THE EFFECTS OF ROADS ON MOVEMENT, FLIGHT DYNAMICS, OCCUPANCY, AND PRODUCTIVITY IN BARN OWLS (*TYTO ALBA*)

by

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ABSTRACT

Barn Owls (*Tyto alba*) are a species of conservation concern in many portions of their cosmopolitan range. One important factor contributing to population declines and sometimes local extirpations is roads, which can cause direct mortality through Barn Owl-vehicle collisions, fragment habitat, limit dispersal and movement, and imperil long-term population viability. However, the effects of roads on Barn Owl reproduction are less clear. Further, the cumulative effects of roads on Barn Owls can be dependent on how they respond to them. Road and traffic responses of animals have been classified into four categories: 1) speeders, who increase speed to cross roads, 2) pausers, who pause before crossing, 3) avoiders, who avoid crossing roads altogether, and 4) nonresponders, who have no response to roads or traffic. Barn Owls, who are frequent victims of road mortality around the world and may even be attracted to the areas along roads for foraging, are hypothesized to be nonresponders. My goals were to examine Barn Owl behavior near roads to assess the extent to which they exhibited traits of nonresponders as well as to assess the possibility that they were attracted to areas near roads. Additionally, I aimed to examine the potential effects of roads on Barn Owl reproduction.

To help understand Barn Owl behavior near roads I attached and recovered GPS data loggers from 19 Barn Owls to obtain location data on their movements. I first conducted a random walk analysis to assess how Barn Owl crossing rates and proximity to roads compared to what would be expected by chance. Additionally, I analyzed

individual road encounters to help understand how flight dynamics affected their decision to cross a road and their behavior when actually crossing. I found that owls crossed fewer roads than expected, especially highways and interstates. Additionally, Barn Owls did not fly closer to roads than expected, including major roads and those of any size. When encountering roads, Barn Owls were more likely to cross when they approached at higher altitudes and when roads were narrower in width. When crossing roads, Barn Owls accelerated to cross when approaching at higher altitudes and slower speeds. They also decreased crossing altitude when approaching at higher altitudes and increased altitude to cross wider roads. These findings suggest that rather than being strict nonresponders, Barn Owls showed evidence of traits more associated with speeders and avoiders.

To assess the potential effect of roads on Barn Owl reproduction I monitored a nest box population of Barn Owls between 2019 and 2022 to record breeding occupancy and productivity (number of fledglings) during two breeding seasons (2020 and 2021). I assessed occupancy in an average of 276 nest boxes per year and found that occupancy was 66%. Nests produced an average of 3.7 fledglings across the two breeding seasons (n = 225 nests). Both breeding occupancy and productivity decreased with proximity to roads. These results suggest that roads have the potential to influence owl populations not only through wildlife-vehicle collisions but indirectly through reductions in occupancy and productivity. Although it is alarming that roads are further impacting Barn Owls through their reproduction, my behavioral research suggests that rather than being strict nonresponders to roads, Barn Owls may avoid them to some degree, as well as reduce their risk of collision when crossing through changes in speed and altitude. Given the continuing expansion of road networks across the globe and the negative effects of roads on Barn Owl reproduction, it is encouraging that Barn Owls may be preadapted to the threat of roads, if not currently evolving adaptations in light of selective pressure, providing hope for the conservation of this species in a new and changing environment.

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LIST OF ABBREVIATIONS

ASY	After Second Year
AUC	Area Under Curve
CCR	Correct Classification Rate
GLMM	Generalized Linear Mixed Model
GPS	Global Positioning System
HY	Hatch Year
KML	Keyhole Markup Language
LMM	Linear Mixed Model
MCMC	Markov Chain Monte Carlo
MST	Mountain Standard Time
REU	Research Experiences for Undergraduates
RMSE	Root Mean Square Error
SY	Second Year

CHAPTER ONE: ROADS AS POTENTIAL NOVEL PREDATORS OF WILDLIFE – ARE BARN OWLS NONRESPONDERS?

Abstract

Roads and the traffic along them may be relatively recent additions to the planet, but they have already produced an array of negative effects on animals that evolved in their absence. One major impact has been direct mortality through wildlife-vehicle collisions, which can lead to the decline and extirpation of animal populations. The effects that roads exert on wildlife to some extent is dependent on how species respond to them. Road and traffic responses of animals fall broadly into four categories: 1) speeders, who increase speed to cross, 2) pausers, who pause before crossing, 3) avoiders, who avoid crossing roads altogether, and 4) nonresponders, who have no response to roads or traffic. Barn Owls (*Tyto alba*), which are frequent victims of road mortality around the world, are hypothesized to be nonresponders. There is also some evidence that Barn Owls are attracted to road verges for foraging which, coupled with their hypothesized nonresponsive behavior, would put them at a high risk of collision. Together, these behavioral traits potentially explain the alarming number of Barn Owl roadway mortalities. My goals were to examine Barn Owl behavior near roads to assess the extent to which they exhibited traits of nonresponders as well as to assess the possibility that they were attracted to roads. I attached and recovered GPS data loggers from 19 Barn Owls to obtain location data on their movements. I first conducted a random walk analysis to assess how Barn Owl crossing rates and proximity to roads compared to what

would be expected by chance. Additionally, I analyzed individual road encounters to help understand how flight dynamics affected their decision to cross a road and their behavior when actually crossing. I found that owls crossed fewer roads than expected, especially highways and interstates. Additionally, Barn Owls did not fly closer to roads than expected, including major roads and those of any size. When encountering roads, Barn Owls were more likely to cross when they approached at higher altitudes and when roads were narrower. When crossing roads, Barn Owls accelerated to cross when approaching at higher altitudes and slower speeds. They also decreased crossing altitude when approaching at higher altitudes and increased altitude to cross wider roads. These findings suggest that rather than being strict nonresponders, Barn Owls showed evidence of traits more associated with speeders and avoiders. Given the continuing expansion of road networks across the globe, the notion that Barn Owls have no defenses for this "novel" predator is concerning. However, my research suggests that Barn Owls indeed respond to roads either through some preadapted behaviors, or potentially some currently evolving adaptations in light of the strong selective pressure exerted by roads. Either way, my finding that they are not strict nonresponders provides some hope for the conservation of this species.

Introduction

Biological invasions and species introductions sometimes have positive effects on ecosystems, for instance, in the cases of pollinators or biological control agents (De Clercq et al. 2011, Hung et al. 2018). However, in other situations they are often accompanied by a suite of negative effects, including competition, disease transmission, or new predator-prey dynamics (Pimentel et al. 2001). The introduction and spread of human-manufactured infrastructure across the landscape, for example wind turbines and power lines, can be viewed much like the introduction of novel predators, to which not all species may be preadapted. One such example of human infrastructure is roads, which are being built and expanded upon across the globe, and already account for billions of animal deaths annually (Loss et al. 2014, Novaes et al. 2018, Schwartz et al. 2020). In some ways roads also operate much like an invasive species, as they perpetually increase in abundance and permeate previously roadless areas. The extent to which native fauna are affected may depend on their behavioral responses to roads and their propensity to adapt to this “new predator” that has been introduced into their environment.

A framework to help understand animal responses to traffic volume and roads, recently proposed by Jacobson et al. (2016), suggests four general types of traffic responses among animal taxa: pausers, speeders, avoiders, and nonresponders. Pausers freeze and slow down when confronting traffic, as seen in many reptiles and amphibians (Andrews and Gibbons 2005, Mazerolle et al. 2005). Ungulates sprint quickly across roads and exemplify the speeder strategy (Pfeiffer et al. 2020). Avoiders tend to refrain from crossing roads at all but the lowest traffic volumes, as documented in secretive species, such as black bears (*Ursus americanus*) and moose (*Alces alces*; Wattles et al. 2018, Zeller et al. 2020). Finally, nonresponders, fail to respond behaviorally to roads or traffic volume; therefore, they are often found in large numbers as victims of wildlife-vehicle collisions. Because of their apparent failure to perceive roads as a threat, populations of species that are nonresponders may be particularly prone to fragmentation and extirpation (Jacobson et al. 2016).

Among birds, and especially raptors, vehicular collisions are particularly common with Barn Owls (*Tyto alba*), which "fall prey" to roads in large numbers globally (Moore and Mangel 1996, Ramsden 2003, Baudvin 2004, Gomes et al. 2009, Boves and Belthoff 2012, Payan et al. 2013, Belthoff et al. 2015, Pande et al. 2018). Thus, Barn Owls have been hypothesized to be nonresponders (Jacobson et al. 2016). Moreover, telemetry and mortality data indicate that Barn Owls frequently engage with roads and traffic in the winter months when prey are perhaps scarce elsewhere, and they are more likely to approach and cross highways when the verges contain suitable foraging habitat (Grilo et al. 2012, 2014). This information, coupled with higher road mortality rates of owls in the winter, suggests that not only may Barn Owls be failing to respond to the threats posed by highway traffic, but they could actually be attracted to roads (Boves and Belthoff 2012). Interestingly, if roads are viewed in the framework of predator-prey dynamics, then favorable foraging habitat and abundant rodents along roads perhaps could also be viewed as something analogous to a predator luring prey (Atkinson 1997).

I aimed to understand Barn Owl behavior near roads by studying movement of individuals within a population of Barn Owls in southern Idaho, USA, where some of the highest rates of roadway mortality have been reported (Boves and Belthoff 2012, Belthoff et al. 2015, Regan et al. 2018, Arnold et al. 2019). My first objective was to investigate the extent to which Barn Owls were nonresponders to roads or assess the degree to which they exhibited traits of other response types. I also quantified how often Barn Owls crossed roads and compared the rate to expected values generated using a random walk analysis, in addition to analyzing details of their flight behavior, such as change in crossing speed and altitude when they encountered and crossed roads. My second objective was to evaluate the extent to which roads may have attracted Barn Owls, so I examined the average proximity to roads and road crossing rates of flight tracks in comparison to random paths. I also investigated how behavior varied when accounting for the sex of the owl and the type and width of the road encountered.

Methods

<u>Study Area</u>

I studied a nest box population of Barn Owls in southwestern Idaho (43.6° N, -116.7° W), primarily in Ada, Canyon, Gem, and Owyhee counties. The study area spanned roughly 3,000 km^2 and was comprised mostly of agriculture (50%) and grasslands/pasture (30%) with a small amount of developed areas (10%), shrub/scrub (8%), and other land cover classes in low proportions. Nest boxes numbered > 300 and were built and installed by Canyon County Weed and Pest Control in 2011 - 2021 as part of an integrated pest management program aimed at reducing gophers (*Thomomys* spp.) and other rodents. Boxes were of identical design, constructed of plywood, mounted ~ 4 m-high on steel poles, and with the entrance hole facing northeast. They occurred along irrigation ditches and canals, within vineyards and orchards, on the borders of row crop fields and pastures, and occasionally in more residential and suburban areas as depicted in chapter two.

<u>Owl Capture and Tracking</u>

I captured adult Barn Owls by hand at nest boxes during the winter months of 2019 and 2020 for attachment of data loggers to collect movement data. I used GiPSy-4® and GiPSy-5® data loggers (27 x 13.5 x 4 mm and 23 x 12.5 x 5 mm, respectively) that weighed < 3 g (Figure 1.1; TechnoSmart 2017). Each type of unit could record the coordinates of up to 4,000,000 locations, in addition to date, time, altitude, and instantaneous ground speed. To help balance my need for detailed movement data and extend battery life to track owls for up to 10 nights each, I programmed GiPSy-5 data loggers to turn on every night and record one location fix per second from 1800 to 2000 h (MST), which generally corresponded to the onset of nightly Barn Owl activity (Marti et al. 2005). I reduced the location fix rate to once per minute from 2000 to 0000 h, after which time the data loggers shut off for the night. I programmed the GiPSy-4 data loggers, which had a shorter maximum battery life, to turn on every other night and record one location fix per minute from 1800 to 0000 h. Under these duty schedules both types of data logger were able to collect approximately nine nights of data before batteries died.

I attached data loggers to adult Barn Owls using a modified double loop backpack style (Figure 1.2; Smith and Gilbert 1981, Regan 2016). Each backpack was comprised of a data logger inserted into a clear waterproof heat-shrink tube case (50 mm length, 19 mm diameter). I threaded 110 cm of Teflon ribbon (0.5 cm wide) through one end of the heat-shrink tube and sealed the tube around the Teflon using heat and pressure prior to field attachment; this side of the case was ultimately placed closest to an owl's head. I then inserted the data logger into the heat-shrink tube case and sewed the lower end shut using dental floss and a sewing needle to close the case. After attachment, excess Teflon ribbon was cut with scissors prior to release of the owls. Complete packages weighed < 12 g and were removed from owls upon recapture.

To recapture owls to retrieve location and movement data from the data loggers, I revisited nest boxes as early as one month later and continued to regularly monitor boxes during the following breeding season and subsequent winter if tagged owls were not present on previous visits. Upon recapture, I removed the entire backpack that contained the data logger and returned owls to the box from which I captured them. I also searched roads throughout the study area in an ad hoc fashion for dead owls and inspected any roadkilled Barn Owls I found for backpacks. I offloaded location coordinates from data loggers and read them into R (R Core Team 2021), where all analyses were conducted.

