance do not consider sampling error and evenness in their calculations, we also calculated two species indices: one for total species richness and the other for species diversity. We used the Jackknife 1 Estimator of species richness, which calculates total species richness based on the amount of unique species in each observation (Magurran 2004), as a third response variable. The Jackknife 1 Estimator accommodates for incomplete sampling (Magurran 2004) and was chosen because of its performance in estimating total species richness with real data (Walther & Morand 1998). Finally, to assess species diversity, we used the Brillouin Index, which accommodates non-random sampling owing to differences in bird detection (Southwood & Henderson 2000). The Brillouin Index is a more desirable alternative to the popular Shannon index, which requires knowledge of the absolute number of species (Magurran 2004). For both total species richness and diversity, non-parametric indices were chosen because their performance is not affected by the underlying species abundance distribution (Magurran 2004). The ANOVAs were conducted using R (R Development Core Team 2007). For the species indices, we also used the Vegan Package (Oksanen et al. 2007) and the biodiversity script developed by Meredith (2006).

The PERMANOVA used in the second analysis to test the hypothesis that community composition differed near and far from the road is a non-parametric analog to a MANOVA where F-ratios are calculated from a matrix of the dissimilarities between the community composition at each site and where the test statistic p-values are obtained by permutations (Anderson 2001). The advantage of using a PERMANOVA over measures of species richness and diversity is that it can detect differences is species composition between two communities even when species richness and species evenness does not differ. We used the FORTRAN program PERMANOVA version 1.6 (Anderson 2001) with road type, habitat type, and distance to the road as three fixed factors, 9999 permutations of the residuals under a reduced model, and the Bray-Curtis dissimilarity measure. The Bray-Curtis dissimilarity measure is a city-block distance measure representing the dissimilarity between two communities. This can be visualized as a right-angle triangle where the Euclidean distance between two communities forms the hypotenuse and the sum of the two legs (sides a and b) equals the city-block distance. The city-block distance over the maximum distance obtainable between the two communities yields the Bray-Curtis dissimilarity measure. Because PERMANOVA results do not indicate the direction of the dissimilarity, we also compared summed abundance of individual species using Chi-squares (Zar 1999) where distance to the road or road type were significant factors, alone or within an interaction.

To provide a graphical overview of the relationships among the community data assessed analytically by the PERMANOVA, we used the ordination method of Nonmetric Multidimentional Scaling (NMS). Because NMS avoids assumptions about a linear relationship among variables and is robust to a large number of zero values, it can more accurately represent differences in community composition than other ordination methods (Clarke 1993; McCune & Grace 2002). We performed the NMS on the autopilot setting, the slow and thorough analysis, and Bray-Curtis dissimilarity measures in the PC-Ord program (McCune & Mefford 1999).

Using PERMANOVA, we analysed the effect of our predictor variables (road type, habitat type and road distance) on bird abundance of individual species for the entire bird community, as described above, and for three sub-divided communities (Table 1) based on foraging, nesting, and song guilds. Here again, the PERMANOVA had the advantage of identifying possible differences in species composition. For all guilds, we also compared summed abundance near to and far from the road using a Chi-square test (Zar 1999). For division into these guilds, we grouped birds that nest or forage in open areas, on the ground and in shrubs (hereafter ground guild) and contrasted them with birds that nest or forage in shrubs and trees (hereafter arboreal guild) using the information in Birds of North America Online. For song guilds, we categorized birds by song frequency in relation to traffic frequency. The highest sound pressure exerted by traffic noise is found at frequencies ≤ 1 KHz with the second highest sound pressure at frequencies up to 4 KHz, beyond which it is drastically reduced (Huisman & Attenborough 1991; Skiba 2000). Given these different sound pressures, we created three groups of birds based on songs corresponding to these frequencies. Birds were categorized as having low frequency songs (≤ 1 KHz), moderate frequency songs (> 1 KHz and ≤ 4 KHz), and high-frequency songs (> 4 KHz). We estimated song frequencies from the information in Birds of North America Online and the online Macauley Library (Cornell Lab of Ornithology). For song guilds, we only used species that were present in at least 10 sites and that matched closely the low, moderate and high frequencies. As a result, each song guild was comprised of two species.

In the third analytical approach, we focused on the value of particular species for indicating differences in the bird community owing to road proximity. For this, we employed an Indicator Species Analysis (ISA) (Dufrêne & Legendre 1997) which multiplies the relative abundance by the relative frequency of each species in a given group to obtain the indicator value. The significance of these indicator values was evaluated with a Monte Carlo test with 1000 randomizations. The indicator values, ranging from 0 to 100, specify how likely the presence of a species is to indicate a particular road distance. The ISA analysis was done with the PC-Ord program. Throughout all the analyses, we used a significance level of 0·10 to balance type 1 and type 2 errors (Zar 1999).

Results

Across the two seasons and 72 sites, we identified a total of 75 species and 1981 individuals from a total of 288 point counts. The results of a three-way ANOVA on noise levels revealed that the noise adjacent to the road (mean ± *SD*: 40·4 ± 2·1 dB) was significantly greater than the noise level distant from the road (36·4 ± 2·1 dB; $F_{1,60}$ = 32·58, P < 0·0001). When the two highways were considered separately, this difference was only present for the highway (near: 46·0 ± 5·3 dB; far: 37·2 ± 6·7 dB; $t_{2,70}$= 6·17, P < 0·001) but not for the secondary road (near: 34·9 ± 3·1 dB; far: 34·5 ± 2·7 dB; $t_{2,70}$= 0·59, P = 0·55; Fig. 2.1). The results on the secondary road were expected because few cars were recorded during sound readings due to the voluntary closure. There was also a significant difference in noise level between the highway (41·6 ± 7·5 dB) and the secondary road (34·7 ± 2·9 dB; $F_{1,60}$ = 72·84, P < 0·0001). Furthermore, there was a significant interaction between road type and habitat type ($F_{1,60}$ = 3.48; P < 0.04) as well as road proximity and road type ($F_{1,60}$ = 27·05; P < 0·0001). The difference in noise near to and far from the highway (24·32 %) was greater than the difference between the two road types (19·95 %). Noise also differed between the three habitat types with aspen being the noisiest (39·6 ± 5·5 dB) followed by pine (37·6 ± 7·3 dB) and then spruce (37·1 ± 6·8 dB; $F_{2,60} = 3·62$, $P = 0·03$).

Among these point counts, species richness varied from 9 to 28 (Fig. 2.2 a) and the average richness pooled over the four visits was 16·2 (*SD*: 3·0) for species near to and 16·9 (4·6) for species far from the highway, and 18·3 (3·9) for species near to and 16·4 (4·1) for species far from the secondary road. The results from our three-way ANOVA showed that there was no effect on species richness of road type ($F_{1,60} = 1·11$, $P = 0·29$) or road proximity ($F_{1,60} = 0·49$, $P = 0·48$). However, aspen (mean ± *SD*: 18·8 ± 2·8) and spruce (17·5 ± 4·4) sites had significantly higher species richness than pine sites (14·5 ± 3·1; $F_{2,60} = 10·73$, $P = 0·0001$). There was no interaction between road proximity and road type but there was an interacting effect between road proximity and habitat type ($F_{2,60} = 3·35$, $P = 0·04$) where sites near the road had significantly higher species richness for pine habitat (2·9 species; $t_{2,22} = 2·56$, $P = 0·02$), compared to similar sites located far from the road. By contrast, richness did not differ with road proximity for aspen and spruce habitats ($t_{2,22} \leq -1·17$, $P \geq 0·25$).

These results were qualitatively similar for abundance of individuals at point count sites (Fig. 2.2 b, c). Again, neither road type ($F_{1,60} = 0·20$, $P = 0·65$) nor road distance ($F_{1,60} = 1·82$, $P = 0·18$) affected the maximum abundance, but birds were more abundant at aspen (mean ± *SD*: 31·3 ± 5·0) and spruce (28·3 ± 7·7) sites than at pine sites (22·9 ± 5·3; $F_{2,60} = 14·83$, $P < 0·0001$). Here again, there was an interacting effect of road proximity and habitat type ($F_{2,60} = 7·7$, $P = 0·001$) where sites near the road had significantly higher abundance in pine sites (7·5 birds; $t_{2,22} = 4·97$, $P < 0·0001$), but no significant differences occurred in aspen and spruce sites ($t_{2,22} \leq -1·35$, $P \geq 0·19$) compared to similar sites located far from the road. Furthermore, abundance data showed an interacting effect of road type and road proximity ($F_{1,60} = 2·91$, $P = 0·09$) where bird abundance through posthoc tests tended to be greater near the secondary road (3·7 birds; $t_{2,34} = 1·61$, $P = 0·12$).

When we examined species richness with the Jackknife 1 Estimator, there was no effect of road type ($F_{1,2} = 0·58$, $P = 0·53$) and road proximity ($F_{1,2} = 0·48$, $P = 0·56$), but aspen sites (mean ± *SD*: 53·3± 4·0) had significantly higher species richness than pine sites (39·7 ± 6·6; $F_{2,2} = 10·62$, $P = 0·09$). There were no significant interactions among variables. The Brillouin Index results were qualitatively similar to the species richness results. These results showed a higher diversity in aspen (mean ± *SD*: 2·17 ± 0·12) and spruce (2·08 ± 0·21) sites than in pine sites (1·91 ± 0·20; $F_{2,2} = 14·11$, $P < 0·0001$) as well as a significant interacting effect of road proximity and habitat type ($F_{2,60} = 6·20$, $P = 0·004$) where sites near the road had a higher diversity index for both pine (13·97 %; $t_{2,34} = 3·56$, $P = 0·002$) and aspen (1·86 %; $t_{2,34} = 0·97$, $P = 0·34$) habitats, but a lower diversity index (4·93 %; $t_{2,34} = 1·15$, $P = 0·26$) for spruce habitat.

The PERMANOVA analysis supported the main results from the species richness and abundance assessments. It indicated that the effect of the two road types and the two distances to the road on the community composition was minimal compared to the influence of habitat types (Table 2.2). The community dissimilarity was the greatest between aspen and spruce sites (49·80) followed by aspen and pine (49·46) and then pine and spruce (42·44). Habitat type also had an interacting effect with road type where the dissimilarity between the highway and the secondary road was the lowest in pine habitat (40·83) and the highest in aspen (42·42) and spruce (42·46) habitats. Posthoc tests revealed that within each habitat type, the bird community significantly differed given the road type present ($t_{2,22}= 1·33$, $P = 0·04$, $t_{2,22}= 1·36$, $P = 0·04$, $t_{2,22}= 1·44$, $P = 0·02$). Within each habitat, summed abundance of individual species varied with road type (Table 2.3). Furthermore, there was an interacting effect of habitat type and road distance where communities between the two road distances were the most dissimilar in aspen sites (42·27) followed by spruce (41·34) and then pine (40·45). These road distances dissimilarities were only significant in aspen sites ($t_{2,22}= 1·25$, $P = 0·09$). At these sites, gray jays and Townsend's warblers were more abundant far from the road (Table 2.3). The community dissimilarities resulting from the PERMANOVA were illustrated graphically by the NMS ordination based on a three-dimensional optimal solution with a satisfactory final stress of 17·42 and an instability < 0·00001 (Fig. 2.3).

The PERMANOVA results divided by foraging, nesting and song guilds yielded results that were qualitatively similar to the above analyses of the combined species with three exceptions. First, all song guilds as well as the ground foraging and nesting guilds showed no interacting effects between habitat type and road type. Second, the interacting effect of habitat and road proximity in the ground foraging guild ($F_{2,60} = 2{\cdot}10$, $P = 0{\cdot}008$) and the moderate and high song frequency guilds ($F_{2,60} = 2{\cdot}76$, $P = 0{\cdot}02$; $F_{2,60} = 3{\cdot}79$, $P = 0{\cdot}02$) revealed the greatest dissimilarity between distances to the road in spruce habitat rather than in aspen habitat as was shown by the combined species analyses. Posthoc tests further indicated that sites near and far from the road were significantly dissimilar in pine habitat ($t_{2,22}= 1{\cdot}51$, $P = 0{\cdot}01$) for the ground foraging guild, in pine ($t_{2,22}= 1{\cdot}68$, $P = 0{\cdot}09$) and spruce ($t_{2,22}= 1{\cdot}88$, $P = 0{\cdot}002$) habitat for the moderate frequency song guild, and in spruce ($t_{2,22}= 1{\cdot}66$, $P = 0{\cdot}04$) and aspen ($t_{2,22}= 2{\cdot}19$, $P = 0{\cdot}10$) habitat for the high frequency song guild. We compared summed bird abundance between the two road distances for these guilds and found a greater number of birds at sites near the road for the foraging guild ($\chi^2 = 6{\cdot}84$, d.f. = 1, $P = 0{\cdot}009$), the moderate frequency guild in pine habitat ($\chi^2 = 6{\cdot}15$, d.f. = 1, $P = 0{\cdot}01$) and the high frequency guild in spruce habitat ($\chi^2 = 4{\cdot}45$, d.f. = 1, $P = 0{\cdot}03$). There was no difference in the summed bird abundance between sites near to and far from the road for the moderate frequency guild in spruce habitat ($\chi^2 = 0{\cdot}29$, d.f. = 1, $P = 0{\cdot}59$) and the high frequency guild in aspen habitat ($\chi^2 = 0{\cdot}82$, d.f. = 1, $P = 0{\cdot}36$). Third, birds with low and high frequency songs differed by road type ($F_{1,60} = 6{\cdot}10$, $P = 0{\cdot}008$; $F_{1,60} = 2{\cdot}52$, $P = 0{\cdot}09$). Here, we compared species abundance for these guilds and found that the cedar waxwing, which has a high frequency song, was likely responsible for the PERMANOVA result of the high frequency guild because it was significantly more abundant at highway sites ($\chi^2 = 7{\cdot}1$, d.f. = 1, $P = 0{\cdot}008$). Species with low frequency songs, which we predicted would be most affected by traffic noise, were more abundant on the secondary road than the highway ($\chi^2 = 4{\cdot}50$, d.f. = 1, $P = 0{\cdot}03$).

Finally, although both the PERMANOVA and NMS indicated that habitat was stronger in determining community composition than distance to the road, the indicator species analysis revealed three species that were indicative of the community near the road: the blue-headed vireo (Indicator value = 29·3, $P = 0·04$), the American robin (Indicator value = 52·8, $P = 0·08$) and the chipping sparrow (Indicator value = 52·6, $P = 0·09$).

Discussion

We investigated the composition of bird communities near and far from two road types in Banff National Park with the prediction that a high-traffic road, the highway, would have the greatest impact on community composition in all types of habitats along the highway and especially at sites located near to the road. Our results only partially support this hypothesis. In contrast to our hypothesis, we found no direct effect of road type or road distance, but found that habitat type was important in structuring avian communities. In support of our hypothesis, low and high song guilds revealed dissimilarity by road type and we found that road type can influence community composition if we considered its interacting effect with habitat type.

In contrast to our hypothesis that road proximity would alter community composition, measures of species richness, abundance of individuals, the Jackknife 1 Estimator, the Brillouin Index and the PERMANOVA all found no direct effect of road type or road distance. Instead, these metrics revealed that habitat type was the most important factor in structuring avian communities. A similar result was reported for subtropical forests in eastern Australia in which habitat, but not road presence, predicted the composition of bird communities (Maron & Kennedy 2007). Maron & Kennedy compared sites at < 50 m and > 300 m from a low-traffic road in three different habitat types. Their study revealed that only one species, the eastern yellow robin (*Eopsaltria australis*), differed in abundance with road proximity. Different habitats in North America also vary in community composition. In Texas, hardwood forest contained more species than mixed pine and hardwood, and both forest types had greater species richness than pine forests (Shackelford & Conner 1996). In our study, aspen habitat contained the highest number of species and the highest abundance of individuals. Others have also reported that aspen habitat in Canada supports larger and more diverse avian communities than does pine habitat (Hobson & Bayne 2000). These results could stem from the greater vegetative diversity, particularly in the understory, of deciduous forests (Barbier, Gosselin & Balandier 2008).

Although there were no impacts of road distance itself on the bird community, measures of species richness, abundance of individuals, the Brillouin Index and the PERMANOVA all found an interacting effect of distance to the road and habitat type. During our field census, observers may have had the propensity to account for birds outside the 50 m radius. Because of the road presence at sites near to the road, it could have created a bias where counts at sites far from the road would have been artificially increased. However, we would have expected the bias to be constant across habitats, which was not shown in our results. In pine habitats, bird richness, abundance, and diversity were significantly higher near roads, which was the opposite of what we predicted. This increase in diversity resulted from higher numbers of ground foraging birds found adjacent to the road in pine habitat. Three species, the American robin, the dark-eyed junco and the white-crowned sparrow were more abundant near the road in pine habitat. Pine forests cause soil of high acidity, where mainly mosses and Labrador tea *Rhododendron groenlandicum* were observed as the main undergrowth species (M. Dubé, personal observation). Near the road, however, we observed a greater propensity for shrubs and grasses. Elsewhere, it appears that calcareous road dust reduced soil acidity in coniferous forests to result in an increase in graminoids and a decrease in mosses, evergreen shrubs, forbs, and lichens (Myers-Smith et al. 2006). We speculate that the increased diversity of birds in pine forests near the road is a result of similar modifications to the understory community, but we did not collect the vegetation data that would be needed to test this hypothesis. Also, the interior of forests has reduced light at the understory level compared to the edges where light penetrates (Murcia 1995), further supporting the propensity for shrubs and grasses there. Although bird abundance varied with road proximity in pine habitat, the PERMANOVA showed that significantly dissimilar communities near to and far from the road existed only in aspen habitat. In aspen habitat, none of the other metrics (species richness, bird abundance and diversity) varied with road proximity. Also, only two species, the gray jay and the Townsend's warbler, were significantly more abundant at one of the two road distances. Hence, species composition likely caused the dissimilarity observed in aspen habitats. Of the 64 species we observed in aspen habitats, 14 (21·88 %) were found only near to and 9 (14·06 %) were found only far from the road. However, for each of these species, individuals occurred in three sites or less with the exception of the black-billed magpie that was present in four aspen sites near to the road.

With the exception of the aspen community, there was no significant effect of road distance on community dissimilarity and thus species composition. This result may have occurred because there really was no effect of road distance on the species composition or because the effect of distance was inadequately assessed with our study design. In support of the first interpretation, aspen habitats had greater species richness and bird abundance compared to other habitats, as reported above. This increased richness and abundance gives the potential for greater variations between communities at different distances from the road and thus a greater dissimilarity. Alternatively, the noise at which bird population densities start to decline averages 42 dB in woodland habitat (Forman & Alexander 1998) and in our study only sites near the highway reached slightly above that noise level. Hence, the noise level experienced by birds in our study may not have been elevated enough to significantly affect the community. Although the traffic noise during our study was mostly below 42 dB, yearly traffic in Banff National Park, and thus noise pollution, has been increasing since then (Parks Canada unpublished data). Noise levels recorded at the same study site during a similar time of the year in 2007 show averages of 58·3 dB (*SD* = 3·0) near the road and 46·6 dB (*SD* = 3·3) far from the road, which is 78·90 % and 79·82 % higher than during this study, respectively. Others have suggested that traffic noise may be an important factor affecting bird species (Leedy & Adams 1982; Illner 1992; Kuitunen, Rossi & Stenroos 1998). If noise so afflicts birds, the current impact of noise pollution on the bird community could be greater than portrayed by our study because traffic noise is clearly increasing in Banff.

The second interpretation of our results is that birds in Banff are affected by roads, but our study design failed to demonstrate this effect. This interpretation is suggested because average sound meter readings were similar near and far from the road (see results) and because our near and far sites were relatively close (325 m) to one another. Reijnen et al. (1995) distinguished between bird populations living 50 versus 400 m from the road, but found evidence of road effects extending to 1500 m when daily traffic volume was of only 10 000 cars. Further studies should examine community composition at greater distances from the highway and the secondary road.

Although road distance did not affect the Banff bird community in all habitats, song guild analyses identified a significant dissimilarity between road distances for moderate song frequency birds in pine and spruce habitat as well as for high song frequency birds in spruce and aspen habitat. Summed abundances were higher near the road only in pine habitat for the moderate frequency guild and in spruce habitat for the high frequency guild. There is no obvious explanation for why these particular guilds differed in relation to road proximity only in these habitats. However, we can hypothesize that since sound degrades during transmission, because transmission is affected by vegetation and because low and high frequencies are affected differently (Slabbekoorn, Yeh & Hunt 2007), traffic noise, song frequency, tree density and habitat type all interacted to produce these community dissimilarities. Further studies are also needed to determine the exact cause of these dissimilarities near to and far from the road.

Along with the song guild analysis, the ISA identified three species that were indicative of point counts adjacent to the road. The first species, the blue-headed vireo, prefers mature forest with shrubs and small trees in the understory (James 1998). Presumably the edge habitat adjacent to the road promotes the growth of vegetation that is more typical of early successional stages, thus increasing shrubs and pole saplings (Thomas, Maser & Rodiek 1979). The other species – the American robin and the chipping sparrow – are usually associated with edge habitat (Middleton 1998; Sallabanks & James 1999). The American robin's preferred breeding areas are grassy and mixed with shrubs and trees (Sallabanks & James 1999). It is a well adapted species that lives in residential areas and forages mainly on the ground and on foliage (Sallabanks & James 1999). Similarly, the chipping sparrow breeds in grassy and open forest and feeds close to the ground (Middleton 1998).

In addition to road proximity, we predicted that the different traffic levels found on the highway and the secondary road would engender a difference in community composition. Posthoc tests following the PERMANOVA on the two road types within habitat types supported this hypothesis. The highway and the secondary road communities were most dissimilar in spruce and aspen habitat followed by pine habitat. Here again, the lack of a difference in the other metrics (species richness, bird abundance and diversity) suggests that the species composition differs between the highway and the secondary road. In fact, of the 75 species present in the study area, 9 (12·00 %) were only present on the secondary road and 10 (13·33 %) were only present on the highway. For each of these species, individuals occurred in three sites or less with the exception of the winter wren that was present at a total of four highway sites. It is interesting to note that although species abundance did not vary for the community as a whole, some species, such as the European starling and the American crow, were more abundant at highway sites while others, such as the gray jay, were more abundant on the secondary road. A potential reason for the difference in community composition between the two road types is the habitat type surrounding the two roads. Because we lacked road type replication, habitat may have been confounded with road effects.

Two other reasons for the difference in the bird community between the highway and the secondary road may be the effect of traffic noise on bird communication and the visual stimuli provided by car traffic. However, the visual stimulus is unlikely to have an important effect because elsewhere, at identical noise load, bird density at plots with high or low car visibility did not vary (Reijnen et al. 1995). Traffic noise is thus a more plausible explanation given that density of grey partridge *Perdix perdix* decreased when hedgerows prevented the sight of traffic (Illner 1992). In support of this explanation, the cedar waxwing – characterized with a high song frequency – was more abundant near the highway. By contrast, we found that birds with low song frequencies, which would overlap the most with traffic noise, were more abundant near the secondary road than the highway. However, the secondary road is located in the wider part of the valley and this could alternatively explain the higher abundance of Wilson's snipes and the blue grouses, which maintain large territories (Mueller 1999; Zwickel & Bendell 2005). Finally, species with moderate frequency songs did not differ between the two road types. If bird songs overlap with traffic noise, noise may possibly impact populations. Recently, traffic noise was shown to reduce breeding densities of at least 15 % of the bird community in western-central Spain (Peris & Pescador 2004) and authors have suggested that anthropogenic noise reduces the richness of communities (Stone 2000) as well as the pairing success of individuals (Habib, Bayne & Boutin 2007). These effects seem to be most likely to afflict species with low-frequency songs that overlap with road noise (Rheindt 2003). Some birds, however, can adapt to anthropogenic noise. These birds have shorter, more rapid songs with a higher minimum frequency (Slabbekoorn & Boer-Visser 2006). Ultimately, species that cannot modulate their songs may cease to exist near noisy roads (Slabbekoorn & Boer-Visser 2006).