Crossing Frequency

To investigate how often Barn Owls crossed roads and how their proximity to roads both differed from expected, I conducted a random walk analysis to generate data for comparison to observed owl tracks. I first organized location data by date such that each night for each owl represented a nightly track. The fine-scale data (i.e., one fix per second) were filtered so only the first fix of each minute remained, effectively standardizing all data from each hour of the night, and from owls that carried either type of data logger, to one fix per minute. Next, locations that were < 100 m from the previous fix, excluding the starting location for each night, were removed to filter instances where owls were stationary or moved only negligible distances, which allowed for more streamlined random walk generation. I then recorded total distance traveled and number of fixes for each night for each owl. I ultimately included only nights when owls moved $\geq$ 1 km and where ≥ 10 location fixes remained, which prevented short-distance and otherwise negligible flights, such as flying from one perch to another, from skewing analyses. Given that the data loggers recorded data for a maximum of 6 h each night (from 1800 to 0000 h), I refer to each night of data as a ‘tracking night,’ in contrast to a full night of observation.

For comparison to observed tracks, I generated 100 random paths for each observed track using constrained correlated random walk models using the *adehabitatLT* package in R (Calenge 2006). The random paths started in the same location as observed data and were created using the same distribution of step lengths and turning angles, but they were configured in a random order (Figure 1.3). I also applied a habitat constraint using the National Land Cover Database (NLCD, Yang et al. 2018). For a random path of a given night of data, the proportion of fixes that fell in 'suitable' Barn Owl habitat (shrub/scrub, grassland/herbaceous, pasture/hay, and cultivated crops; Salvati et al. 2002, Żmihorski et al. 2020, Castañeda et al. 2021, Huysman and Johnson 2021) was constrained to fall within the range expressed in the observed data for that given owl. For instance, if a given owl had four nights of usable data, and the proportion of fixes spent in suitable habitat was 0.86, 0.94, 0.98, and 0.91 for those nights, then each random path would require a proportion between 0.86 and 0.98. I then calculated how frequently both the random (i.e., expected) paths and observed tracks crossed roads, including major highways (interstates and U.S. and state highways), minor roads (all roads excluding highways and interstates), and those of any size, using publicly available road data (U.S. Census Bureau 2016). Additionally, I calculated the distance from each location fix to the nearest road (both major and any size) and averaged that distance for each night of data for each owl.

To compare the actual number of road crossings to those expected from random paths I used generalized linear mixed models (GLMMs) with the *glmmTMB* package in R (Brooks et al. 2017) using an approach similar to Fey et al. (2016) and Paterson et al. (2019). I used number of road crossings as the response variable, category (expected or observed) and distance traveled (log-transformed) as fixed effects, and individual Barn Owl ID as a random intercept. Because the data were zero-inflated with structural zeros (Blasco-Moreno et al. 2019) and overdispersed, I used a zero-inflated type II negative binomial model. Ultimately, I considered Barn Owls nonresponsive to roads if observed tracks crossed roads at a similar frequency to those of random paths. If owls crossed at a lower or higher frequency I considered this possible avoidance or attractance, respectively.

I also examined the extent to which Barn Owl crossing frequency was related to road class, or sex of the owl. To do so, I constructed separate zero-inflated type II negative binomial GLMMs to investigate the potential effects of road class (response variable: number of road crossings; fixed effects: log-transformed distance traveled, category as expected or observed, road class as major or minor, and the interaction between category and road class; random intercept: Barn Owl ID) and sex (response variable: number of road crossings; fixed effects: log-transformed distance traveled, category as expected or observed, sex as female or male, and the interaction between category and sex; random intercept: Barn Owl ID). An interaction effect between category and road class would indicate Barn Owls responded differently to major and minor roads, whereas an interaction between category and sex would indicate the road responses of male and female Barn Owls differed.

To assess the potential that Barn Owls were attracted to roads, I examined whether the proximity of Barn Owl flight to roads differed between observed and random paths using a type II negative binomial GLMM (response variable: mean distance (to nearest m) to the nearest road; fixed effects: log-transformed total length of road within a

1-km radius of nest box, category as expected or observed; random intercept: Barn Owl ID). A second model constructed in a likewise manner assessed proximity to major roads only (response variable: mean distance to the nearest major road; fixed effects: presence of major roads within a 1-km radius of nest box as yes or no, category as expected or observed, and the interaction between category and presence; random intercept: Barn Owl ID). No “minor roads only” shape file was available, so average minimum distance to minor roads was not analyzed. But if Barn Owls were attracted to major roads then mean distance to road would be considerably smaller for observed tracks as compared to random paths.

All continuous variables were scaled for each model. I assessed the fit of all models with a visual inspection of the residuals using the *DHARMa* package (Hartig 2021), by calculating an approximation of the coefficient of determination (pseudo R^2; Nakagawa and Schielzeth 2012), and using the root mean square error (RMSE). In addition to their importance in accounting for nonindependence in the owl location data given multiple nights of tracks from each owl, I considered random effects warranted if the variance was greater than 0.05 (Shipley et al. 2020). I considered predictor variables to have a meaningful effect if their 95% confidence interval excluded zero and discussed their effects relative to their coefficient size and standard error. A visual inspection of the residuals and the metrics of model fit indicated that all but one model fit appropriately. The exception was the GLMM that addressed minimum distance to roads of any size which had had large residuals and poorer metrics of fit than others. When discussing crossing frequency in the results, I standardize crossings to crossings per km so that results between categories, sexes, etc. are directly comparable.

Crossing Behavior

To assess factors that potentially influenced Barn Owls' decisions to cross roads, and the manner in which they crossed, I used only the fine-scale data (i.e., one location fix per second). Because the GiPSy-4 data loggers were not programmed to record fine-scale data, I used only the data from Barn Owls tracked with GiPSy-5 data loggers in assessing flight dynamics related to crossing.

For analysis, I loaded each night of data for each owl individually into Google Earth Pro as a KML (Keyhole Markup Language) file. Starting at the earliest recorded location fix for a given night, I visually followed each track in temporal order of coordinates until each time a location fix was within 15 m of a paved road, which I defined as the beginning of a road encounter. I further identified each road encounter as: 1) crossings, where the owl completely crossed the road before leaving the 15 m buffer again, or 2) approach-departs, where the owl did not completely cross the road before leaving the 15 m buffer. If an owl flew within the 15 m buffer but stopped moving for three or more consecutive location fixes before ultimately crossing or approaching closer to the road, I considered the road encounter as starting from that last stationary fix.

For each crossing I recorded the ID number of the Barn Owl, date, start and end time of the road encounter, and width of the road encountered (not including road verge) measured at the first point of crossing. I also recorded approach speed in m/s (calculated as the distance between the prior location fix and the fix in question, whose fixes were 1 sec apart) for up to the first three fixes prior to the Barn Owl crossing the road. If only one location fix prior to crossing fell within the 15 m buffer, then only one approach speed was recorded. Crossing speed was measured for as many fixes that fell within the paved road itself before emerging on the other side, but it was typically only one fix. If no location fix occurred directly over the road, then the first fix after crossing the road was recorded as a proxy so that there was always at least one value for crossing speed. I used similar methods as described for approach and crossing speeds to record approach and crossing altitudes. Altitudes (height above ground in m) was measured as the difference of the flying altitude of the owl and the elevation of the terrain directly beneath it. For each approach-depart I recorded the same information but with a few minor differences. Width of the road was measured at the closest location fix to the road rather than at the first point of crossing given that the road was never crossed. Approach speed and altitude were recorded up until the closest location fix to the road, rather than the first point of crossing, and crossing speed and altitude were not recorded because they were irrelevant. For analysis, I averaged approach speeds and altitudes for each encounter for both crossing and approach-depart data and for crossing speeds and altitudes.

To assess factors that potentially affected whether Barn Owls crossed roads, I created a GLMM with the *lme4* package in R (Bates et al. 2015) and used a binomial model with road response (approach-depart = 0, crossing = 1) as the binary response variable, approach altitude, approach speed, and road width as fixed effects, and individual Barn Owl ID as a random effect. All continuous predictor variables were scaled. To assess the fit of this model I calculated area under curve (AUC; Robin et al. 2011). An AUC value greater than 0.75 is considered good model fit whereas a value closer to 1 is considered excellent (Williamson et al. 2020).

To assess whether Barn Owls changed flight speed or altitude when crossing roads, I included only crossing encounters where the average crossing altitude was ≤ 10

m. I reasoned that at crossing altitudes > 10 m Barn Owls were clear of collision danger with even the tallest vehicles (e.g., tractor trailers) and any air turbulence they may cause (Orlowski and Siembieda 2005). Next, I created two new variables, change in speed and change in altitude, by calculating the difference between the crossing speed or altitude and the approach speed or altitude. To assess if Barn Owls adjusted flight speed when crossing I used a linear mixed model (LMM) with change in speed as the response variable, approach altitude, approach speed, and road width as fixed effects, and individual Barn Owl ID as a random effect. Likewise, to assess the extent to which owls adjusted flight altitude, I created another LMM with change in altitude as the response variable, approach altitude, approach speed, and road width as fixed effects, and individual Barn Owl ID as a random effect. All continuous predictor variables were scaled for both models. I evaluated the fit of both models with visual inspections of the residuals and through pseudo R^2 and RMSE. I again considered random effects warranted if the variance was greater than 0.05 and considered predictor variables to have a meaningful effect if their 95% confidence interval excluded zero. Visual inspection of the residuals and metrics of model fit indicated that the binomial crossing model and the change in speed model both had good model fit. However, the change in altitude model had poorer metrics of model fit. I present all means in the results with ± one standard deviation.

Results

Data Collected

Over the winters of 2019 and 2020 I captured and equipped 27 Barn Owls with GPS data loggers, including 14 males and 13 females. As of November 2021, I recovered

19, which included 10 males, 9 females, and all but 3 from birds that were aged as after second year (ASY; Table 1.1, Figure 1.4). There were 8.6 ± 1.7 tracking nights of data (range: 5 – 12, n = 163 nights) recorded per owl, of which 5.9 ± 1.7 tracking nights (range: 2 – 9, n = 113 nights) achieved minimum location fixes and distances moved for inclusion in analyses. All tracking data came from the month of December in both years.

On average, Barn Owls traveled 6.3 ± 5.3 km per tracking night (range: 1.4 – 27.8, n = 113 nights) and crossed 9.4 ± 12.2 roads per tracking night (range: 0 – 69, n = 113 nights). Road crossings included 0.1 ± 0.5 major roads (range: 0 – 4, n = 113 nights) and 9.2 ± 12.1 minor roads per tracking night (range: 0 – 69, n = 113 nights). Males traveled 7.9 ± 6.1 km per tracking night (range: 1.6 – 27.8, n = 64 nights), and females averaged 4.1 ± 2.9 km (range: 1.4 – 17.7, n = 49 nights). Males exhibited 12.4 ± 14.9 road crossings per tracking night (range: 0 – 69, n = 64 nights) compared to females that tallied 5.4 ± 5.2 (range: 0 – 19, n = 49 nights). Distance to the nearest road of any size was 133.6 ± 73.9 m (range: 39.0 – 451.2, n = 113 nights) while minimum distance to the nearest major road was 1,454.6 ± 1,083.1 m (range: 132.9 – 5,166.9, n = 113 nights).

Crossing Frequency

On average, owls crossed 37% fewer roads per km of flight than expected, and all but one individual crossed fewer roads than expected (Figure 1.5). No Barn Owls crossed more major roads than expected and, overall, owls crossed 84% fewer major roads than expected per km of flight (Figure 1.6). In contrast, one Barn Owl crossed more minor roads than expected, and owls averaged 34% fewer minor road crossings per km of flight than expected (Figure 1.7). On average Barn Owls were 6% closer to all roads than expected, compared to 3% closer for major roads only (Figure 1.8, Figure 1.9).

There was meaningful evidence that Barn Owls crossed all roads less frequently than expected (Table 1.2). With flight distance set near its mean at 5 km, Barn Owls crossed 30.9% fewer roads than expected (Figure 1.10) with no overlap between the 95% confidence intervals of observed and expected. Further, there was evidence that Barn Owls avoided crossing major roads more so than minor roads (Table 1.3). With flight distance set near its mean at 5 km, Barn Owls crossed 75.0% fewer major roads than expected, but only 28.4% fewer minor roads (Figure 1.11). Both female and male Barn Owls crossed roads less frequently than expected, but there was no evidence of differences in potential road avoidance between the two (Table 1.4). With flight distance set near its mean at 5 km, female Barn Owls crossed 34.2% fewer roads than expected, whereas males crossed 28.9% fewer (Figure 1.12). Interestingly, males crossed fewer roads than females for both the observed data (6.8% fewer) and the random paths (13.7% fewer).