If acoustic communication in birds is impeded by road noise, there are several ways in which birds might compensate for this effect to limit the differences we found in the bird communities near and far from roads as well as adjacent to the two road types. First, some species can increase the frequency of their songs to minimize the interference caused by traffic noise (Slabbekoorn & Peet 2003). More work is needed to know the extent of these effects, particularly in North America. It would be particularly interesting to know if birds adjust the whole range of song frequency, only their minimum frequency (Slabbekoorn & Peet 2003) or their dominant song frequency, which is better at indicating a bird's sensitivity to traffic noise (Rheindt 2003). A second way that birds may avoid interference from road noise is to shift their singing bouts temporally to avoid the times when traffic noise is loudest (Bergen & Abs 1997). On the secondary road, the voluntary closure allowed birds to go through morning chorus without the presence of traffic noise. Because we censused birds in early morning when traffic volume was lower, a shift in singing behaviour is unlikely to have reduced our detection rates on the highway. Finally, birds may compensate for the overlapping frequencies of their song and traffic by increasing the intensity of their song (Brumm & Todt 2002). These mechanisms, however, have the potential of being costly to the individual and some authors suggest the resulting stress would impact bodily functions (Illner 1992; Reijnen, Foppen & Veenbaas 1997). Investigating this hypothesis would be another profitable avenue of future research even without evidence that the bird community is altered by road proximity. It is interesting to note, however, that if noise is causing the difference in community composition between the two road types, we would have expected to see a difference with road proximity as well. Indeed, noise levels between the two road distances on the highway were greater in magnitude that the difference in noise between the two road types.

In sum, three main conclusions can be drawn from our study in Banff National Park. First, habitat type was the most important factor shaping bird community composition. Species richness and bird abundance were both highest in aspen forests. Maintaining aspen stands in the Park is thus an important avenue to support a diverse bird community. A second main conclusion is that, within the range of our samples, distance to the road resulted in differing bird abundance, richness and diversity in pine habitat and dissimilar communities only in aspen habitat Whether the impacts did not affect species composition in the other habitats or whether both distances were impacted equally by the road presence remains unclear. If an impact existed, planners may need to acknowledge a greater zone of road effects and minimize the presence of high-volume roads in protected areas. Further studies should compare community composition at greater distances from the road where the topography is permitting. Nevertheless, our results may suggest that in a valley delimited by high altitude mountains, a central road could affect the bird community of the whole valley. A third conclusion is that for similar habitat types, communities along the highway and the secondary road were dissimilar, perhaps as a function of road noise. Hence, as traffic keeps increasing worldwide, it has become ever more important to test the effectiveness of noise-mitigation measures.

Table 2.1. Common and scientific names with a classification of species into nesting, foraging and song frequency guilds for all bird species surveyed through point counts in Banff National Park. All guilds contain birds present at a minimum of 10 sites. The low song frequency guild contains birds with song frequencies ≤ 1 KHz. The moderate song frequency guild contains birds with song frequencies > 1 KHz and ≤ 4 KHz. The high song frequency guild contains birds with song frequencies > 4 KHz.

		Nesting	**Foraging**	**Song Frequency**
American crow	*Corvus brachyrhynchos*	Arboreal	Ground	*
American redstart	*Setophaga ruticilla*	Arboreal	Arboreal	*
American robin	*Turdus migratorius*	Arboreal	Ground	moderate
Barn swallow	*Hirundo rustica*	*	Ground	*
Black-billed magpie	*Pica hudsonia*	Arboreal	Ground	*
Black-capped chickadee	*Poecile atricapilla*	Arboreal	Arboreal	*
Belted kingfisher	*Ceryle alcyon*	*	*	*
Brown-headed cowbird	*Molothrus ater*	*	Ground	*
Blue-headed vireo	*Vireo solitarius*	Arboreal	Arboreal	*
Blue grouse	*Dendragapus obscurus*	Ground	Arboreal	low
Blackpoll warbler	*Dendroica striata*	Arboreal	Arboreal	*
Boreal chickadee	*Poecile hudsonica*	Arboreal	Arboreal	*
Brown creeper	*Certhia americana*	Arboreal	Arboreal	*
Cedar waxwing	*Bombycilla cedrorum*	Arboreal	Arboreal	high
Clay-colored sparrow	*Spizella pallida*	Arboreal	Ground	*
Chipping sparrow	*Spizella passerina*	Arboreal	Ground	*
Clark's nutcracker	*Nucifraga columbiana*	Arboreal	Arboreal	*
Common raven	*Corvus corax*	Arboreal	Ground	*
Wilson's snipe	*Gallinago delicata*	Ground	Ground	low
Common yellowthroat	*Geothlypis trichas*	Ground	Ground	*
Dark-eyed junco	*Junco hyemalis*	Ground	Ground	*
Downy woodpecker	*Picoides pubescens*	Arboreal	Arboreal	*
Dusty flycatcher	*Empidonax oberholseri*	Arboreal	Arboreal	*
European starling	*Sturnus vulgaris*	Arboreal	Ground	*
Fox sparrow	*Passerella iliaca*	*	Ground	*
Golden-crowned kinglet	*Regulus satrapa*	Arboreal	Arboreal	*
Great gray owl	*Strix nebulosa*	Arboreal	Ground	*
Gray jay	*Perisoreus canadensis*	Arboreal	*	*
Hammond's flycatcher	*Empidonax hammondii*	Arboreal	Arboreal	*
Hairy woodpecker	*Picoides villosus*	Arboreal	Arboreal	*
Hermit thrush	*Catharus guttatus*	Ground	Ground	*
House wren	*Troglodytes aedon*	Arboreal	Ground	*

Killdeer	*Charadrius vociferus*	Ground	Ground	*
Least flycatcher	*Empidonax minimus*	Arboreal	Arboreal	*
Lincoln's sparrow	*Melospiza lincolnii*	Ground	Ground	*
MacGillivray's warbler	*Oporornis tolmiei*	Ground	Ground	*
Mountain chickadee	*Poecile gambeli*	Arboreal	Arboreal	*
Northern flicker	*Colaptes auratus*	Arboreal	Ground	*
Northern waterthrush	*Seiurus noveboracensis*	Ground	Ground	*
Orange-crowned warbler	*Vermivora celata*	Ground	Arboreal	*
Olive-sided flycatcher	*Contopus cooperi*	Arboreal	Ground	*
Osprey	*Pandion haliaetus*	Arboreal	*	*
Pine grosbeak	*Pinicola enucleator*	Arboreal	*	*
Pine siskin	*Carduelis pinus*	Arboreal	Arboreal	*
Pileated woodpecker	*Dryocopus pileatus*	Arboreal	Arboreal	*
Rose-breasted grosbeak	*Pheucticus ludovicianus*	Arboreal	Arboreal	*
Red-breasted nuthatch	*Sitta canadensis*	Arboreal	Arboreal	*
Ruby-crowned kinglet	*Regulus calendula*	Arboreal	Arboreal	*
Red crossbill	*Loxia curvirostra*	Arboreal	Arboreal	*
Red-naped sapsucker	*Sphyrapicus nuchalis*	Arboreal	Arboreal	*
Red-tailed hawk	*Buteo jamaicensis*	Arboreal	Ground	*
Ruffed grouse	*Bonasa umbellus*	Ground	Ground	moderate
Rufous hummingbird	*Selasphorus rufus*	Ground	Arboreal	*
Red-winged blackbird	*Agelaius phoeniceus*	Ground	Ground	*
Savannah sparrow	*Passerculus sandwichensis*	Ground	Ground	*
Sora	*Porzana carolina*	Ground	Ground	*
Song sparrow	*Melospiza melodia*	Ground	Ground	*
Spruce grouse	*Falcipennis canadensis*	Ground	Arboreal	*
Swainson's thrush	*Catharus ustulatus*	Arboreal	Ground	*
Tennessee warbler	*Vermivora peregrina*	Ground	Arboreal	*
Townsend's warbler	*Dendroica townsendi*	Arboreal	Arboreal	*
Tree swallow	*Tachycineta bicolor*	Arboreal	Ground	*
Varied thrush	*Ixoreus naevius*	Arboreal	Ground	*
Warbling vireo	*Vireo gilvus*	Arboreal	Arboreal	*
White-crowned sparrow	*Zonotrichia leucophrys*	Ground	Ground	*
Western tanager	*Piranga ludoviciana*	Arboreal	Arboreal	*
Willow flycatcher	*Empidonax traillii*	Arboreal	Arboreal	*
Wilson's warbler	*Wilsonia pusilla*	Ground	Arboreal	high
Winter wren	*Troglodytes troglodytes*	*	Ground	*
White-throated sparrow	*Zonotrichia albicollis*	Ground	*	*
White-winged crossbill	*Loxia leucoptera*	Arboreal	Arboreal	*
Western wood-pewee	*Contopus sordidulus*	Arboreal	Arboreal	*
Yellow-bellied sapsucker	*Sphyrapicus varius*	Arboreal	Arboreal	*

Yellow warbler	*Dendroica petechia*	Arboreal	Arboreal	*
Yellow-rumped warbler	*Dendroica coronata*	Arboreal	Arboreal	*

* indicates a species that could not be categorized in the above mentioned guilds.

Table 2.2. PERMANOVA on the bird community composition of Banff National Park for the three main variables of interest (road, habitat, distance) and their interactions.

Source	df	SS	MS	F	P
Road	1	1224·54	1224·54	1·46	0·12
Habitat	2	15629·04	7814·52	9·32	0·0001
Distance	1	839·83	839·83	1·00	0·46
Road x Habitat	2	3592·50	1796·25	2·14	0·0003
Road x Distance	1	792·97	792·97	0·95	0·51
Habitat x Distance	2	2523·15	1261·58	1·50	0·05
Road x Habitat x Distance	2	1329·05	664·52	0·79	0·76
Residual	60	50308·22	838·47		
Total	71	76239·30			

Table 2.3. Significant Chi-square tests on the summed abundance of individual species where PERMANOVA results on the whole bird community of Banff National Park had distance to the road or road type as significant factors, alone or within an interaction.

		Species	Greater abundance	p-value
Aspen				
	Road distance			
		Gray jay	Far from the road	0·01
		Townsend warbler	Far from the road	0·04
	Road type			
		American crow	Highway	0·02
		Cedar waxwing	Highway	0·03
		Clark's nutcracker	Highway	0·03
		Common raven	Highway	0·03
		Hammond's flycatcher	Secondary road	0·03
Spruce				
	Road type			
		Blue-headed vireo	Highway	0·10
		Brown creeper	Highway	0·02
		Wilson's snipe	Secondary road	0·06
		European starling	Highway	0·002
		Gray jay	Secondary road	0·10
		Mountain chickadee	Secondary road	0·005
		Northern waterthrush	Secondary road	0·06
		White-crowned sparrow	Secondary road	0·03
Pine				
	Road type			
		Gray jay	Secondary road	0·08
		Red-breasted nuthatch	Secondary road	0·03
		Swainson's trush	Highway	0·08
		Varied trush	Highway	0·06

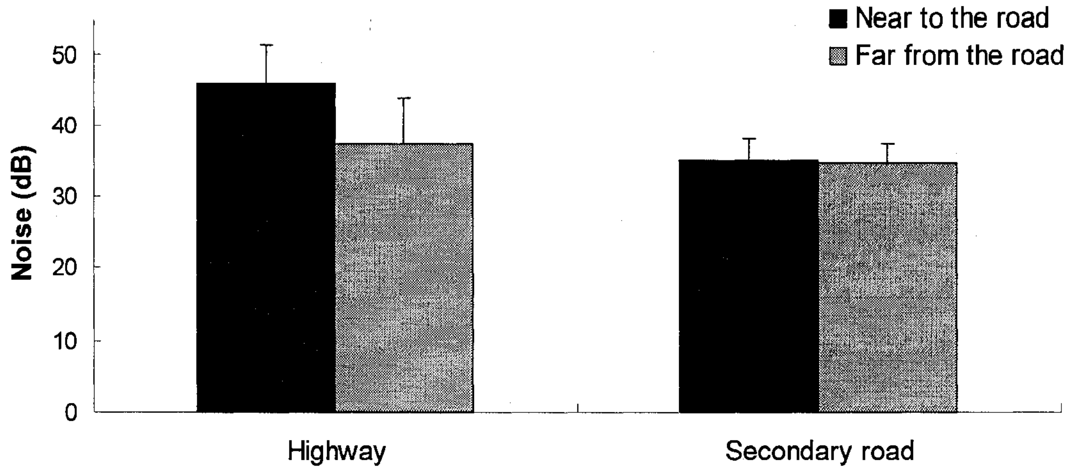


Figure 2.1. Noise meter readings in dB (mean ± SD) as a function of two road types (highway and secondary road) and two road distances (50 and 400 m)

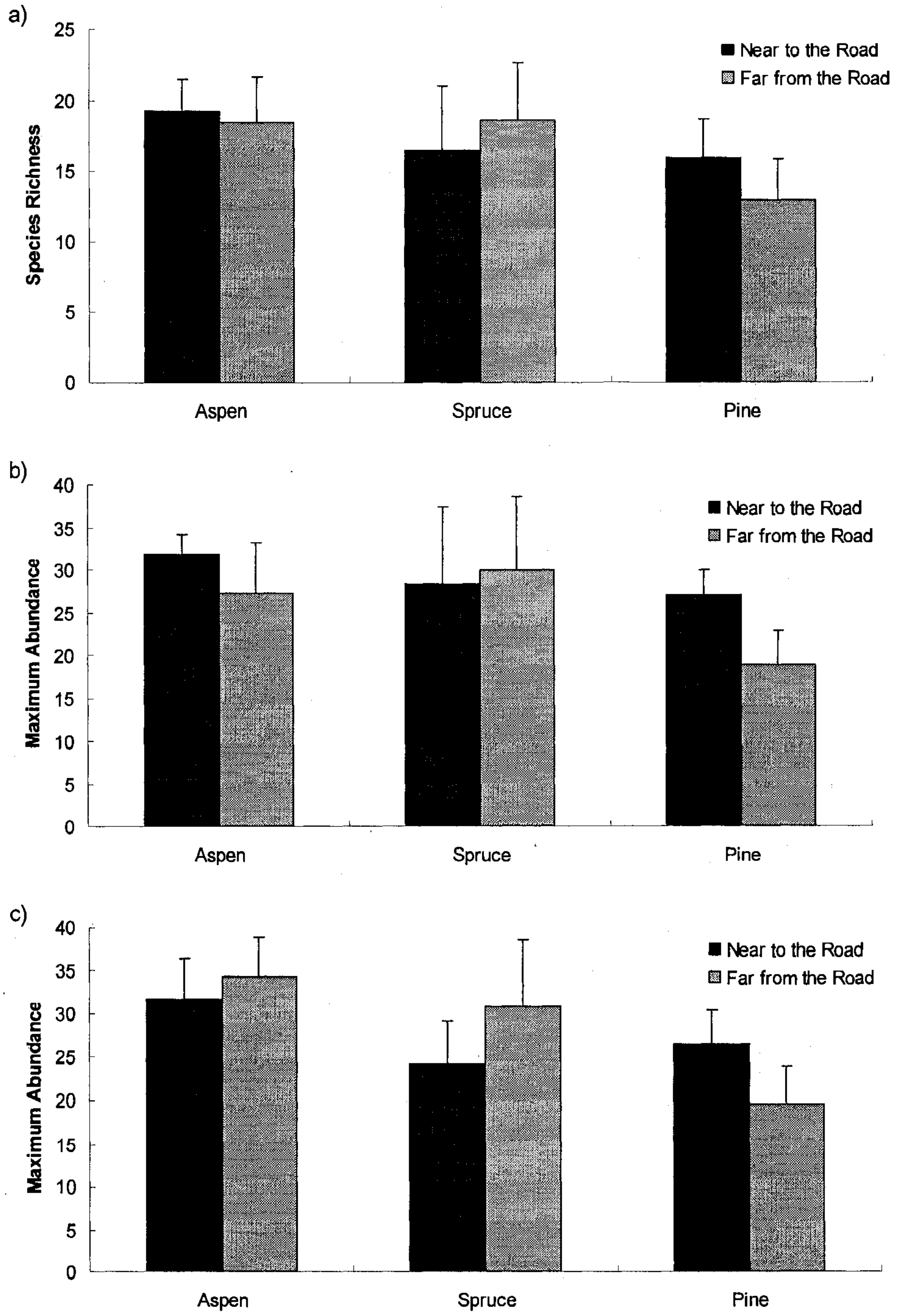
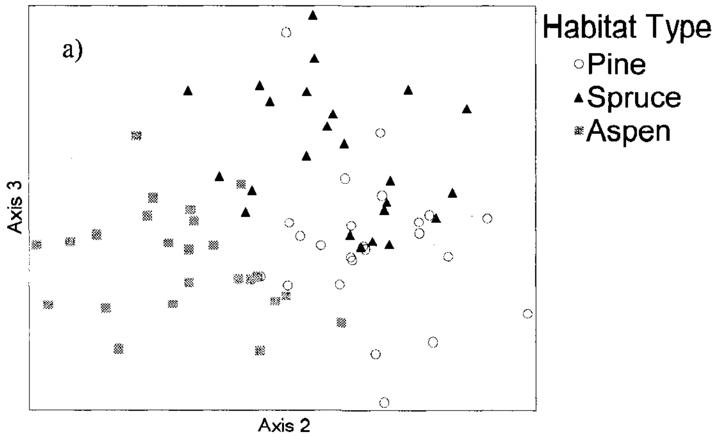
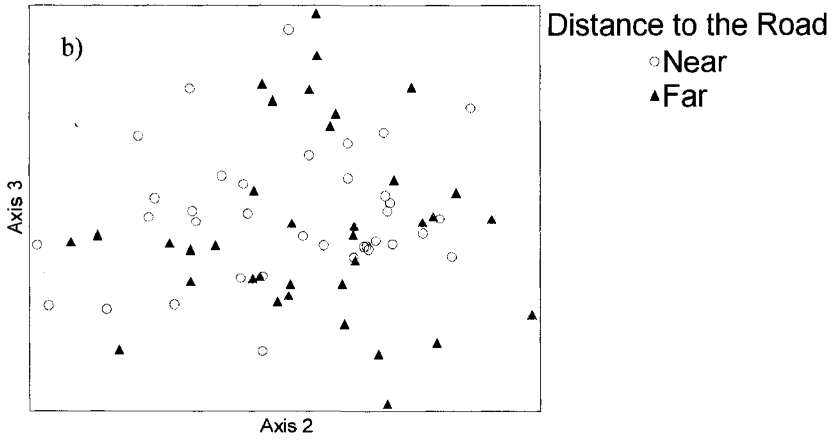
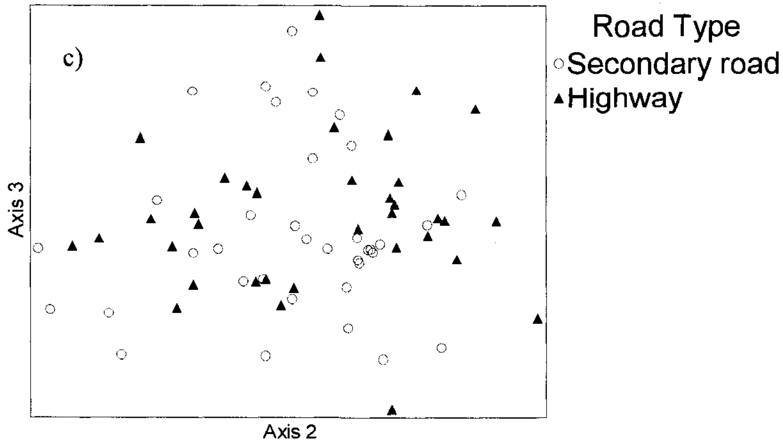


Figure 2.2. Species richness and associated SD obtained from point counts in Banff National park as a function of habitat type (Aspen, Spruce, Pine) and road distance (near, far). Road type (highway, secondary road) was combined when estimating means since they did not differ significantly (a). Maximum abundance obtained through point counts in Banff National park as a function of habitat type (aspen, spruce, pine) and road distance (near, far) for the secondary road (b) and the highway (c).


a)
Habitat Type
○Pine
▲Spruce
▨Aspen
Axis 3
Axis 2


b)
Distance to the Road
○Near
▲Far
Axis 3
Axis 2


c)
Road Type
○Secondary road
▲Highway
Axis 3
Axis 2

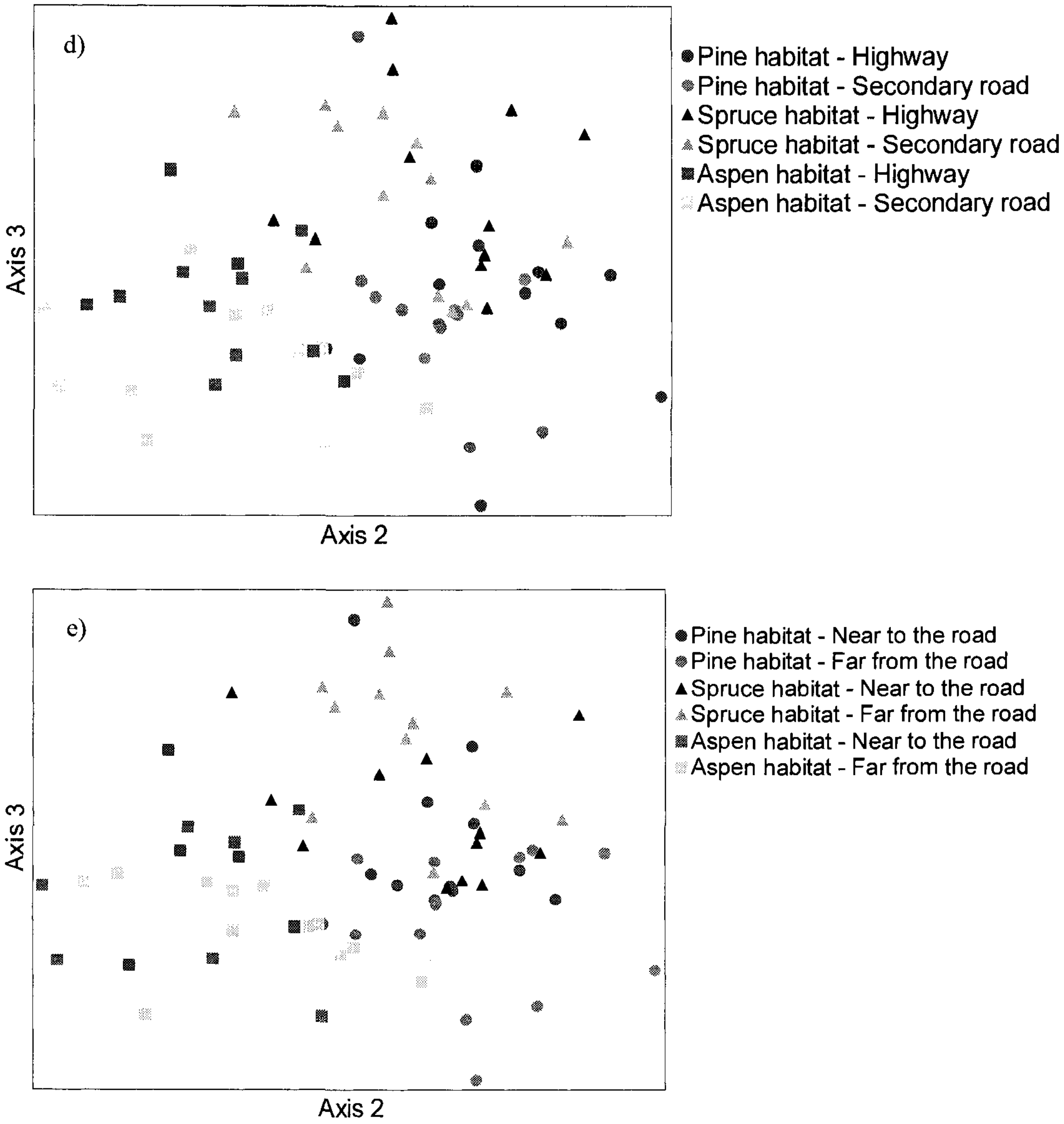


Figure 2.3. NMS ordinations of the bird community in Banff National Park showing axis two and axis three of a three-dimension best solution. These axes were chosen to best represent visual segregation of the interspersion. The interspersion shows a segregation of the community composition per habitat types with aspen stands being the most distinct (a). The interspersion of sites reveals no segregation by road distance (b) or road type (c). The ordination of sites shows an interacting effect of habitat and road type (d) as well as habitat and distance to the road (e).

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Chapter 3 – Effects of a high-traffic road on the age and health of males for two passerine species*

Introduction

Roads have detrimental direct and indirect effects on bird populations around the world. Direct effects impact bird populations mainly through road-kills (Dhindsa et al. 1988; Mumme et al. 2000) and habitat loss (Forman et al. 2002). These direct effects are often exacerbated with indirect effects, which encompass barriers to movement (Thiollay 1999; Laurance et al. 2004), changes in microclimate and vegetation structure at road edges (Forman et al. 2002; Male and Nol 2005), and noise pollution (Leedy and Adams 1982; Illner 1992; Kuitunen et al. 1998). Although they are generally harder to measure, many of these indirect effects can limit the viability of populations living near roads (Forman et al. 2003).