There was no evidence that Barn Owls flew closer to all roads than expected (Table 1.5). With total length of road set at its mean, Barn Owl's flight tracks were 6.4% closer to roads than expected (Figure 1.13). There was also no evidence that Barn Owls flew closer to major roads than expected (Table 1.6). Barn Owls with major roads absent from a 1-km radius had flight tracks that were 3.3% closer to major roads than expected, whereas those with major roads present within a 1-km radius flew 12.9% closer (Figure 1.14).

Crossing Behavior

Thirteen owls had encounter data useful for analysis of flight dynamics (Table 1.7). There were 24.8 ± 22.3 road encounters per owl (range: 7 – 88, n = 322 encounters) including 155 approach-departs and 167 crossings. Approach speed for road crossings averaged 6.8 ± 1.8 m/s (range: 1.7 – 15.3, n = 167 encounters) and 6.0 ± 1.8 m/s (range: 1.3 – 17.0, n = 155 encounters) for approach-departs (Figure 1.15). Approach altitude averaged 14.9 ± 20.0 m (range: 0.0 – 93.3, n = 167 encounters) for crossings and 4.5 ± 6.7 m (range: 0.0 – 55.0, n = 155 encounters) for approach-departs (Figure 1.16). Finally, road width averaged 10.2 ± 3.3 m (range: 4.5 – 27.4, n = 167 encounters) for crossings and 11.4 ± 4.4 m (range: 6.2 – 30.0, n = 155 encounters) for approach-departs (Figure 1.17).

There was meaningful evidence that owls were more likely to cross roads as their approach altitude increased (Table 1.8, Figure 1.18). There was also evidence that owls were less likely to cross wider roads, but no evidence that approach speed influenced crossing probability. For crossing altitudes ≤ 10 m, owls increased their speed to cross by 0.54 ± 1.05 m/s (range: -4.38 – 4.45, n = 108 encounters) and had a mean altitude change of -0.10 ± 1.05 m (range: -5.00 – 2.67, n = 108 encounters). There was meaningful evidence that owls accelerated to cross roads when approaching at higher altitudes and that they accelerated to cross when approaching at slow speeds (Table 1.9, Figure 1.19). There was no evidence that road width affected change in speed. There was meaningful evidence that owls decreased altitude to cross roads when approaching at higher altitudes and that they increased altitude when crossing wider roads (Table 1.10, Figure 1.20). There was no evidence that approach speed was associated with any change in altitude when crossing.

Discussion

Barn Owls, which throughout their global range are frequent victims of road mortality (Belthoff et al. 2015), are hypothesized to be nonresponders to roads, meaning they should fail to respond to roads and traffic in any meaningful way (Jacobson et al. 2016). My goals were to examine the behavior of Barn Owls near roads to assess the extent to which they exhibited traits of nonresponders as well as to assess the possibility that roads potentially attracted them. I found that owls crossed fewer roads than expected and that they especially avoided crossing major roads. There was no evidence that sex of an owl affected road avoidance. Additionally, Barn Owls did not appear to fly closer to roads than expected, including major roads and roads of any size. When encountering roads, Barn Owls were more likely to cross when approaching at higher altitudes and when roads were narrower. When crossing roads Barn Owls accelerated when approaching at higher altitudes or at slower speeds. They also decreased altitude when approaching at higher altitudes and increased altitude for wider roads.

Crossing Frequency

My finding of considerably lower road crossing rates than expected indicates that Barn Owls be avoiders as opposed to strict nonresponders. This finding is consistent with another study from southern Idaho also conducted during the breeding season, where male owls with nests located within 3 km of a major interstate highway (I-84) never approached within 1 km of the highway, despite making movements > 3 km from their nests (Regan 2016). Regan (2016) also reported that Barn Owls are more likely to use habitat that is closer to minor roads, however, this is not necessarily indicative of their crossing behavior around such roads. That difference in apparent avoidance behavior between the interstate highway and smaller roads in Regan (2016) seems commensurate with the greater avoidance of major versus minor roads I observed. Similarly, in Portugal, Barn Owls avoid highways more as the traffic intensity increases, and are less likely to move toward the highway the closer they are flying to it (Grilo et al. 2012). These findings also align with mine, where Barn Owls crossed 75% fewer highways than expected in southern Idaho. Grilo et al. (2014) found that high Barn Owl road mortality is associated with low occurrence, suggesting that many mortalities might be attributed to younger birds dispersing or foraging along verges given the absence of food elsewhere. This finding fails to support their nonresponder hypothesis, where occurrence would be high in areas where road mortality was high. Likewise, my results suggest Barn Owls were not entirely nonresponsive to roads, and the data suggest they may in fact avoid them to some extent.

Many roadway mortality studies show a strong female bias in roadkill counts of Barn Owls: 74% of roadkilled owls in California were female (Moore and Mangel 1996), 68% in Portugal (Grilo et al. 2014), 61% in France (Massemin et al. 1998), and 58% in Idaho (Boves and Belthoff 2012). One possible explanation for this pattern is that females show less avoidance behavior near roads compared to males, but that difference was not evident in my study. The lack of a pattern could be explained by the fact that none of the females from which I recovered data loggers were dispersing. Female Barn Owls typically disperse longer distances than males (Marti 1999, Almasi et al. 2021), which has been used to potentially explain female-biased road mortalities in this species (Moore and Mangel 1996, Boves and Belthoff 2012). Of the 13 data loggers I attached to females, all nine that were recovered were found at or near the same nest box where they were deployed, meaning that all the tracking data I recorded came from females who did not disperse after instrumentation, or those who had already finished dispersal. If female biased mortality is primarily caused by greater distances traveled during dispersal rather than sex-dependent behavioral differences near roads after dispersal, then this would help explain my findings. Although none of the owls tracked in my study dispersed, it is interesting that males traveled almost double the nightly distances of females during the hours they were tracked. The number of crossings per km did not differ, but the greater distance covered by males resulted in their crossing over twice the number of roads per night. All else being equal, this would suggest that males rather than females were at a higher risk of road mortality unless another aspect of their biology (e.g., smaller size than females, different energy needs, etc.) plays an important role.

There was no evidence that Barn Owls flew closer to roads than expected, even when isolating analysis to major roads only. These findings, coupled with apparent road crossing avoidance, seem to counter any notion that Barn Owls in my study were attracted to roads and/or the habitat along them. Grilo et al. (2012) found that when Barn Owls in Portugal approach major roads, or even cross them, the vegetation of the nearby verges is more likely to be suitable for hunting. Likewise, Barn Owls prefer roadside verge over all other habitat types in British Columbia, Canada (Hindmarch et al. 2017), and higher rates of road mortalities have been linked to areas of highway with more suitable foraging habitat and greater numbers of small rodents in the roadside verges in southern Idaho (Arnold et al. 2019). However, my results appear to suggest that while Barn Owls were likely not attracted to areas along roads, they were not avoiding them either. Effectively, Barn Owls avoided crossing roads to a degree, but they did not appear to avoid the areas near them.

Random walk analyses have been used to assess road avoidance in snakes (*Boiga irregularis*, *Elaphe obsoleta*, *Heterodon platirhinos*, *Sistrurus catenatus*; Row et al. 2007, Shepard et al. 2008, Robson and Blouin-Demers 2013, Siers et al. 2014), turtles (*Emydoidea blandingii*, *Gopherus agassizii*, *Terrapene* spp.; Proulx et al. 2014, Peaden et al. 2017, Paterson et al. 2019), hedgehogs (*Erinaceus europaeus;* Rondinini and Doncaster 2002), squirrels (*Sciurus vulgaris*; Fey et al. 2016), moose (Wattles et al. 2018), wolves (*Canis lupus*; Whittington et al. 2004), and bears (Zeller et al. 2020). To my knowledge, mine is the first study to apply this approach to understanding road interactions in birds. One possible limitation of random walk analyses to investigate crossing behavior in birds is that, unlike the terrestrial animals previously studied, birds can also avoid roads on a third axis (altitude). That is, if birds fly higher than the height of traffic, they have effectively avoided roads, although tracking data would still indicate this as a road crossing. Although this could be perceived as a downside to my analysis, it can also strengthen the conclusion that Barn Owls avoided roads. That is, even without accounting for avoidance through altitude, Barn Owls in my study crossed roads less often than expected. If some of those crossings were effectively null given a high flight altitude, then this could only increase the importance of the already notable avoidance tendencies, i.e., my results are a conservative estimate of avoidance.

Crossing Behavior

When approaching roads at collision-prone altitudes (≤ 10 m) the probability that Barn Owls crossed was around 0.5. But as approach altitude increased to levels safely above the flow of traffic, the probability increased to nearly 1. Low flight height inherently makes birds more susceptible to collisions (Erritzoe et al. 2003, Lima et al. 2015) and, indeed, avian species with high flight are less susceptible to road mortality (Rytwinski and Fahrig 2015). In my study, Barn Owls often flew at higher altitudes and more directly when leaving roost sites for presumptive foraging areas, only lowering altitude once at their destination (pers. observ.). This behavioral strategy would explain these findings and help Barn Owls avoid collisions when crossing roads on the way to hunting grounds.

Barn Owls were also less likely to cross wider roads. Owls had a ~ 0.75 probability of crossing the narrowest roads, which were approximately 5 m in width, but a ~ 0.25 probability to cross the widest roads (~ 30 m wide). Generally, wider roads have more lanes and traffic, which inherently increases the risk of vehicular collision for an owl during a crossing. This tendency to avoid crossing wider roads aligns with the random walk analysis findings of an increased avoidance of major roads. It is also congruent with behavior seen in other animals such as moose and bears (Wattles et al. 2018, Zeller et al. 2020), other bird species (Husby and Husby 2014), and previously in Barn Owls (Grilo et al. 2012, Regan 2016).

When crossing roads, Barn Owls could respond in several ways: increase their speed like a speeder, decrease speed like a pauser, increase altitude like an avoider, maintain speed and altitude like a nonresponder, or some combination of these options. In my study, Barn Owls tended to increase their speeds when crossing roads, and much more so when traveling at slower speeds. These results intuitively make sense and indicate Barn Owls may exhibit tendencies of speeders. When approaching roads at slow speeds accelerating to cross would minimize time spent in the collision zone, however, when already flying rapidly there is no need to increase speed further. Crossing roads at faster speeds occurs in other species of animal (Andrews and Gibbons 2005, Wattles et al. 2018, Zeller et al. 2020), and likely is a mechanism to reduce the risk of traffic collision by spending less overall time in the road (Jacobson et al. 2016). There is scant literature on the behavioral responses of birds during actual road crossings (Rytwinski and Fahrig 2015), but increasing speed to evade predators is certainly a common escape mechanism in animals, including in birds (Husak and Fox 2006, van den Hout et al. 2010), which also accelerate or even attempt to outfly approaching aircraft as a means to escape (Kelly et al. 1999, Lima et al. 2015).

Barn Owls increased their crossing speed more when crossing roads at higher altitudes; this was counterintuitive because a higher altitude would generally mean less danger and therefore a reduced need to accelerate to cross quickly. Barn Owls have been known to preferentially select roadside areas (Hindmarch et al. 2017). So, it is also possible that lower altitude flights represented foraging, when an owl might not be inclined to increase speed to cross as it is actively searching for prey. Indeed, there was little change in speed at heights of 1.5 to 4.5 m above the ground, flight altitudes at which Barn Owls often hunt (Marti et al. 2005), but owls did accelerate at higher altitudes, possibly because they were not foraging and therefore undistracted and capable of noticing the potential threat of a road in their flight path.

I also investigated factors that affected change in altitude by Barn Owls when they approached roads at collision-prone altitudes. However, the model fit was poor, so results should not be overinterpreted. There was evidence that Barn Owls were more likely to decrease altitude when approaching at higher altitudes, and they tended to remain level when approaching from lower altitudes. There was also evidence that owls increased altitude when crossing wider roads versus no change for narrower ones. The slight descending behavior when approaching at high altitudes is subtle, and it is possible that a descent of less than a meter, when already flying nearly ten meters above the road, is not biologically relevant. More importantly, these data suggest that when approaching roads at lower altitudes, and thus at a greater risk of collision, Barn Owls do not increase altitude to cross. Elevating when crossing wider roads however is intuitive because once again, as wider roads typically represent highways and other major thoroughfares, it is likely that these roads had the most traffic and were most likely to elicit a response. By increasing altitude owls may be avoiding potential collisions with vehicles while still crossing the road. A study that investigated avian behavior around vehicles in Europe classified birds that increased height to fly above traffic together with birds that turned away, because both actions effectively avoided the chance of collision (Husby and Husby 2014). Sudden shifts in altitude by birds also occur in response to approaching aircraft, allowing individuals to avoid collision by decreasing or increasing height (Lima et al. 2015). This is especially pronounced at low altitude interactions where the most common avian response is to climb in altitude (Dolbeer et al. 2004).