Although some studies link road edges to heightened bird density (Ferris 1979; Clark and Karr 1979), more indicate that the density of bird populations decreases near roads (Räty 1979; van der Zander et al. 1980; Illner 1992; Reijnen and Foppen 1994; Reijnen et al. 1996). The mechanism of this decline is suggested by a Dutch study on Willow Warblers (*Phylloscopus trochilus*). For this species, the edge habitat provided by roads is less suitable for breeding than interior habitat (Reijnen and Foppen 1994) and it is more likely to be occupied by younger individuals (Foppen and Reijnen 1994). Other authors have shown that younger individuals are less likely to be paired (Van Horn et al. 1995; Bayne and Hobson 2001), which in turn causes a reduction in productivity and, ultimately, population density. In Willow Warblers, this reduction can be significant; the proportion of younger (second year) birds was 50 % higher near the road, causing the annual offspring production to decrease by 40 % (Reijnen and Foppen 1994).

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* I used "we" throughout this chapter to reflect all contributors.

It is likely that roads elsewhere also cause changes in the demography, and hence productivity, of bird populations that live near to them. Unfortunately, demographic studies are time-consuming to conduct, and counts of abundance may be affected by variability in observers (Sauer et al. 1994) as well as environmental conditions (Robbins 1981). To date, there have been no detailed demographic studies of the effects of roads on birds in North America (reviewed by Forman et al. 2003). An alternative to demographic studies of road effects on bird populations is to use physiological parameters of health as proxies for eventual impacts on populations. For birds, traffic noise appears to cause stress (Illner 1992; Reijnen and Foppen 1994), and initial studies of the relationship between bird health and road proximity are suggestive of such effects. In Spotted Owls (*Strix occidentalis*), levels of fecal corticosteroids were higher within 400 m of logging roads (Wasser et al. 1997) and in Mexican Spotted Owls (*Strix occidentalis lucida*), noise from chain saws and helicopters increased flushing behaviour (Delaney et al. 1999). Also, laying hens subjected to noise had higher levels of chronic stress (Campo et al. 2005). Because health parameters such as stress response and body condition are linked to disease resistance, survival, and reproductive success (Siegel 1985; Haramis et al. 1986; Smith and Moore 2003), they may provide important estimators for the longer-term effects of roads.

Several body parameters can provide indications of bird health. Body mass is the most easily measured and it is usually positively correlated with fecundity and survival (Haramis et al. 1986; Brittas 1988; Smith and Moore 2003) as well as with brood care investment (Hanssen et al. 2003) although it fluctuates daily (Clark 1979). Morphological measures can reveal developmental stress that occurred during ontogeny via fluctuating asymmetry. Fluctuating asymmetry is defined as a deviation from perfect symmetry in bilateral traits of an organism (Van Valen 1962) and it can be used to estimate the stress on individuals stemming from both environmental and genetic sources (see reviews by Palmer and Strobeck 1986; Leary and Allendorf 1989; Parsons 1990). Although feathers are molted each year, fluctuating asymmetry of primary feathers in flycatchers is believed to arise from stochastic events affecting feather follicles in early development, which can produce continued asymmetry through annual molts (Stige et al.

2005). Other environmental stressors, such as food deprivation, can affect feather development during molt and lead to fluctuating asymmetry (Swaddle and Witter 1994). More chronic stressors have been linked to cardiovascular and gastrointestinal diseases as well as metabolic and immune function derangements (Siegel 1985). For birds, this kind of stress is reflected in elevated ratios of heterophil white blood cells to lymphocytes (Gross and Siegel 1983). Similarly, elevated heterophil counts indicate high stress, and low lymphocyte counts indicate stress and immunosuppression (Siegel 1985; Maxwell 1993; Maxwell and Robertson 1998). Variation in the total number of white blood cells of an individual can also reflect ongoing immunological processes such as bacterial and viral infections (Campbell and Dein 1984).

Here, we assess the effects of roads on bird health – as a potential indicator of longer-term population impacts – and on age distribution. We studied territorial male birds of one migrant and one resident species living near and far from a major highway and determined whether they differed in age, body mass, fluctuating asymmetry and several haematological measures: heterophil to lymphocyte ratios, as well as counts of heterophils, lymphocytes and total white blood cells. We hypothesized that birds living near the road would endure prolonged stress that would be reflected in these parameters. We further hypothesized that the resident species would be subject to greater stress because of its year-round presence in the area. Accordingly, we predicted that birds living near the highway would be younger, exhibit lower body mass and higher fluctuating symmetry as well as higher heterophil to lymphocyte ratios, higher heterophils, lower lymphocytes and higher total white blood cells than those living further from the highway. We also predicted that resident birds would show greater age segregation and difference in body mass, developmental and chronic stress than migratory birds.

Methods

STUDY SITE

Our study was conducted from May - July 2007 along the TransCanada Highway (hereafter "highway") in Banff National Park, Canada (51° 8', 115° 24') between the east entrance to the park and Castle Junction. The highway conveyed up to 19,500 cars daily, on average, for the months of May, June and July 2006 (Parks Canada unpublished data). The area along this high traffic-volume road is characterized by forested stands dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Englemann spruce (*Picea englemannii*), and trembling aspen (*Populus tremuloides*). In addition to the forested habitat that characterizes the valley bottom, there are several lakes, the Bow River and its tributaries, and the town of Banff, which has over 8,000 residents (Town of Banff 2007).

PROTOCOL AND SAMPLING

We captured male Ruby-crowned Kinglets (*Regulus calendula*; hereafter "kinglet"), a yearly migrant, and Red-breasted Nuthatches (*Sitta canadensis*; hereafter "nuthatch"), generally a year-long resident, at sites near to (approximately 50 m) and far from (approximately 400 m) the highway. Birds were caught throughout the day from approximately 0600 until 1600 MST. These species were chosen primarily because of their abundance in the area (St. Clair 2003) but also because of the ease of identifying them visually or by ear. Our capture method consisted of luring birds into mist nets by using species-specific taped playback calls, to which only males typically respond. Birds were usually processed within 20 min and always within an hour of capture time. Since cold morning temperatures interfered with blood clotting and thus potentially birds' health, we spread our capture efforts throughout the day and avoided early mornings on cold days.

After capture, birds were weighed to the nearest 0.1 g using an electronic scale, banded with Canadian Wildlife Service / U.S. Fish & Wildlife Service bands and aged as second year (SY) or after second year (ASY; Pyle 1997). Age assessments were verified blindly through photographs by a third-party to ensure accuracy (M. A. Gahbauer, pers. comm.). For each bird, we measured wing chord, bill length (from the nares to the tip), the right tarsus length and, to calculate fluctuating asymmetry, the left and right primaries. All measurements were taken by the same person throughout the study. We obtained blood samples by puncturing the ailar vein with a 0.27 gauge, 0.5 inch-long needle and collecting less than 1 cc of blood in a heparinised microhematocrit tube. We immediately made blood smears following a two-wedge slide method (Campbell 1988). All blood smears were air-dried and later stained with a Wright stain and buffered with a 2 % solution of Giemsa stain in deionized water (Sigma). We performed both absolute and differential white blood cell (WBC) counts. For the differential counts, we tallied all WBC (heterophils, lymphocytes, monocytes, eosinophils and basophils) until we reached a total of 100 WBC. From the counts obtained, we then calculated the heterophil to lymphocyte ratio (H:L). For the absolute counts, we calculated the total WBC as well as the number of heterophils and lymphocytes per 10 000 RBC. To assess the number of red blood cells, we first categorized each field of view as having a low, medium or high red blood cell count and use the average number of red blood cells in each of these three categories. To obtain the averages, we manually counted each RBC in 20 fields of view for each of the previously mentioned categories. The mean number of cells for low, medium and high counts was 330 ± 62, 612 ± 125 and 873 ± 104, respectively. Each of the three categories were significantly different from one another (low and medium: $t_{2,38} = -9.018$, $P < 0.0001$; medium and high: $t_{2,38} = -7.1987$, $P < 0.0001$). Finally, we scanned a random subset of 10 slides twice, and assessed the repeatability of our differential and absolute counts with an intraclass correlation coefficient (ICC) from a two-way ANOVA to identify consistency rather than absolute agreement among measurements (McGraw and Wong 1996). The noise at point count sites was also measured by averaging sound readings taken with a TES-1350A sound meter (TES Electrical Electronic Corporation) every 5 seconds for a 1 minute period.

STATISTICAL ANALYSES

To evaluate if younger birds of each species were more abundant near the highway, we used a one-tailed G-test of independence with, for kinglets, the Yates correction for continuity (Zar 1999). To determine if lower body condition was associated with road proximity, we built general linear models using the Hosmer and Lemeshow (2000) model-building approach. Briefly, we first identified the significant main effects by fitting a univariate regression with each independent variable and only retaining variables that were significant at ≤ 0.25. These significant variables were then forced into a multivariate model for which we set alpha at 0.10 to accommodate generally small sample sizes and the conservation context of our work. The remaining significant variables were fitted in a reduced model and all biologically plausible interactions were added, one at a time, and kept in the model if they were significant. In this way, we modelled the dependent variable mass against five independent variables: distance to the road, bird age, Julian date, time of day and an index of body size. We additionally tested for interactions between date and distance, time and distance, date and time, date and age, distance and age, body size and age, and distance and body size. We obtained an index of body size by using the first principal component (PC1) of a Principal Component Analysis (PCA) that reduced beak length, tarsus length and wing chord to a single variable as a more reliable measure of body size than any single measure (Greene 2001). Because PCA results can be greatly influenced by outliers (McCune and Grace 2002), we did not include data that were more than two standard deviations from the mean.

To test the hypothesis that birds with higher developmental stress settled closer to the highway, we tested for a difference in fluctuating asymmetry between the two road distances with an *F*-test. After Palmer (1994), we used FA4, the variance of the differences between the right and left ninth primaries, as well as FA5, the variance of that same difference but where the mean is assumed to be zero, as indices of fluctuating asymmetry. We conducted skewness and kurtosis tests to verify the presence of antisymmetry. Skewness and kurtosis tests are one-sample *t*-tests where t is equal to the skewness or kurtosis divided by its appropriate standard error and compared to the t-distribution with infinite degrees of freedom (Palmer 1994). We also plotted the absolute value of the difference between the right and left primaries against tarsus length to test for dependence with body size (Palmer 1994). We further tested for directional asymmetry by conducting a one-sample *t*-test on the difference between the right and the left ninth primaries (Palmer 1994).

Finally, to determine if birds with higher stress and lower immunocompetence were found near the highway, we modelled our independent variables with each of our four dependent variables of haematological health: H:L, total WBC, absolute heterophils and absolute lymphocytes. Our independent variables in each model, as well as the interactions tested, were identical to the one used above with the exception of the index of body size, which was not used in this model. Mass was used instead because it is affected by corticosteroid levels (Hiebert et al. 2000), which are also known to impact the number of leukocytes (Siegel 1985). To meet the linear model's assumptions of normality, H:L for both species were square-root transformed. Total WBC for the nuthatch was also square-root transformed and both total WBC and absolute lymphocytes for the kinglet were log transformed. Additionally, the model for H:L of kinglets was corrected for heteroscedasticity with an heteroscedasticity-corrected covariance matrix of type HC3 (Long and Ervin 2000). All analyses were performed using R (R Development Core Team 2007) with the exception of the PCA, which was conducted using the PC-Ord program (McCune and Mefford 1999).

Results

Between May 8 and July 11, 2007, we captured 24 male kinglets and 37 male nuthatches. Of these birds, 12 kinglets and 17 nuthatches were captured near the road and 12 kinglets and 20 nuthatches were captured far from the road. The average noise adjacent to the road (57.32 dB ± 3.27) was significantly greater than the average noise far from the road (47.37 dB ± 3.94; $t = 6.72$, df = 22, $P < 0.0001$).

Among the kinglets, 19 (79.17%) were SY and 4 (16.67%) were ASY. In SY kinglets, 10 (52.63 %) were caught near the highway and 9 (47.37%) were caught far from the highway. For nuthatches, 17 (45.95%) were SY and 19 (51.35%) were ASY. In SY nuthatches, 10 (58.82%) lived near the highway and 7 (41.18%) far from the highway. One bird of each species was aged as after hatching year. For nuthatches, significantly more young birds were found living near the road ($G = 1.74$, df = 1, $P = 0.10$), but not for kinglets ($G = 0.21$, df = 1, $P = 0.33$; Fig. 3.1).

Body mass ranged from 5.75 g to 6.60 g for kinglets (mean ± SD, 6.17 ± 0.21 g) and from 9.80 g to 11.00 g for nuthatches (mean ± SD, 10.50 ± 0.41 g). There was no difference in body mass as a function of road proximity for either species ($t < 0.66$, $P > 0.52$). When body mass was examined with the covariate of body size (PC1), body mass of nuthatches and PC1 were negatively correlated ($\beta = -0.27$, $t = -3.30$, df = 18, $P = 0.002$; Fig. 3.2) and there was a significant interaction between body size and road proximity ($t = 1.91$, df = 18, $P = 0.06$; Fig. 3.2). Because high PC1 values represent small body sizes and low PC1 values represent large body sizes, this interaction reveals that nuthatches exhibit a stronger relationship between body mass and body size near the road than they do far from the road. The PC1 of the PCA accounted for 46.06% of the variation in size traits in kinglets and 53.09% in nuthatches.

Levels of developmental stress, reflected in the fluctuating asymmetry of morphological measures, did not differ in birds that settled near vs. far from the road for either species (Table 3.1). We verified the adequacy of using the difference in length between the left and right ninth primaries as a trait for fluctuating asymmetry. The trait met most assumptions in that it displayed no significant skewness (kinglet: $t = 0.79$, df = ∞, $P > 0.10$; nuthatch: $t = 0.79$, df = ∞, $P > 0.10$) or kurtosis (kinglet: $t = 0.22$, df = ∞, $P > 0.10$; nuthatch: $t = 1.65$, df = ∞, $P > 0.10$), and was not correlated with body size (kinglets near to the road: $\beta = 0.10$, $t = -1.49$, df = 11, $P = 0.17$; kinglets far from the road: $\beta = -0.02$, $t = -0.12$, df = 11, $P = 0.90$; nuthatches near to the road: $\beta = 0.05$, $t = 0.318$, df = 16, $P = 0.76$; nuthatches far from the road: $\beta = 0.02$, $t = 0.22$, df = 19, $P = 0.83$). However, the difference in length between the left and right ninth primaries displayed directional asymmetry for nuthatches but not for kinglets (Table 1), which means that some variation in this trait could have a genetic rather than environmental basis in nuthatches (Palmer

1994). Given that FA5 is biased when a trait shows directional asymmetry (Palmer 1994), FA5 was not used for nuthatches.

Hematological measures revealed no effect of road proximity, but they varied with time of day and date. For both species, there was no difference between the two road distances in stress and immunocompetence measured by H:L ($t < 0.55$, $P > 0.59$; Fig 3.3), heterophil counts ($t < 0.31$, $P > 0.76$), lymphocyte counts ($t < 0.71$, $P > 0.48$) or WBC ($t < 0.33$, $P > 0.75$) as a function of road distance. However, H:L were negatively correlated with date in kinglets ($\beta = -0.009$, $t = -2.04$, df = 21, $P = 0.05$) but not in nuthatches ($t = 0.74$, df = 35, $P = 0.46$; Fig. 3.4). By contrast, heterophils were positively correlated with date for both kinglets ($\beta = 0.06$, $t = 1.72$, df = 21, $P = 0.10$) and nuthatches ($\beta = 0.12$, $t = 2.40$, df = 35, $P = 0.02$). For kinglets, lymphocytes were also positively correlated with date ($\beta = 0.009$, $t = 3.59$, df = 21, $P = 0.002$) and time of day ($\beta = 0.04$, $t = 1.70$, df = 21, $P = 0.1$). Finally, WBC were positively correlated with date for kinglets ($\beta = 0.008$, $t = 2.93$, df = 21, $P = 0.008$). Of all the birds caught, we collected blood samples from all but one bird of each species and repeatability for the differential and absolute leukocyte counts were all highly significant, indicating high intra-observer reliability ($F > 6.49$, df = 9 and 9, $P < 0.01$).

Discussion

We studied the effects of the TransCanada Highway in Banff National Park on one demographic and a series of physiological parameters with the prediction that more SY birds would live near the highway and that proximity to the road would engender lower body mass, higher levels of developmental and chronic stress as well as lower lymphocyte-mediated immunocompetence. Our results only supported the prediction of an age difference; in nuthatches, SY birds were more likely to live near the road. Young Willow Warblers in the Netherlands are also more likely to live near a road (Reijnen and Foppen 1994). In Alberta, Canada a greater proportion of SY Ovenbirds (*Seiurus aurocapilla*) were found in noisier areas (Habib et al. 2007) and, in our study, locations in proximity to the road had significantly higher noise levels.

Understanding the mechanism of this difference in age distribution would require more study, but several processes could account for it. To begin with, SY birds may be more abundant near the road because these territories are associated with higher mortality risks. In Golden Eagles (*Aquila chrysaetos*) and Bonelli's Eagles (*Hieraaetus fasciatus*), the proportion of young males can act as a surrogate for mortality rates (Carrete et al. 2006). In our study, mortality may be higher at territories near the road for two reasons. First, the birds may be subject to higher predation due to edge proximity (Gates and Gysel 1978) or because high noise levels may interfere with predator detection (Habib et al. 2007). Second, birds living near roads are faced with the possibility of being killed by cars. Road-kill surveys in Banff show a high number of birds being killed along the TransCanada Highway (Clevenger et al. 2003). Because young birds are more likely to live near the road, they are presumably also more likely to be killed in this way. Passerines are short-lived and it has been suggested that SY birds with territories near the road may not live long enough to reproduce (Foppen and Reijnen 1994). Higher mortality risks near the road may cause habitat to be of lower quality. This lower quality habitat could further explain why SY nuthatches are more abundant near the road. Indeed, the ideal despotic distribution (Fretwell and Lucas 1970) predicts that young birds, having a lower social status (Davies and Lundberg 1984), are displaced from good quality territory by ASY birds that have greater dominance and experience. As opposed to kinglets, nuthatches are yearly residents and had a longer time to assess territory quality and segregate between SY and ASY.

Dispersal may also account for the difference in age distribution of nuthatches. In the Netherlands, SY male Willow Warblers that live near roads disperse three to four times longer distances than males far from the road (Foppen and Reijnen 1994). Dispersal probability in SY is correlated with breeding success (Foppen and Reijnen 1994) and because SY birds show lower reproductive success near the road (Reijnen and Foppen 1994), which could be due to lower pairing success (Saether 1990; Bayne and Hobson 2001; but see Habib et al. 2007), it may cause SY birds to disperse more (Foppen and Reijnen 1994).

In contrast to the relationship between road proximity and bird age, body mass did not vary with road proximity for either species. One reason why mass did not differ near and far from the road may be that roads, and their associated traffic, may not interfere with overall energy obtained by birds through foraging. Although traffic vibrations are thought to affect emergence of earthworms (Tabor 1974), kinglets feed mainly on spiders, insects, fruit and seeds (Ingold and Wallace 1994) and nuthatches on arboreal arthropods during the breeding season (Ghalambor et al. 1999). As for the impact of traffic pollution on arthropods, it was shown to decrease species richness in some groups but to be beneficial to others (Przybylski 1979). Also, in Ovenbirds, anthropogenic noise did not affect body mass, even though younger birds lived in noisier sites (Habib et al. 2007). Body mass was more strongly correlated with body size near the road in nuthatches, further suggesting that there is no limiting effect of road proximity on foraging success. Although body mass did not differ with distance to the road, it increased throughout the day in kinglets. This result was expected as mass in birds generally increase by 5 to 10 percent with food consumption throughout the day (Clark 1979). The accumulated mass is then lost during the night (Clark 1979).

In accordance with the results obtained for body mass, our results showed no difference in the level of developmental stress between birds with territories near to or far from the road as measured with fluctuating asymmetry. This result may have occurred because birds with higher developmental stress did not settle in greater number near the highway or because fluctuating asymmetry was inadequately assessed by our study. Our first interpretation suggests that birds near to and far from the road may have a similar level of fitness (Thornhill 1991; Møller 1992). However, the birds near to the road may raise offspring that will show more developmental asymmetry than offspring far from the road due to the significantly higher noise in proximity to the road. In support of this hypothesis, fluctuating asymmetry increased in rats that were born in a noise-stressed environment (Gest et al. 1983). Also, noise level is associated with traffic as well as road proximity and, in a study on Western Fence Lizards (*Sceloporus occidentalis*), fluctuating asymmetry increased at sites where off-highway vehicles were present (Tull and Brussard 2007). The second interpretation suggests that although a difference in developmental stress with road proximity exists, our study did not detect this difference. It is possible that the resolution of our measurements was not detailed enough as we measured to the nearest 0.5 mm, or that the chosen trait was symmetrical simply by chance, or that the errors in measurement – which were not evaluated with a second observer – were too great (Palmer 1994).

Similar to the results obtained for body mass and developmental stress, there was no effect of road proximity on chronic stress and immunocompetence as indicated by our four blood measures. These results could indicate that road proximity has no effect on nuthatches and kinglets. Another potential reason why blood measures did not differ with road proximity is that birds in our whole study area may have been affected by road noise and hence exhibit chronic stress and immunosuppresion. When comparing the averages for heterophils, lymphocytes and H:L of both kinglets and nuthatches to a study that compared these same measures in urban and rural Rufous-collared Sparrows (*Zonotrichia capensis*; Ruiz et al. 2002), the level of chronic stress and immunocompetence exhibited by our birds is more similar to urban birds than rural birds. Urban birds had higher heterophils and H:L as well as lower lymphocytes than rural birds (Ruiz et al. 2002). Within the 400 m of the road surface for which we measured birds, all individuals may have suffered from low lymphocyte-mediated immunocompetence and high levels of stress (Gross and Siegel 1983; Siegel 1985; Maxwell 1993; Maxwell and Robertson 1998). These levels of leukocytes could negatively impact breeding populations because elevated H:L ratios are linked to a higher production of corticosterone, which decreases lymphocytes in the blood (Vleck 2001), and this high level of corticosterone can negatively affect offspring development (Hayward and Wingfield 2004). Further work would be needed to know whether these measures differ from birds living elsewhere in the park and if the observed counts are similar across a greater range of species.

Hematological measures of health did not differ with road distance but varied with date and time of day. In kinglets, there was a decrease in H:L and an increase in the number of heterophils, lymphocytes and total WBC during the breeding period. Both an increase in total WBC and a decrease in H:L through the breeding season were observed elsewhere (Mazerolle and Hobson 2002). Our results suggest that lymphocytes were increasing at a greater rate than heterophils during the breeding season because H:L decreased while heterophils and lymphocytes increased. Lymphocytes are indicative of acquired immunity and because this type of immunity is more costly to deploy and maintain (Apanius 1998), kinglets were likely in better health towards the end of the breeding season. At the start of the season, the higher H:L and the lower lymphocyte and total WBC counts could be lingering effects of the kinglets' migratory state. When migrating, birds have a lower lymphocyte and total WBC counts as well as higher heterophil counts and H:L (Owen and Moore 2006). Lymphocytes, H:L and total WBC of nuthatches did not vary throughout the summer probably because they are generally year-long residents (Ghalambor and Martin 1999). Both nuthatches and kinglets showed an increase in heterophils during the season. Although elevated heterophil counts can indicate high stress (Siegel 1985), this is unlikely the case in this study because, for kinglets, H:L – the most reliable indicator of chronic stress (Gross and Siegel 1983) – decreased during the same period.

Date was not the only variable influencing hematological measures; kinglets' lymphocyte counts also increased with time of day. Fluctuation in WBC levels during the day is still poorly understood. Because birds' immune system can be negatively affected by the level of testosterone (Zuk 1996) others have suggested that daily variation in testosterone could explain fluctuation in WBC (Mazerolle and Hobson 2002). Hence, the daily variation in our data is not explained by the typical long-term stress meaning we associate with lymphocytes fluctuation but rather by daily variations in testosterone.

In sum, we can infer three main conclusions from our study of road effects. First, distance to the road was reflected only in the demographic measure of age and only for one species: younger nuthatches were more likely to live near the road. The prevalence of SY birds near the highway could conceivably create a population sink in that area if young birds do not live to reproduce. None of the three variables that were assumed to reflect the stress exerted by road proximity – body mass, fluctuating asymmetry and blood-born measures – differed as a function of road distance. The persistent correlation between blood measures and date suggests that kinglets, a migratory species, were in better health at the end of the breeding season whereas nuthatches, a year-round resident, remained in similar health throughout the season. Further work should compare health measures at greater distances from the road and in a wider range of species to assess the robustness of our results that roads have little effect on the health of bird.

Table 3.1. Fluctuating asymmetry expressed as both FA4 and FA5 indices, directional asymmetry, skewness and kurtosis of the difference between the right and left ninth primaries of Red-breasted Nuthatches and Ruby-crowned Kinglets living near to and far from the road.