Although Barn Owls have been hypothesized to be nonresponders to roads given their high mortality rates and evidence found in previous movement studies, my results seem to suggest that they also have traits of avoiders and speeders. One possible explanation for this discrepancy is a change in both field and statistical methodology. Although Barn Owl movement has been tracked before, most previous studies have done so at relatively low resolution, whereas those that have collected higher resolution data have not analyzed behavior in relation to roads (Grilo et al. 2012, Regan 2016, Hindmarch et al. 2017, Castañeda 2018, Almasi et al. 2021, Slankard et al. 2021). Analyzing Barn Owl movement near roads with resolution as fine as one fix per second gave a finer understanding of how owls respond to roads. When coupled with a random walk analysis, which has never been used with avian tracking data before, the results provide new insight into the behavior of Barn Owls near roads that suggests they are not simply nonresponders.

The most pressing question that remains, however, is that if Barn Owls do in fact have behavioral mechanisms to deal with the threats of roads and traffic, perhaps by avoiding them when possible, why are they dying alongside roads in such great numbers and in so many locations across their range? I can think of a number of potential reasons: 1) of the occasions that Barn Owls do cross roads, the likelihood of mortality is extremely high (see Ramsden 2003, Grilo et al. 2012), 2) high mortality rates are mostly representative of dispersing juveniles and females (see Boves and Belthoff 2012), whereas the owls from my study were mostly established in their territories, 3) major roads and their verges are serving as ecological traps that are attracting and “depredating” owls (see Hindmarch et al. 2017), 4) owl populations are healthy and high road mortality is reflective of large populations with high breeding output and generally high annual mortality (but see Grilo et al. 2014), or 5) any combination of these. Future studies may help to further understand Barn Owl behavior near roads and evaluate why owls are dying in such great numbers and what measures can be taken to prevent it.

Future Directions

One significant addition to the understanding of Barn Owl behavior in relation to roads would be the incorporation of traffic data into the analyses instead of using roads as a proxy (as done in my study). Behavioral responses of birds to oncoming traffic have been studied, but only in a few species that were either diurnal, captured and observed in captivity, baited to roads with carcasses, or observed opportunistically from a moving vehicle (Mukherjee et al. 2013, Devault et al. 2014, 2018, Husby and Husby 2014). Barn Owls, however, are nocturnal and typically hunt on the wing (Marti et al. 2005), rendering opportunistic or baited observations of their interactions with actual traffic difficult or impossible. One more practical approach could be the use of captive birds perhaps in combination with flight trials near experimental moving vehicles. Further, the use of captive birds is also promising for investigating the effectiveness of potential mitigation efforts such as berms, trees, and pole barriers (Bard et al. 2002, Belthoff et al. 2015, Kociolek et al. 2015, Zuberogoitia et al. 2015).

Current limitations in technology coupled with the relatively small mass of Barn Owls and their nocturnal behavior make the remote uploading of fine-scale telemetry data difficult (Marti et al. 2005, Bridge et al. 2011, Hooten et al. 2017, Dahlgren et al. 2018). However, when technology allows, deploying units that do not need to be recovered like the data loggers I used would allow for the tracking of young owls and females that may be more prone to dispersal, as well as owls that ultimately die from vehicular collisions. Information on the movement of these individuals could potentially reveal different patterns of behavior dependent on sex and age, as well as reduce potential survivor bias that could exist in studies such as my own where data from roadkilled owls likely goes unrecovered.

Lastly, there is evidence that Barn Owl populations are more affected by recently constructed highways than established thoroughfares (Ramsden 2003), and although birds can adapt to new road construction, it can come at the cost of initially high mortality rates (Mumme et al. 2000). Given the continuous expansion of road networks around the globe (Dulac 2013), studying the flight behavior of established populations before and after the construction of new roads might be telling.

Conclusions

The outlook for Barn Owl populations is grim in some respects; road mortality rates as low as 5% can be enough to reduce Barn Owl populations by 50% (Borda-de-Água et al. 2014), and major roads have depleted and even extirpated some populations (Ramsden 2003). Although a few studies of Barn Owl behavior suggest that owls may avoid roads and traffic to some degree (Grilo et al. 2012, 2014, Regan 2016), globally high rates of roadway mortality have led to the hypothesis that they are nonresponders, meaning they fail to respond behaviorally to roads or traffic (Jacobson et al. 2016). The notion that as nonresponders Barn Owls may have no pre-adaptations or evolved mechanisms to deal with this threat paints a bleak picture for the future of this species in a rapidly developing world. On the other hand, my data suggest they exhibit at least some traits more typical of speeders and avoiders, in contrast to being strict nonresponders. That is, although Barn Owls did not avoid areas near roads, they crossed roads less than expected, avoided more dangerous major roads, and often flew at altitudes well above the collision zone when crossing, suggesting they share similarities with avoiders. Further, when they were in the collision zone, they accelerated flight speeds to cross, especially for larger roads, suggesting they also share traits with speeders. Thus, despite the substantial roadway mortality of Barn Owls, these results offer some encouragement. With global road networks expanding year after year (Dulac 2013), the thought that Barn Owls lack any response mechanism to these dangerous entities is alarming. But perhaps they already had a method for dealing with this threat. Or perhaps we are seeing outcomes of several decades of the selective pressure of road mortality acting on a fast growing, high biotic potential species, as observed in other birds affected by road mortality (Brown and Brown 2013). Either way, with Barn Owl populations around the globe facing increased exposure to roads, it is somewhat reassuring to know that they may be evolving a toolset for persistence.

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Tables

Table 1.1 A list of GPS data loggers deployed in 2019 and 2020 and information on the sex and age class of the tagged Barn Owls with nightly statistics for those recovered, in southern Idaho, USA. Nightly statistics are measured for each tracking night, which included a maximum of 6 h of observation (between 1800 and 0000 h).

Owl ID	Sex	Age[1]	Deploy Date	Recovery Date	# Nights of Data	# Roads Crossed/Night	Avg. Distance/Night (km)
N1-1	F	SY	12/13/2019	1/2/2020	6	3	2.8
N1-2	M	ASY	12/11/2020	1/8/2021	2	9	3.9
N2-1	F	HY	12/13/2019	4/17/2020	4	3.8	3.6
N3-1	M	ASY	12/13/2019	10/16/2020	9	1.9	4.9
N4-1	M	ASY	12/13/2019	10/24/2020	6	15.2	12.8
N5-1	M	ASY	12/14/2019	1/2/2020	9	12.3	6.5
N5-2	F	ASY	12/11/2020	2/26/2021	4	4.3	2.6
N6-1	F	ASY	12/14/2019	1/2/2020	4	9.3	5.2
N7-1	M	ASY	12/17/2019	1/2/2020	6	3	5.2
N7-2	F	ASY	12/14/2020	1/8/2021	7	1.1	3.2
N9-1	M	ASY	12/19/2019	1/5/2020	5	12.6	4.5
N10-1	F	HY	12/19/2019	4/17/2020	5	5.8	3.4
N10-2	F	ASY	12/14/2020	4/23/2021	7	4.3	2.4
N11-1	M	ASY	12/14/2020	1/15/2021	7	18.4	7.6
N12-1	M	ASY	12/16/2020	1/15/2021	6	2.3	3
O1-1	F	ASY	12/17/2019	1/17/2020	6	8.8	7.9
O1-2	M	ASY	12/14/2020	1/8/2021	8	17	13.5
O2-1	F	ASY	12/17/2019	4/17/2020	6	9.8	6.1
O4-1	M	ASY	12/19/2019	1/17/2020	6	32.7	13.8
N2-2	F	SY	12/11/2020	*NA*			
N4-2	F	ASY	12/11/2020	*NA*			
N6-2	M	SY	12/12/2020	*NA*			
N8-1	F	ASY	12/17/2019	*NA*			
N9-2	M	HY	12/14/2020	*NA*			
O2-2	M	ASY	12/16/2020	*NA*			
O3-1	M	ASY	12/17/2019	*NA*			
O4-2	F	HY	12/16/2020	*NA*			

[1] HY indicates hatch year, SY is second year, and ASY is after second year

Table 1.2 A summary of the model investigating Barn Owl road crossings in southern Idaho, USA as a function of the category (expected or observed) and distance traveled, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Expected (Intercept)	2.31	2.15	2.46	0.08	
Observed	-0.37	-0.49	-0.25	0.06	
Scaled log of Distance	0.73	0.71	0.74	0.01	
ZI Model Intercept	-3.22	-3.35	-3.09	0.07	
Random Intercept					0.12
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R^2**	**Marginal Pseudo R^2**		
	7.18	0.55	0.45		

Table 1.3 A summary of the model investigating Barn Owl road crossings in southern Idaho, USA as a function of the category (expected or observed), road class (major or minor), and their interaction, as well as distance traveled, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Expected, Major Roads (Intercept)	-0.86	-1.04	-0.69	0.09	
Observed	-1.40	-1.93	-0.86	0.27	
Small Roads	3.14	3.10	3.17	0.02	
Observed x Small Roads	1.06	0.51	1.61	0.28	
Scaled log of Distance	0.72	0.70	0.73	0.01	
ZI Model Intercept	-2.97	-3.13	-2.81	0.08	
Random Intercept					0.14
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R^2**	**Marginal Pseudo R^2**		
	5.91	0.84	0.81		

Table 1.4 A summary of the model investigating Barn Owl road crossings in southern Idaho, USA as a function of category (expected or observed), sex (female or male), and their interaction, as well as distance traveled, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Expected, Female (Intercept)	2.39	2.16	2.61	0.11	
Observed	-0.42	-0.61	-0.23	0.10	
Male	-0.15	-0.45	0.16	0.16	
Observed x Male	0.08	-0.16	0.32	0.12	
Scaled log of Distance	0.73	0.71	0.75	0.01	
ZI Model Intercept	-3.22	-3.35	-3.09	0.07	
Random Intercept					0.12
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R^2**	**Marginal Pseudo R^2**		
	7.17	0.53	0.43		

Table 1.5 A summary of the model investigating minimum distance to roads of Barn Owls in southern Idaho, USA as a function of category (expected or observed) and total length of roads in a 1-km radius of the nest box with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Expected (Intercept)	4.88	4.77	5.00	0.06	
Observed	-0.07	-0.13	0.00	0.03	
Scaled log of Total Road Length	-0.19	-0.31	-0.08	0.06	
Random Intercept					0.06
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R^2**	**Marginal Pseudo R^2**		
	61.3	0.44	0.17		

Table 1.6 A summary of the model investigating minimum distance to major roads of Barn Owls in southern Idaho, USA as a function of category (expected or observed), presence of major roads within a 1-km radius (absent or present), and their interaction, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Expected, Major Roads Absent (Intercept)	7.51	7.29	7.73	0.11	
Observed	-0.03	-0.13	0.07	0.05	
Major Roads Present	-0.89	-1.23	-0.55	0.17	
Observed x Major Roads Present	-0.11	-0.26	0.06	0.08	
Random Intercept					0.14
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R2**	**Marginal Pseudo R2**		
	495.7	0.67	0.38		

Table 1.7 A list of GPS data loggers with flight dynamics data and their associated counts of approach-departs, crossings, and total encounters for Barn Owls in southern Idaho, USA. Sex, age, and year of movement data are listed in Table 1.1 for each.

Owl ID	# Approach-Departs	# Crossings	Total Encounters
N1-2	3	4	7
N2-1	2	8	10
N3-1	18	7	25
N4-1	31	17	48
N5-1	48	40	88
N5-2	6	13	19
N6-1	10	4	14
N7-1	1	6	7
N7-2	6	3	9
N9-1	5	13	18
N10-1	11	15	26
N10-2	12	22	34
N11-1	2	15	17
Total	155	167	322

Table 1.8 A summary of the model investigating Barn Owl crossing probability (approach-depart = 0, crossing = 1) in southern Idaho, USA as a function of approach altitude, approach speed, and road width, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Intercept	0.61	0.20	1.09	0.22	
Scaled Approach Altitude	0.97	0.54	1.50	0.24	
Scaled Approach Speed	0.30	-0.01	0.63	0.16	
Scaled Road Width	-0.47	-0.83	-0.15	0.17	
Random Intercept					0.10
Metrics of Model Fit:	**AUC**				
	0.76				

Table 1.9 A summary of the model investigating change in speed of Barn Owls when crossing roads in southern Idaho, USA as a function of approach altitude, approach speed, and road width, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Intercept	0.87	0.26	1.47	0.30	
Scaled Approach Altitude	1.11	0.07	2.15	0.54	
Scaled Approach Speed	-0.66	-0.89	-0.43	0.12	
Scaled Road Width	0.18	-0.12	0.46	0.15	
Random Intercept					0.26
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R^2**	**Marginal Pseudo R^2**		
	0.87	0.42	0.22		

Table 1.10 A summary of the model investigating change in altitude of Barn Owls when crossing roads in southern Idaho, USA as a function of approach altitude, approach speed, and road width, with a random intercept for Owl ID and including metrics of model fit.