	N		Fluctuating asymmetry (FA4)		Fluctuating asymmetry (FA5)		Directional asymmetry		Skewness ± SE	Kurtosis ± SE
	Near	Far	F	P	F	P	t	P		
Red-breasted Nuthatch	17	20	1.02	> 0.50	Not applicable		2.83	0.007	-0.31 ± 0.39	-0.17 ± 0.76
Ruby-crowned Kinglet	12	12	1.16	> 0.50	1.13	> 0.50	-1.23	0.23	0.37 ± 0.47	-1.52 ± 0.92

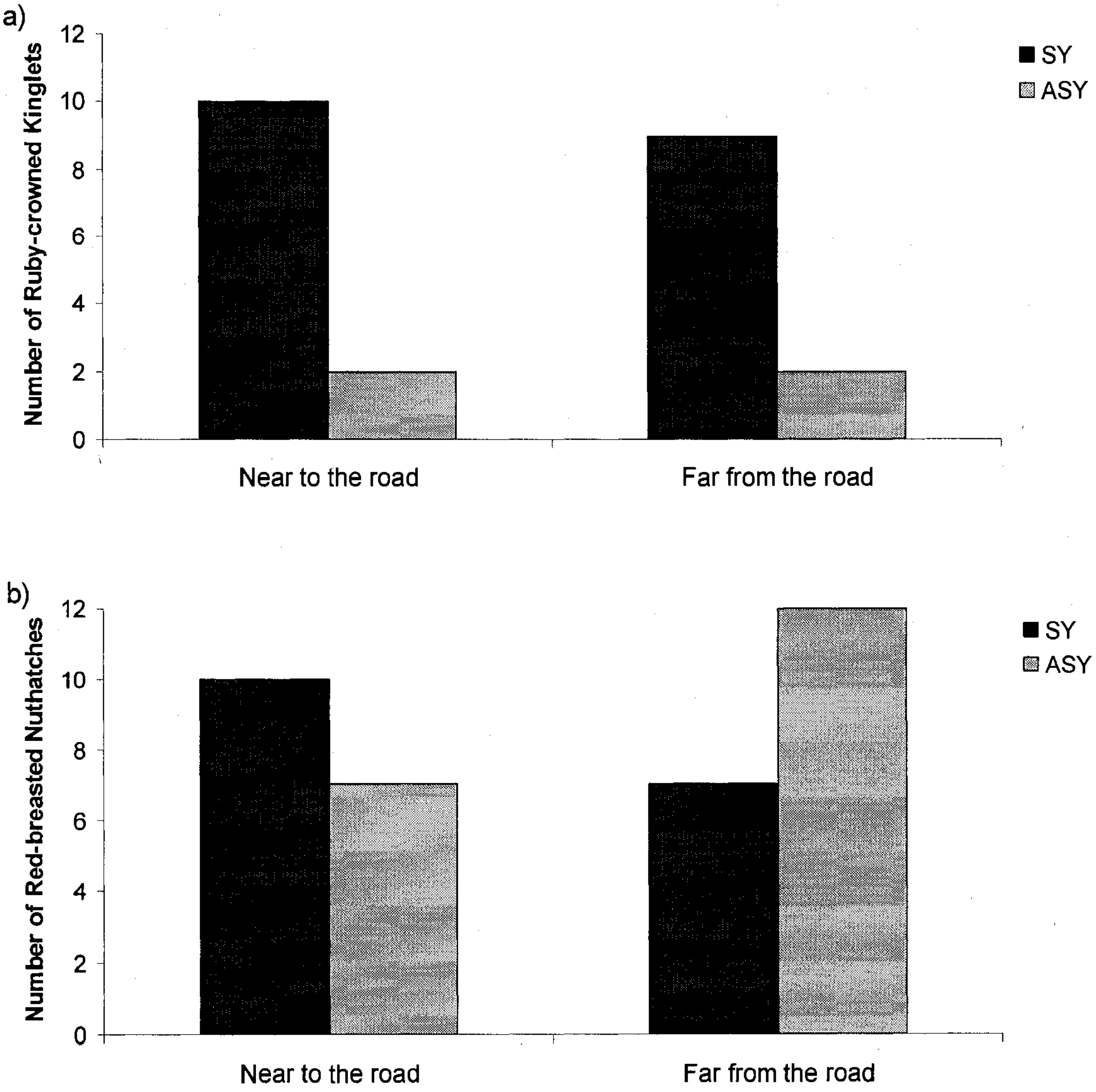

Figure 3.1. Number of male birds in each age class captured in Banff National Park as a function of road proximity (approximately 50 versus approximately 400 m) for (a) Red-breasted Nuthatch and (b) Ruby-crowned Kinglet.

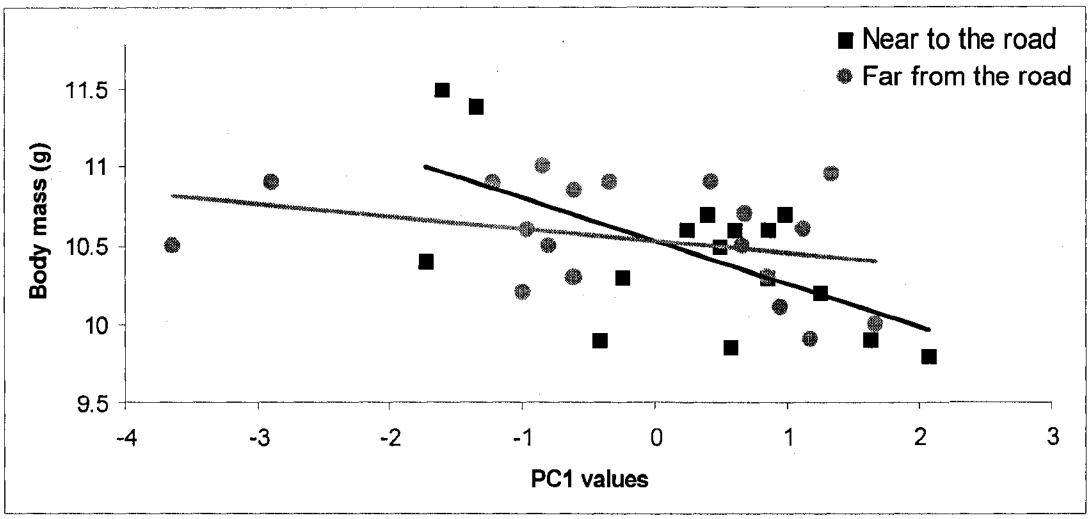

Figure 3.2. Body mass of Red-breasted Nuthatches obtained from mist net captures near to and far from the road in Banff National Park as a function of PC1 values where high PC1 values indicate small body size and vice versa (near: $P = 0.01$, $r^2_{adj} = 0.33$; far: $P = 0.18$, $r^2_{adj} = 0.05$).

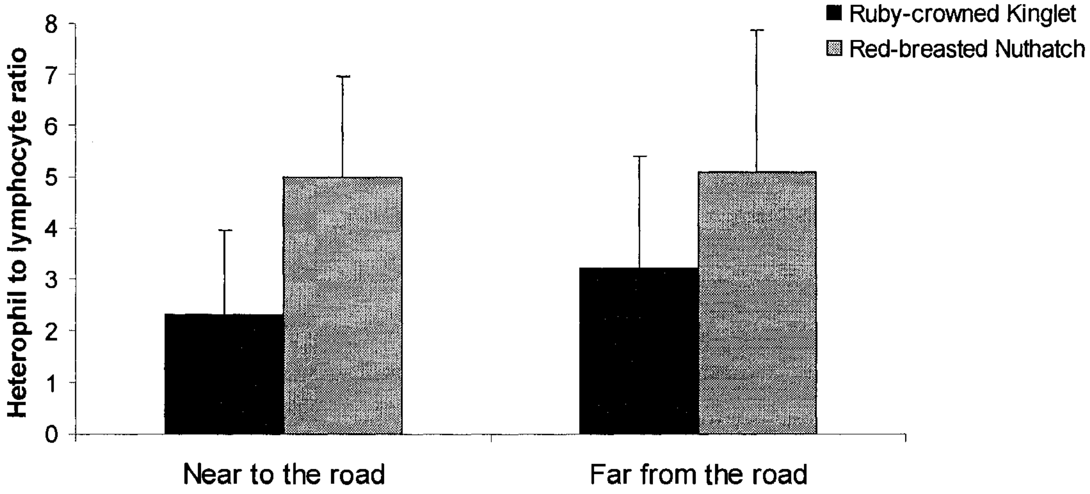

Figure 3.3. Ratio of heterophils to lymphocytes as a function of road distance (approximately 50 versus approximately 400 m) in Ruby-crowned Kinglets and Red-breasted Nuthatches obtained from mist net captures in Banff National Park.

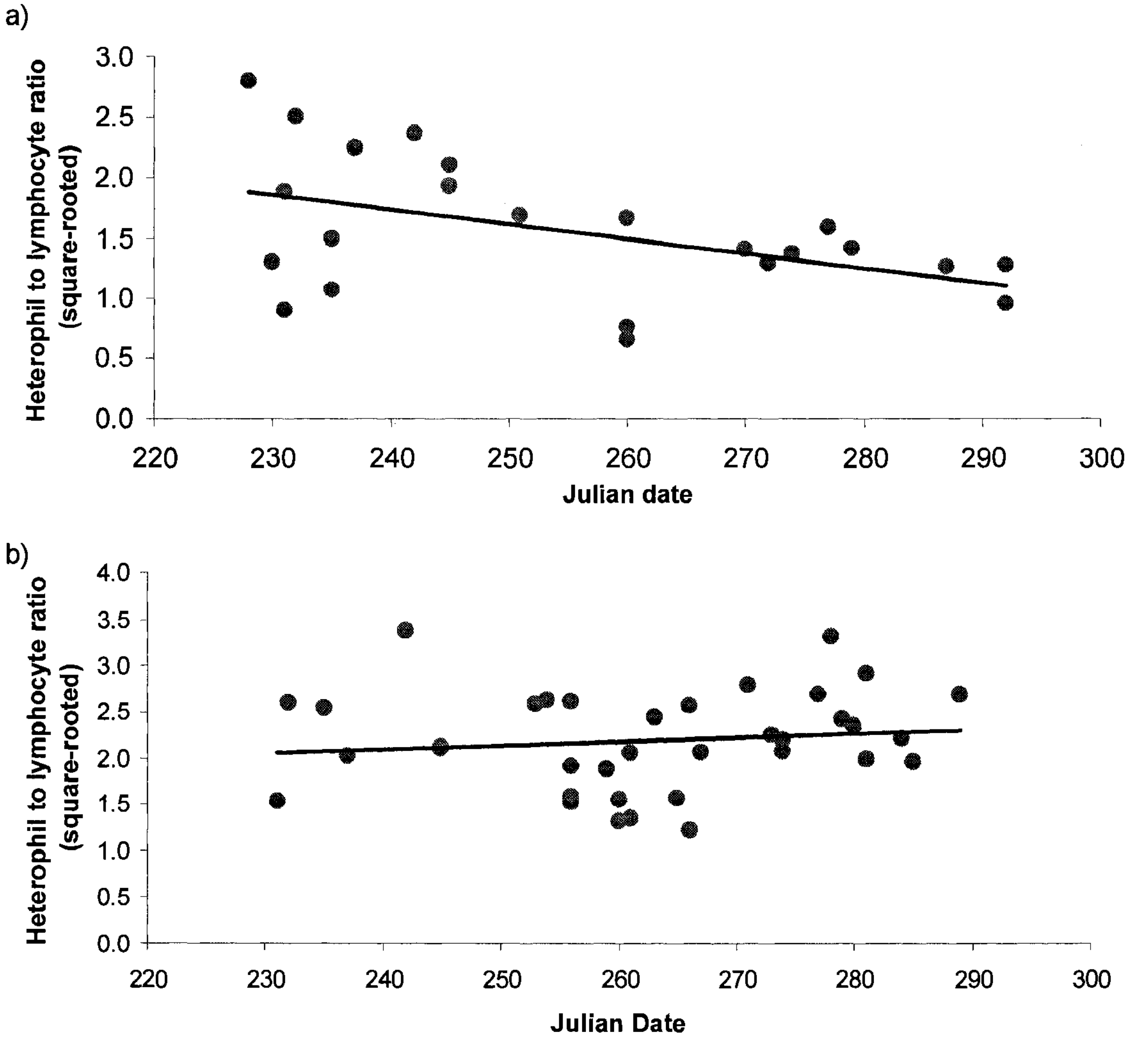

Figure 3.4. Heterophil to lymphocyte ratios obtained from mist net captures in Banff National Park as a function of Julian date of (a) Ruby-crowned Kinglets ($\beta = -0.009$, $t_{2,21} = -2.04$, $P = 0.05$) and (b) Red-breasted Nuthatches ($\beta = 0.004$, $t = 0.74$, df = 35, $P = 0.46$

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Chapter 4 – General Discussion

Birds are known to be negatively affected by a variety of direct and indirect road effects (Forman et al. 2003). With this thesis, I extended the existing knowledge on road impacts by investigating two understudied aspects of road effects: impacts on community composition and physiological measures of health. To assess road impacts on community composition, I compared species richness, bird abundance, diversity, and dissimilarity between communities in three habitat types (aspen, spruce, pine) near to and far from a highway and a secondary road. I also examined how bird abundance for foraging, nesting and ground guilds responded to road impacts. For males of two species – red-breasted nuthatches and ruby-crowned kinglets – I further assessed the effects of road proximity on age distribution and three health parameters: body mass, fluctuating asymmetry and blood measures. Here, I review my findings on road effects and conclude by synthesizing my results in relation to habitat fragmentation more generally, as well as suggesting avenues for future research.

Community composition differed mainly by habitat type and this is most clearly shown by two results. First, species richness, bird abundance and the Brillouin index of diversity were greater in aspen habitats than in spruce and pine habitats. Second, there existed significant dissimilarity, as shown through the PERMANOVA, between the three habitat types. The greatest dissimilarity existed between aspen and spruce habitats, closely followed by the dissimilarity between aspen and pine habitats. Both of these results likely stem from the greater undergrowth plant diversity in deciduous forests (Barbier et al. 2008) compared to coniferous forest. A more diverse undergrowth creates greater environmental complexity, which allows more species to become established (Molles 2002).

In aspen and pine habitats, distance to the road affected community composition. In aspen habitat, the communities near to and far from the road were significantly dissimilar through the PERMANOVA analysis, although species richness, abundance and the Brillouin index of diversity did not vary significantly. In pine habitat, richness, abundance, the Brillouin index of diversity, and the abundance of ground foraging birds were higher near the road. One explanation for this interaction between habitat and road proximity in aspen habitat is that the greater number of species in aspen habitat increased the likelihood of detecting a difference in species composition between sites that were near versus far from the road. This would not explain the difference in pine habitats. In this habitat, it is possible that sites near the road have more understory plants (Murcia 1995) and reduced soil acidity (Myers-Smith et al. 2006). Hence, this modified vegetation might be favoured by ground-foraging birds.

Although habitat type was the most important factor shaping bird community composition, road type also had an effect. Within similar habitats, the communities along the highway and the secondary road were dissimilar as shown by the PERMANOVA. The dissimilarity likely came from a difference in species composition because species richness, abundance and the Brillouin index of diversity did not vary between the two road types. This dissimilarity may have been due to differences in noise levels adjacent to the two roads. Because traffic volume is correlated with road noise (Ma et al. 2006), the noise levels we detected were significantly higher beside the highway (mean ± *SD*: 41·58 ± 7·49 dB), in contrast to the secondary road (34·68 ± 2·93 dB). Noise pollution is expected to affect bird populations because sound is so important to bird communication (Coffin 2007).

The potential effect of noise on birds is further illustrated by the analysis of the abundance of birds belonging to different song guilds. I found that two species of birds with low-frequency songs – those overlapping the most with traffic noise – were more abundant near the quieter secondary road. Conversely, one of two species with high-frequency songs was more abundant along the noisier highway. Two species with moderate-frequency songs did not differ between the two road types. Others have suggested noise to be an important factor affecting birds (Leedy and Adams 1982, Illner 1992, Kuitunen et al. 1998). Although these studies examined the effects of road noise on breeding densities, this thesis could indicate the potential for noise to affect community composition as well, a finding which supports other studies on the effects of road noise on community composition. (Slabbekoorm and Peet 2003, Slabbekoorn and Boer-Visser 2006).

In the first part of this thesis, my findings suggested that habitat was the main factor shaping the bird community. Even the effect of road proximity was limited to specific habitat and associated modifications. The lack of an effect of road proximity across all habitat types may mean that no such effect occurs, or that our two distance classes were too similar to detect it. If, as hypothesized above, noise is one factor that is responsible for the difference in community composition between the highway and the secondary road, I would have expected to also see a significant interaction between road type and road proximity. One possible explanation for the lack of an interaction between road type and road proximity in the community data is that the variation in community composition between the three habitat types may have dwarfed the significance of the interaction.

In the first part of the thesis, I focused on the effects of roads on community composition, whereas in the second part of the thesis I showed that age distribution varied with road proximity. This is demonstrated by the disproportionately high presence of young red-breasted nuthatches near the road. In eagles, high numbers of young birds were interpreted to be a surrogate for mortality rates (Carrete et al. 2006). Hence, one reason why more young birds were found near the road may be because their territories were associated with higher mortality rates. This could occur if edges create ecological traps (Gates and Gysel 1978) because noise levels there interfere with predator detection (Habib et al. 2007) or because birds living near roads are more likely to be killed by cars (Clevenger et al. 2003).

Even though age distribution varied with road proximity, none of the other health parameters I measured (including mass, fluctuating asymmetry and hematology) did. The sample sizes for this part of the thesis were relatively small and the variation of the hematological data was substantial. Hence, even though we set our alpha at 0.10, it is possible that our study lacked the power to detect an effect. However, the lack of variation in mass could also indicate that road proximity does not interfere with foraging.

Also, the similar level of fluctuating asymmetry near to and far from the road could indicate similarity in fitness for birds at both distances (Thornhill 1991; Møller 1992). Likewise, my hematological measures failed to detect a significant difference in stress and immunosuppression between the two distances. The similarity in mass, fluctuating asymmetry and hematology at both road distances could indicate that road proximity has no effect on red-breasted nuthatches and ruby-crowned kinglets. A second explanation is that all birds in the study area may have been subjected to relatively equal levels of stress, regardless of their proximity to the road. Indeed, the level of the hematological indicators of chronic stress and immunosuppression obtained in the study birds were similar to the ones recorded in urban rufous-collared sparrows from a study in Chile (Ruiz et al. 2002). Urban birds had higher H:L and heterophils as well as lower lymphocytes than rural birds (Ruiz et al. 2002). This could indicate that birds in my whole study area could live in an environment that is more indicative of urban rather than rural habitat and suffer a reduction in fitness due to elevated stress (Hanssen et al. 2003, Boonstra 2004). More studies would be needed to understand the full range of hematological measures in birds as well as in the context of my own results.

By comparing the results obtained in both parts of this thesis, two main interpretations are possible. The first suggests that the effects I observed indicate that roads cause no further effects than those resulting from the edges caused by fragmentation if no pavement and no cars were present on the highway and the secondary road. The second suggests that roads cause effects that are more severe than those expected from fragmentation alone. I will discuss the support for each interpretation below.

In support of the first interpretation, fragmentation creates edges of modified vegetation structure and plant composition (see review by Murcia 1995), which could account for the observed differences in community composition between the two road distances in aspen and pine habitats. The presence of edges could also account for the disproportionately high number of young red-breasted nuthatches near the road because this habitat is of lower quality as suggested by a close relative: the Eurasian nuthatch (*Sitta europaea*) (Bani et al. 2006). Young birds generally have a lower social status

(Davies and Lundberg 1984) and, according to the ideal despotic distribution (Fretwell and Lucas 1970), older (ASY) birds are able to push young (SY) birds out of better territories. Hence, because the habitat is of lower quality, more young birds occur near roads and younger birds of some species have lower reproductive outputs (Reijnen and Foppen 1994). However, if SY birds of several species consistently produced fewer offspring in proximity to the road, I would have expected the abundance of birds to have been lower there, which it was not. This could indicate that the habitat near the road is not of markedly lower quality or that young birds do not have a noticeably lower reproductive output. Another possibility is that even though habitats closer to the road were of lower quality and that lower reproductive output was found there, this may not have been reflected in bird abundance. This could occur if areas near the road were sinks for some bird species but that they remained ecologically stable and maintained at current population densities due to regular immigration from a source (Pulliam 1988). A source is characterized by an excess of births to deaths and a net emigration of individuals (Watkinson and Sutherland 1995) and it would likely be situated further from the road. Due to a low reproductive success in young birds near the road (Reijnen and Foppen 1994) and because of a higher mortality risk at edges (Gates and Gysel 1978), road proximity could cause bird territories to be sinks. In sum, the presence of roads may not affect birds beyond what would be expected by fragmentation alone as three of the thesis results – differences in community composition with road proximity in aspen and pine habitats, as well as age distribution – can possibly be explained by the habitat modification at edges.

The second interpretation of the thesis results is that the roads and cars bring effects that surpass what fragmentation edges could cause. These effects could be attributed to the presence of traffic noise. As mentioned above, the difference in community composition between the two road types may be due to noise. This claim was consistent with the analysis on song guilds, which showed that birds with songs overlapping the most with road noise were more abundant near the secondary road. Moreover, ruby-crowned kinglets and red-breasted nuthatches near and far from the highway potentially exhibited leukocytes values that were more representative of urban birds and a profound difference between forest and urban areas is the presence of anthropogenic noise. Hence, I speculate that the presence of anthropogenic noise may affect the whole study area along the highway. If anthropogenic noise has an impact, the study area surrounding the highway may have lost species that, because they cannot modulate their song, ceased to exist (Slabbekoorn and Boer-Visser 2006). This could explain the difference in community composition between the highway and the secondary road.

From here, I would like to consider areas of future research. To further test the hypothesis that noise is a main factor affecting community composition, subsequent research could compare community composition between the highway and the secondary road to the values reported in this thesis. This may be profitable because the volume of noise is changing rapidly. At the time the community composition data were collected, the average noise levels along the highway were near the 42 dB threshold (Forman and Alexander 1998). Since then, noise along the highway has increased by 26.03 %, on average, above 1999-2000 levels to 58.27 dB near to and 46.59 dB far from the road, which is well above the 42 dB threshold at which bird density starts to decline in woodland forest (Forman and Alexander 1998). It is also likely that the noise increased along the secondary road. If noise drives the observed difference in community composition between the two road types, it should also create a difference between the community in 1999-2000 and today's community.

Another area of future research could be the study of thresholds. Ecological thresholds are defined as the critical value of an independent variable for which an ecological system shifts from one equilibrium to the next (Muradian 2001). At a community level, different equilibria correspond to different species assemblages (Scheffer et al. 1993). At a population level, it would correspond to different stable densities (Loenardsson 1994). These definitions vary at differing spatial and temporal scales and this is the greatest challenge facing the applicability of threshold studies (Muradian 2001). Nevertheless, the idea of thresholds has been prominent in the fragmentation literature for more than 10 years where it revealed information such as the level of habitat fragmentation at which populations can become disjunct (With and Crist 1995) and extinction thresholds in relation to habitat destruction (Bascompte and Solé 1996). I believe that the identification of thresholds could be beneficial in the context of road effects as well. For example, the threshold at which bird breeding densities start to decline in woodland is believed to be 42 dB (Forman and Alexander 1998). If we could identify community and species-specific thresholds at which, for example, noise interferes with bird communication given specific habitat, then managers could more effectively apply mitigation measures.

Finally, a downfall of mensurative studies, such as the ones present in this thesis, is that variation in the ecology of different sites can confound and limit the study's outcomes (McGarigal and Cushman 2002). Detailed vegetation surveys were not conducted and I could not examine the effects of vegetation quantitatively in this thesis. Vegetation may have affected habitat quality through food availability, provision of nesting habitat, and amelioration of noise pollution. Each of these could have exerted considerable confounding effects and may have prevented me from detecting significant differences in either community composition or bird health as a function of road proximity.

In sum, habitat drove most of the patterns observed in this study. However, roads affected the age distribution of nuthatches. Community composition differed as a function of road proximity in aspen and pine habitat, perhaps because of edge effects. Community composition also differed between roads of varying traffic volume, possibly as a function of road noise. Because Canada has more road length per person than any other country in the world (Forman et al. 2003), more research of the effects of roads on wildlife is needed. Since birds represent a large component of terrestrial diversity (Hickman et al. 2003) and since they are sensitive to habitat loss and fragmentation (Fahrig 2003), they will continue to provide an excellent system for assessing the broader ecological effects of roads.

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