Covariate	Estimate	2.5%	97.5%	SE	Variance
Intercept	-0.96	-1.55	-0.36	0.31	
Scaled Approach Altitude	-1.42	-2.54	-0.30	0.58	
Scaled Approach Speed	0.17	-0.10	0.42	0.13	
Scaled Road Width	0.32	0.01	0.62	0.16	
Random Intercept					0.11
Metrics of Model Fit:	**RMSE**	**Conditional Pseudo R^2**	**Marginal Pseudo R^2**		
	0.94	0.18	0.09		

Figures

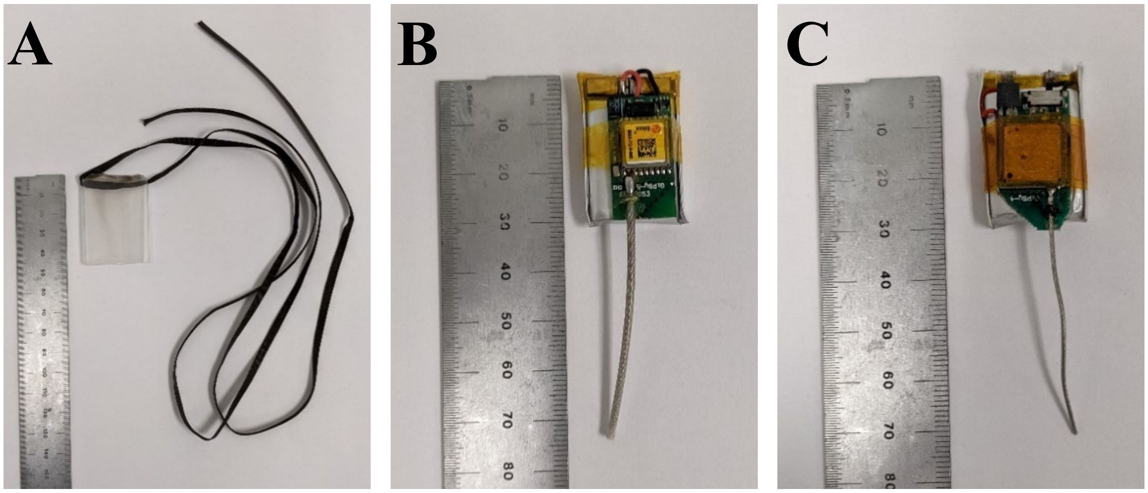

Figure 1.1 A) Unsealed harness, B) GiPSy-5®, and C) GiPSy-4® data loggers used for tracking movements of Barn Owls in southern Idaho, USA to assess behavior near roads.

Figure 1.2 A backpack containing a GiPSy-5® data logger attached to an adult female Barn Owl near Homedale, Idaho, USA.

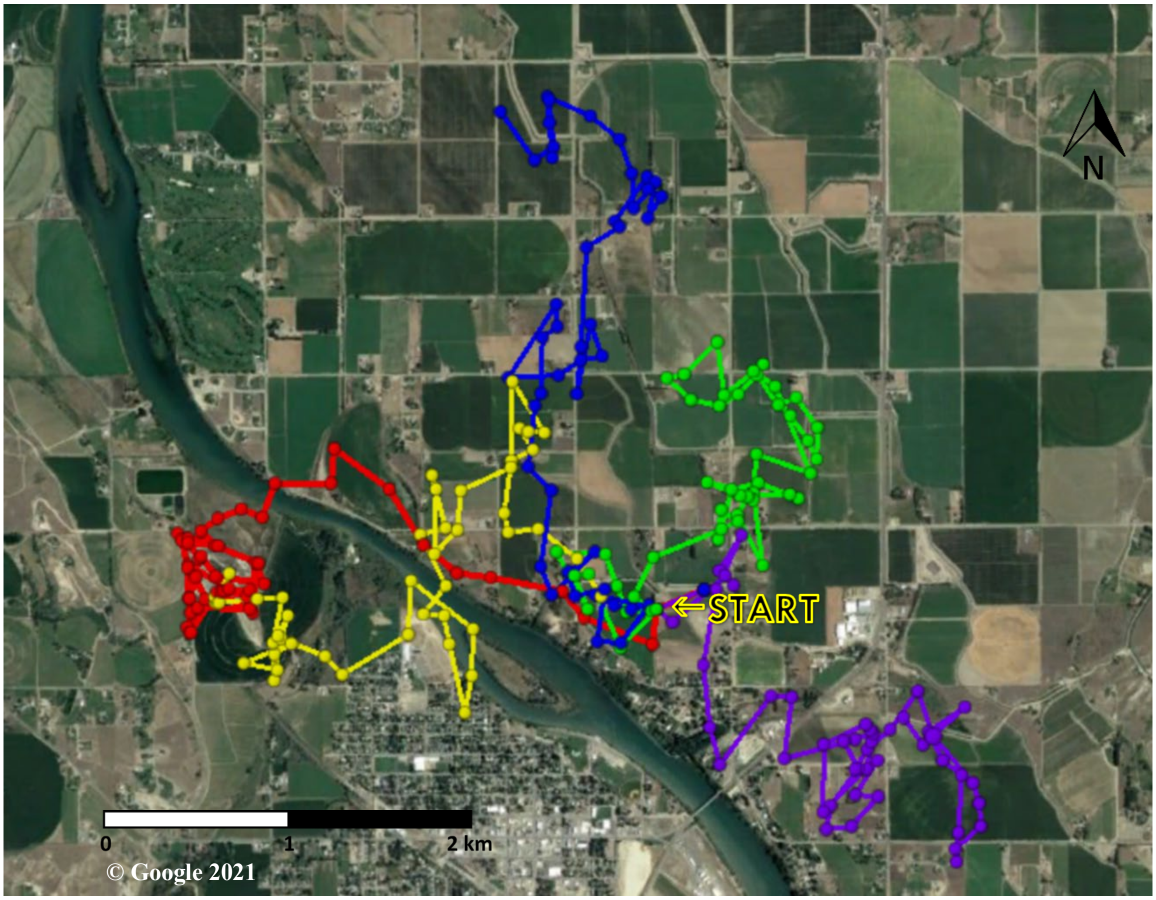

Figure 1.3 A comparison of an observed track (in red) for an instrumented Barn Owl with four random walk paths (other colors) in Canyon and Owyhee counties, Idaho, USA. The starting point (identical for each) is also indicated.

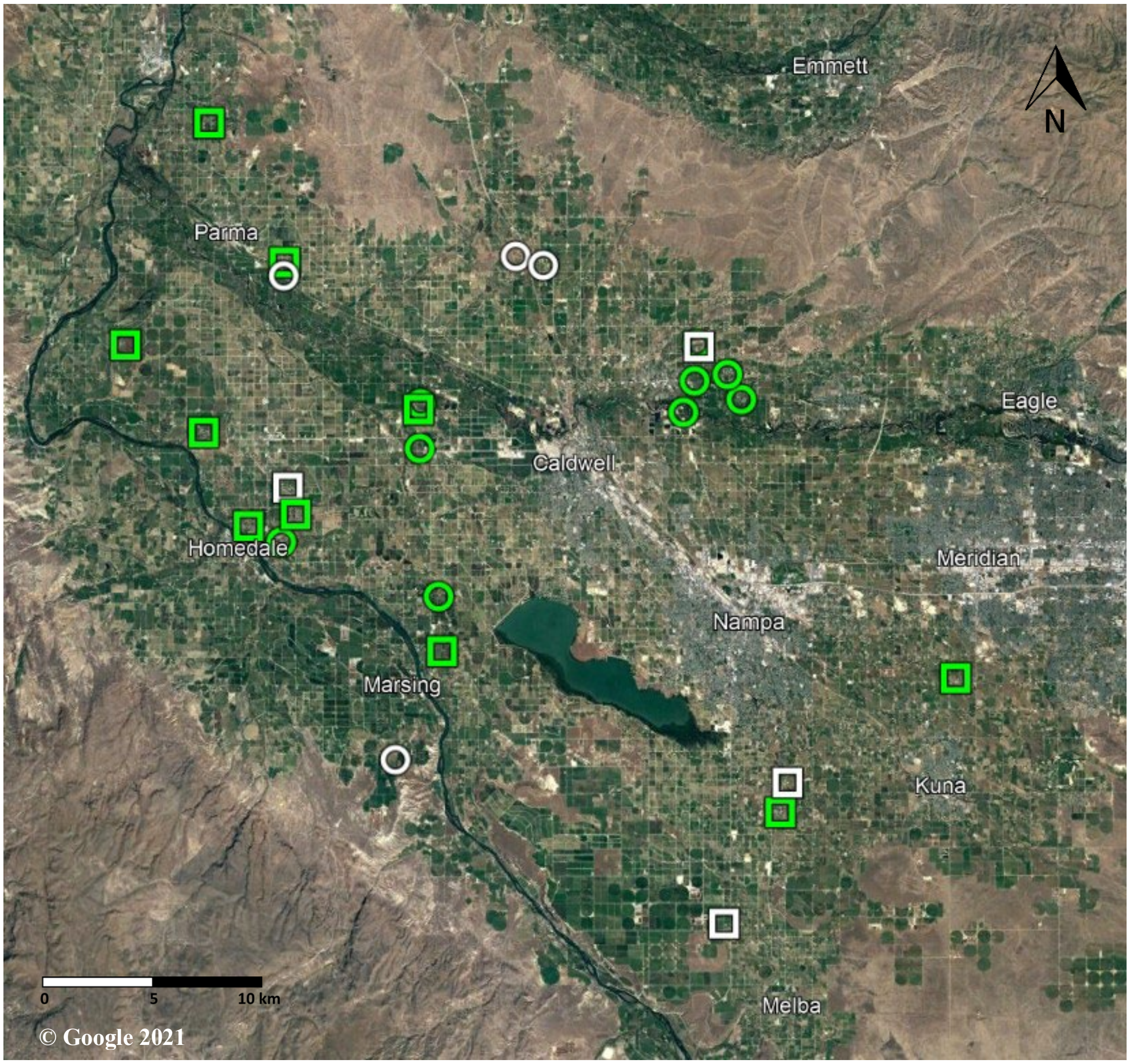

Figure 1.4 The nest box locations where GPS data loggers were attached to Barn Owls in Canyon County and the surrounding areas in southern Idaho, USA. Circles represent locations where females were instrumented and squares males, and green and white symbols represents recovered and unrecovered data loggers, respectively.

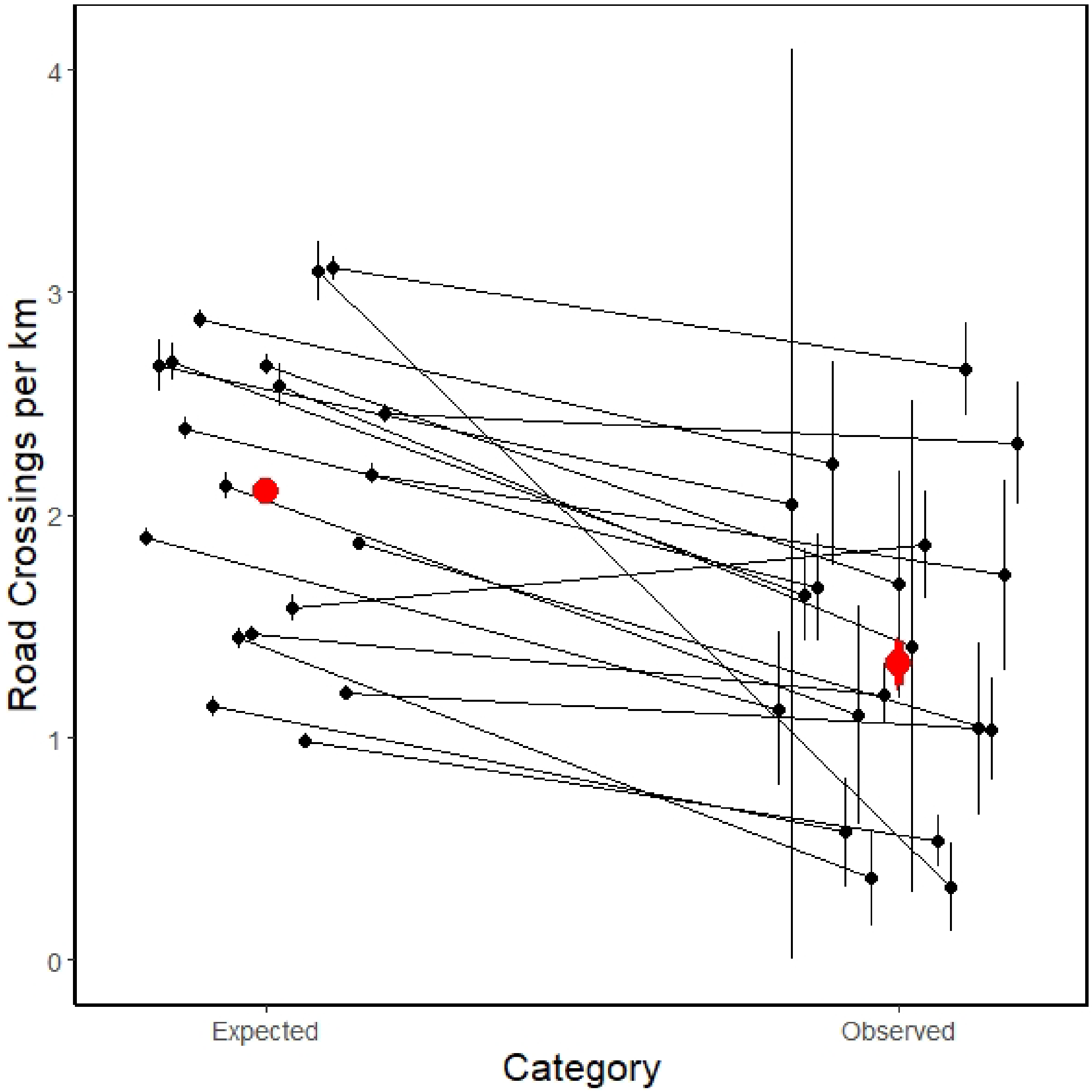

Figure 1.5 A comparison of the number of road crossings per km traveled between the observed (actual) and expected (random walk generated) data for Barn Owls in southern Idaho, USA. Each set of connected points represents an individual owl, with standard error bars included. The red points represent the overall average across all owls with associated standard error.

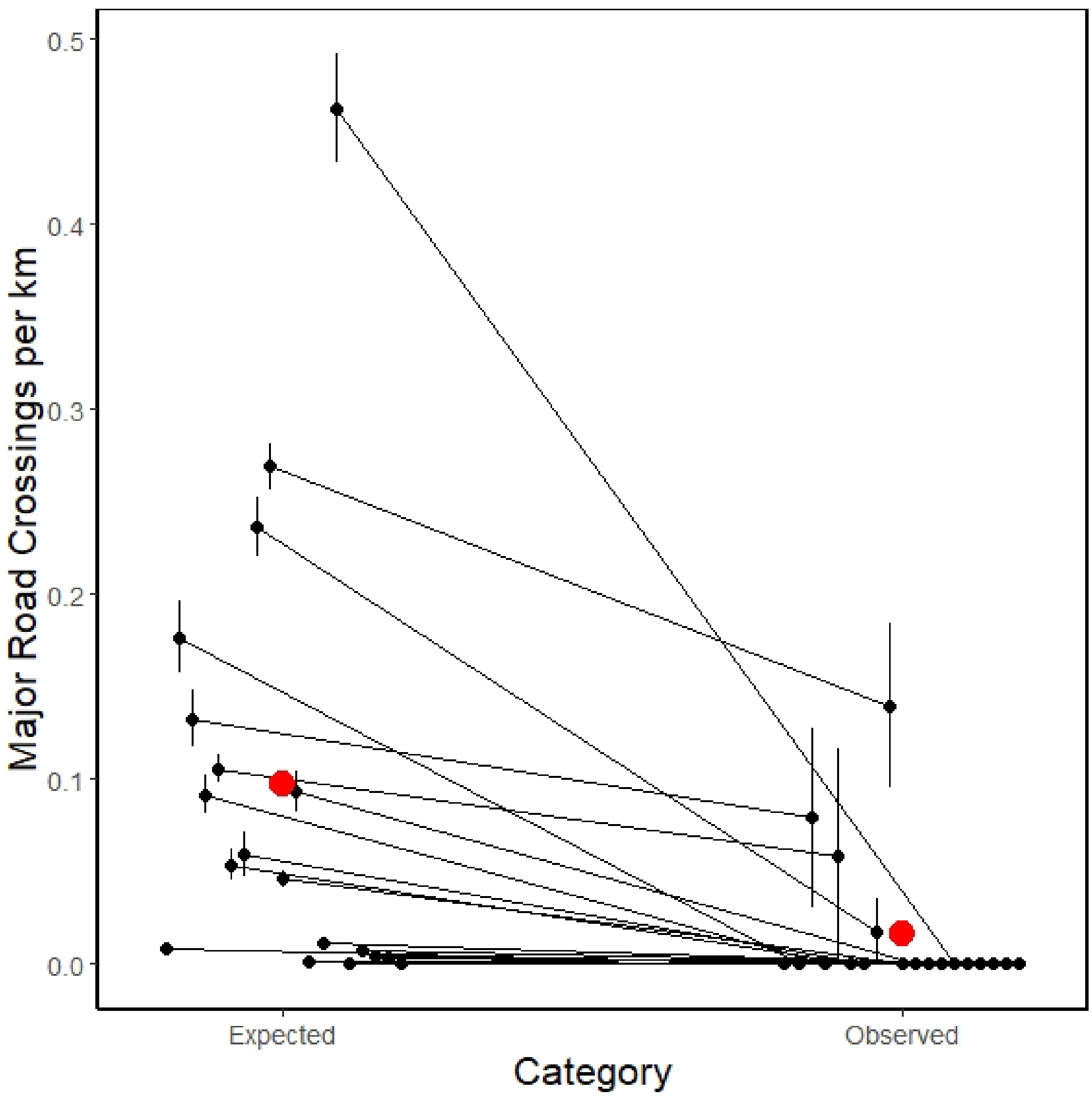

Figure 1.6 A comparison of the number of major road crossings per km traveled between the observed (actual) and expected (random walk generated) data for Barn Owls in southern Idaho, USA. Each set of connected points represents an individual owl, with standard error bars included. The red points represent the overall average across all owls with associated standard error.

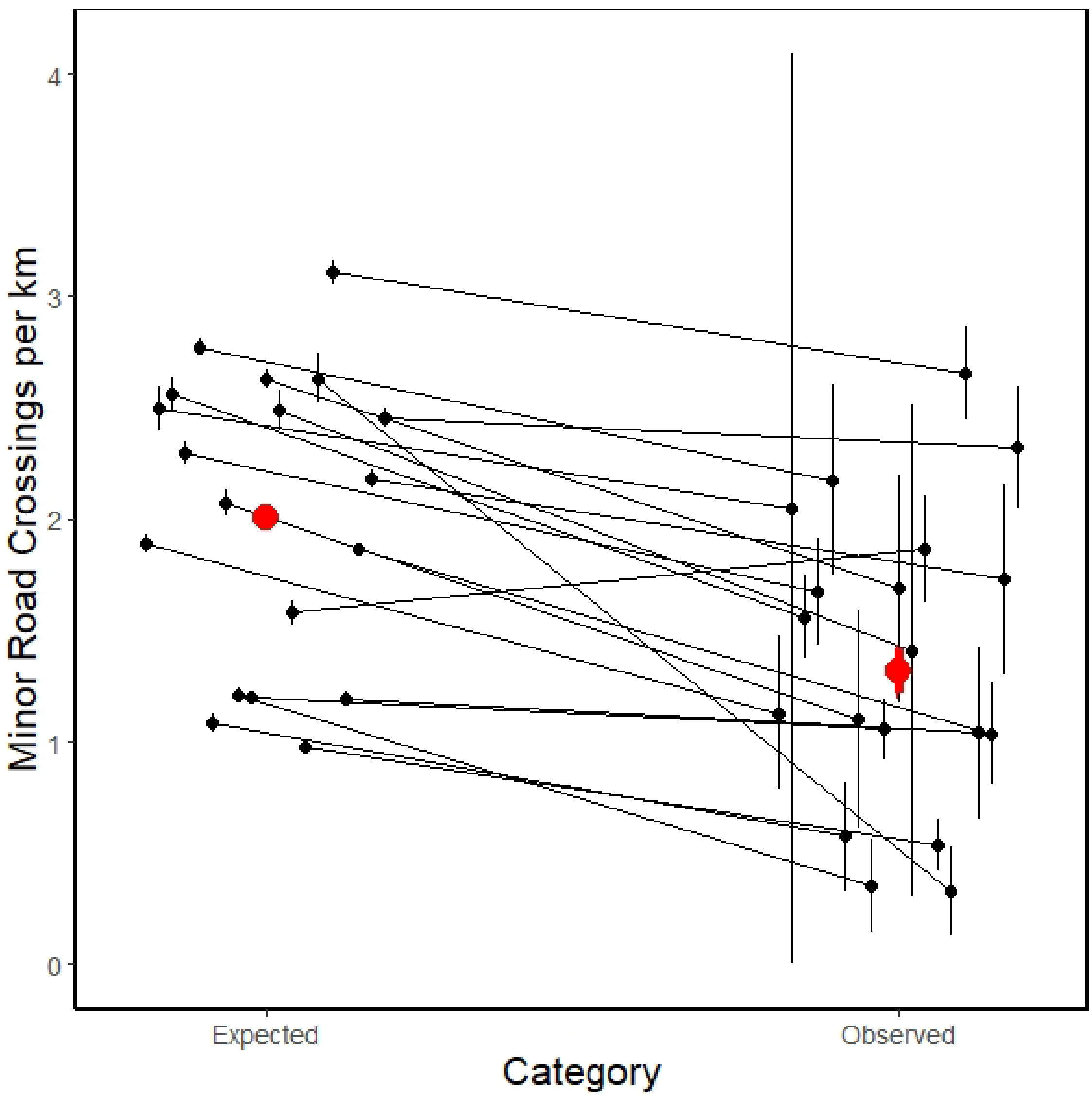

Figure 1.7 A comparison of the number of minor road crossings per km traveled between the observed (actual) and expected (random walk generated) data for Barn Owls in southern Idaho, USA. Each set of connected points represents an individual owl, with standard error bars included. The red points represent the overall average across all owls with associated standard error.

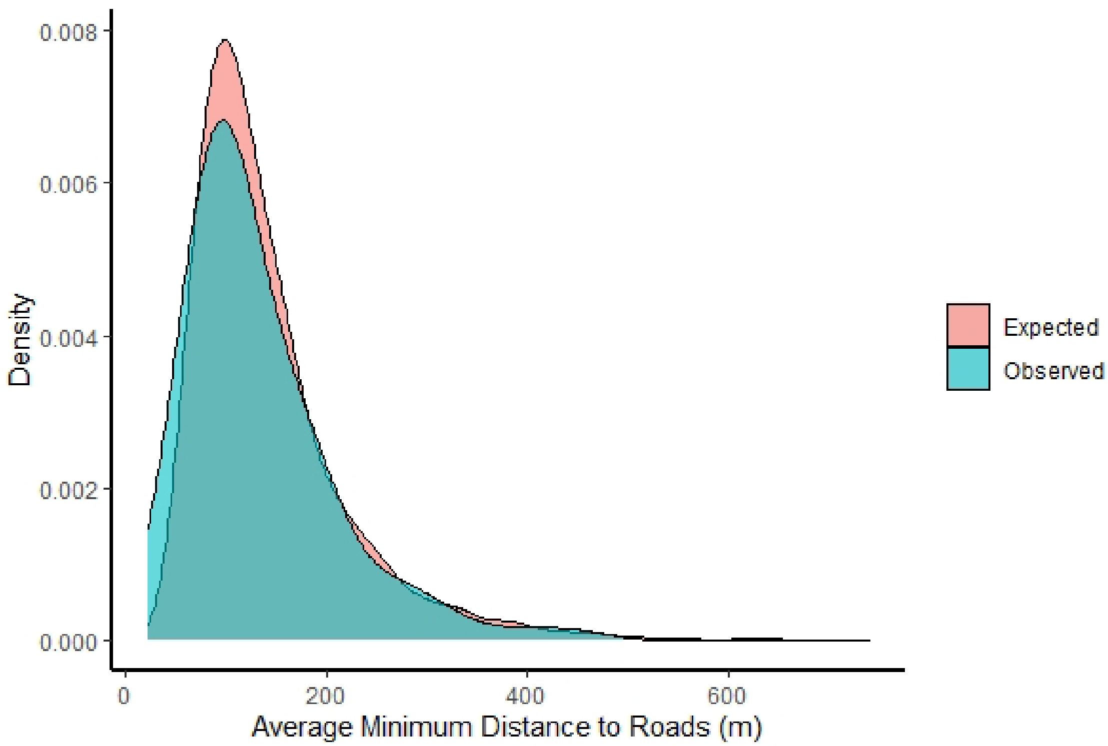

Figure 1.8 A density plot of the average minimum distance of Barn Owls to roads in southern Idaho, USA for observed (teal) and expected (red) data.

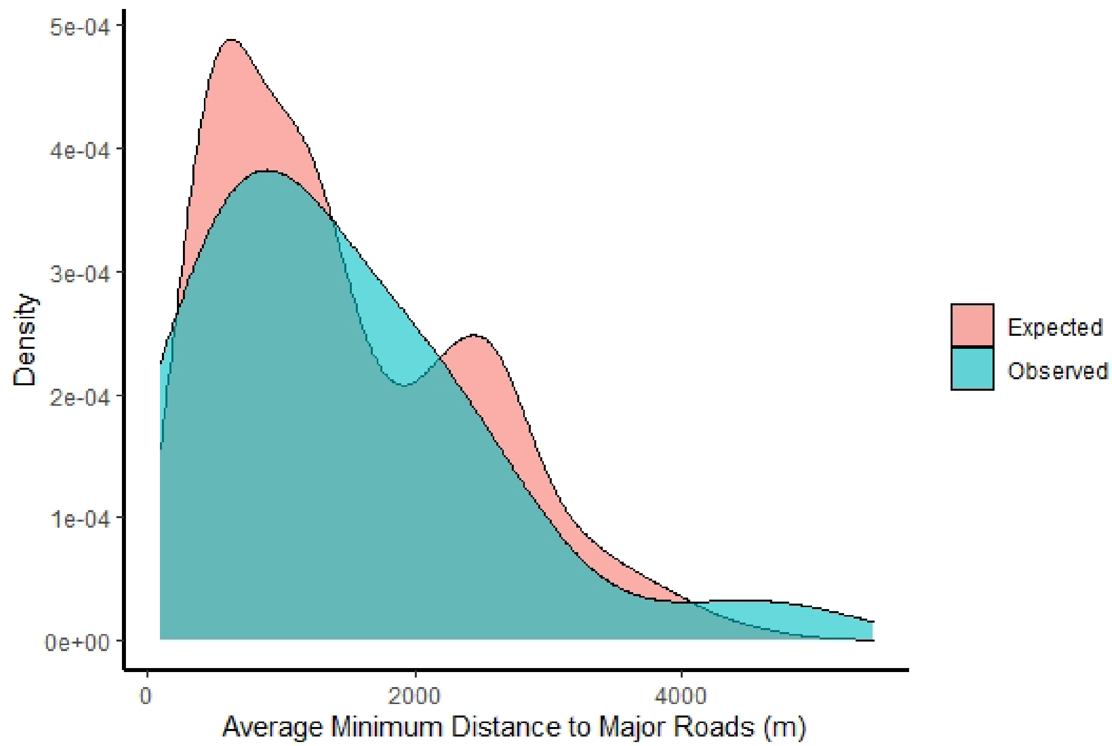

Figure 1.9 A density plot of the average minimum distance of Barn Owls to major roads in southern Idaho, USA for observed (teal) and expected (red) data.

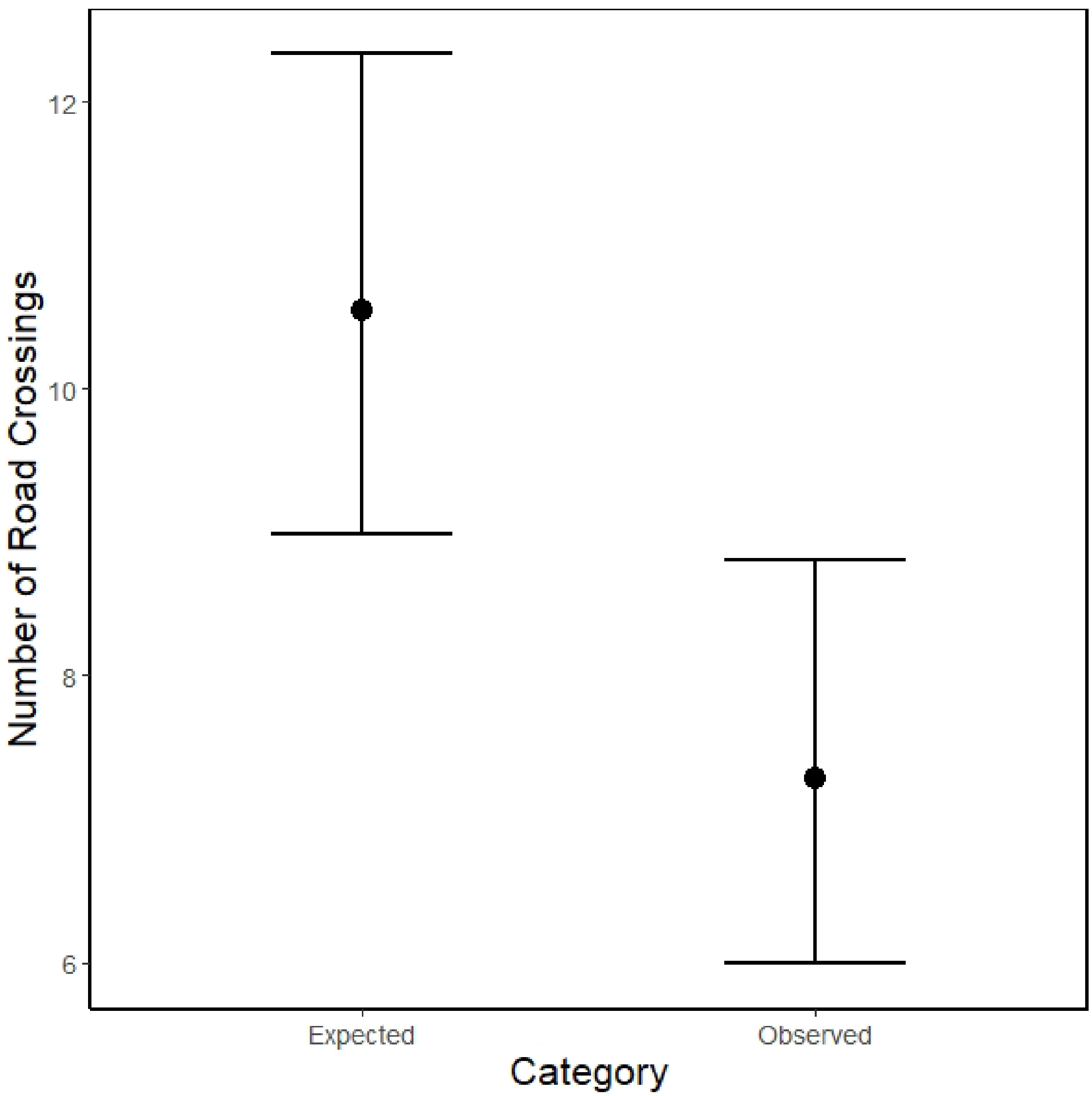

Figure 1.10 The number of road crossings of Barn Owls in southern Idaho, USA as a function of category (expected or observed), with 95% confidence intervals and distance traveled set at 5 km.

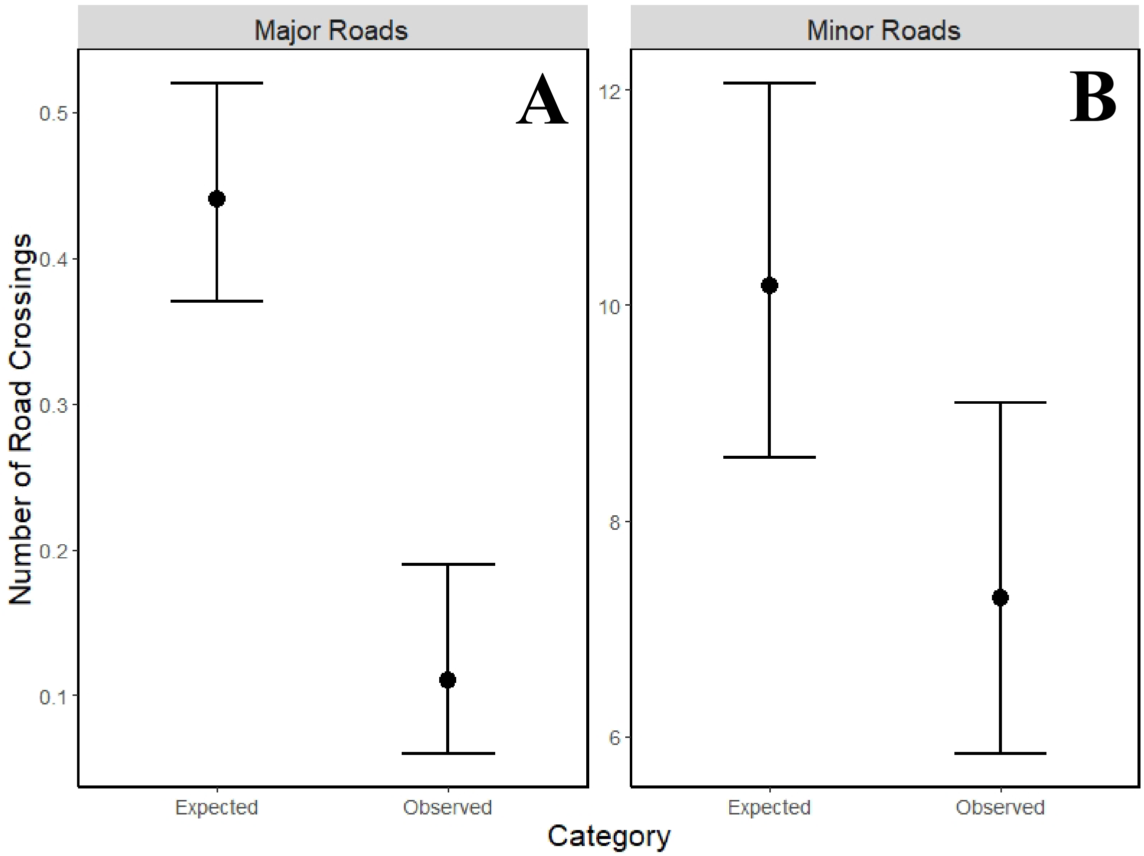

Figure 1.11 The number of road crossings of Barn Owls in southern Idaho, USA as a function of the interaction of category (expected or observed) and road class (major or minor) with 95% confidence intervals and distance traveled set at 5 km. Major roads are shown on the left (A) and minor roads on the right (B). Note that the Y axes are on different scales.

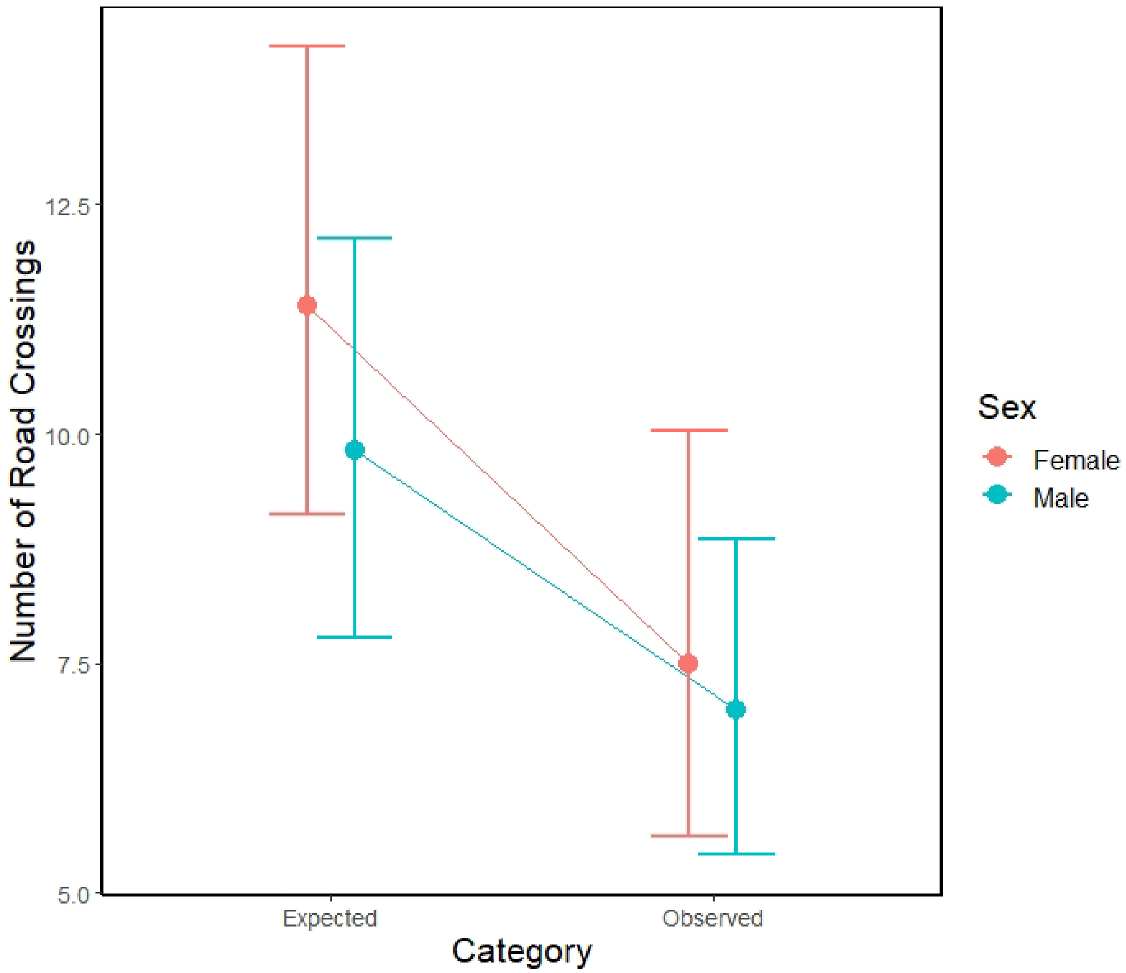

Figure 1.12 The number of road crossings of Barn Owls in southern Idaho, USA as a function of the interaction of category (expected or observed) and sex (female or male) with 95% confidence intervals and distance traveled set at 5 km. Females are shown in red, males in teal.

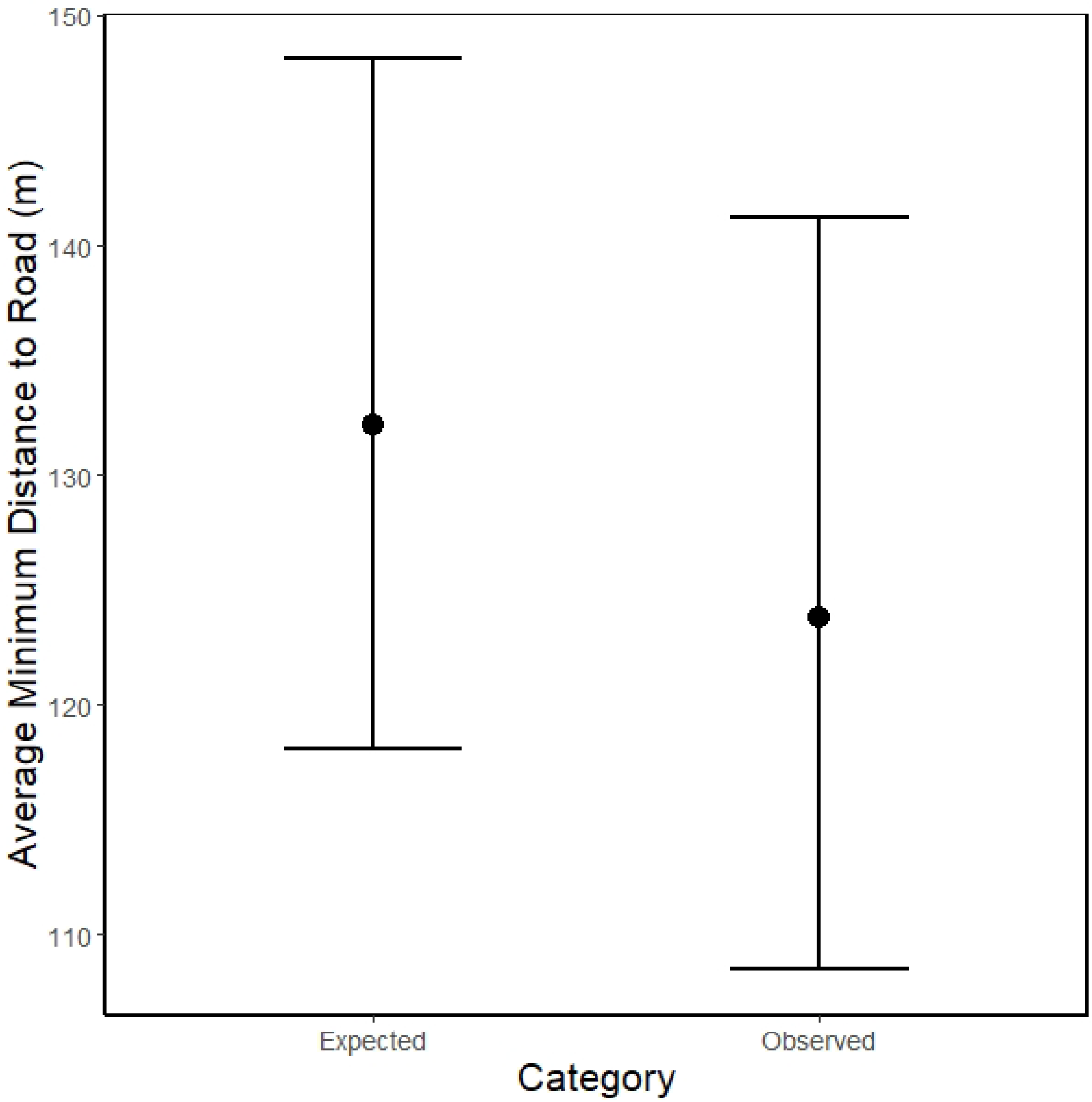

Figure 1.13 The minimum distance to roads of Barn Owls in southern Idaho, USA as a function of category (expected or observed) with 95% confidence intervals and total length of roads set at its mean.

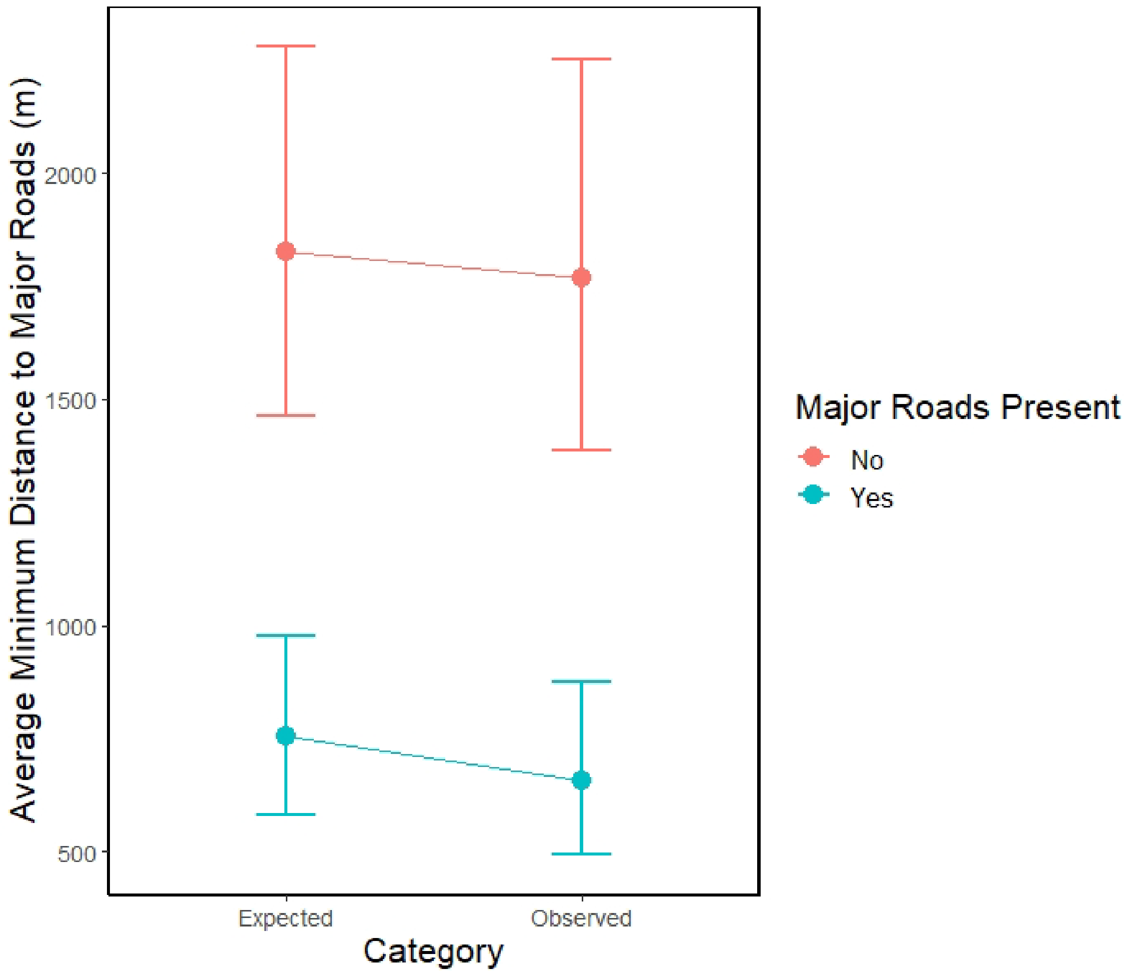

Figure 1.14 The minimum distance to major roads of Barn Owls in southern Idaho, USA as a function of the interaction of category (expected or observed) and presence of major roads within a 1-km radius (no or yes) with 95% confidence intervals. Major roads absent is shown in red and major roads present in teal.

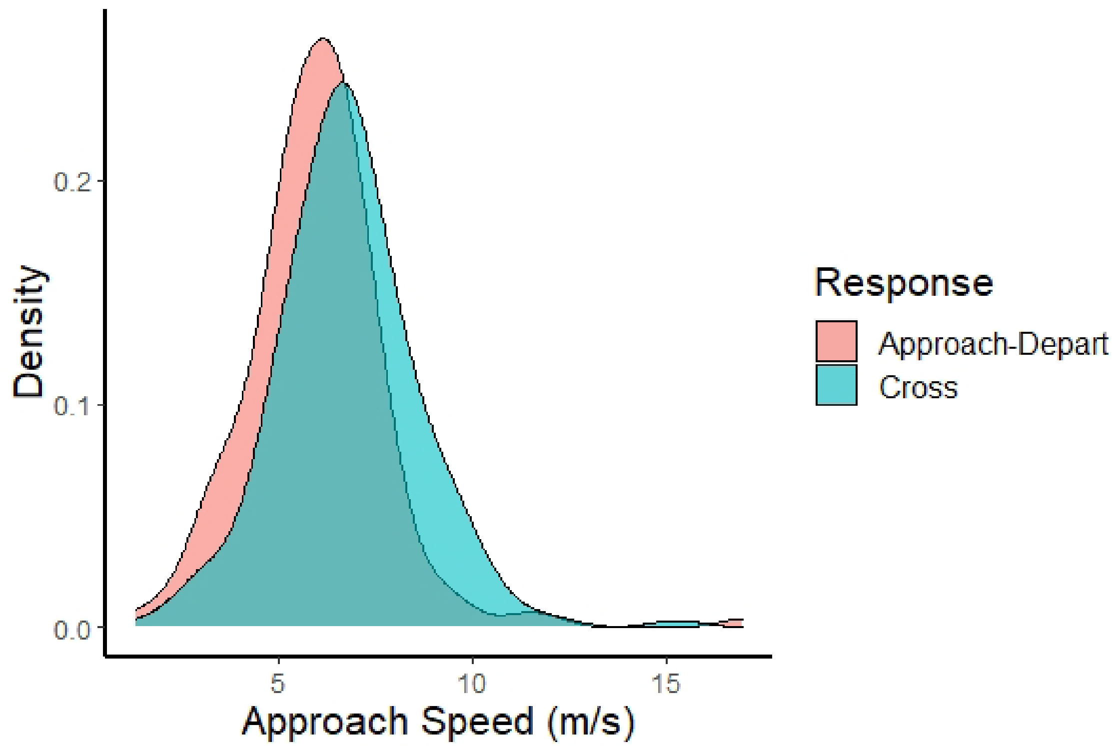

Figure 1.15 A density plot of the approach speed of Barn Owls to roads in southern Idaho, USA when they cross (teal) or approach-depart (red).

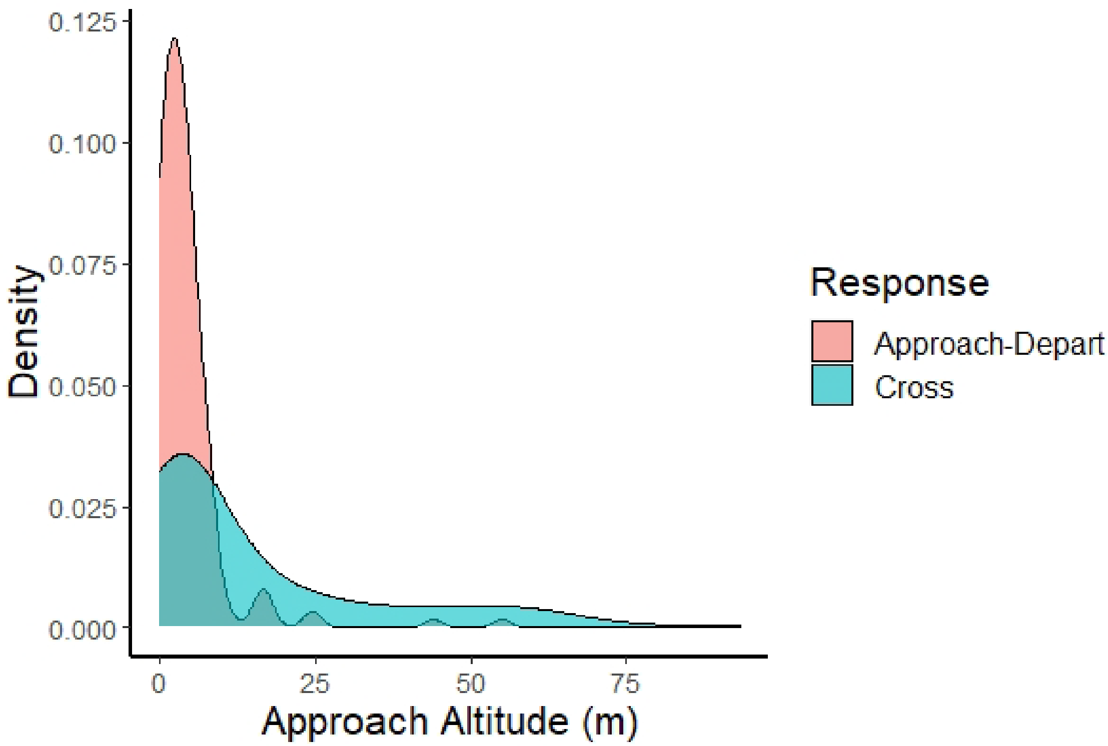

Figure 1.16 A density plot of the approach altitude of Barn Owls to roads in southern Idaho, USA when they cross (teal) or approach-depart (red).

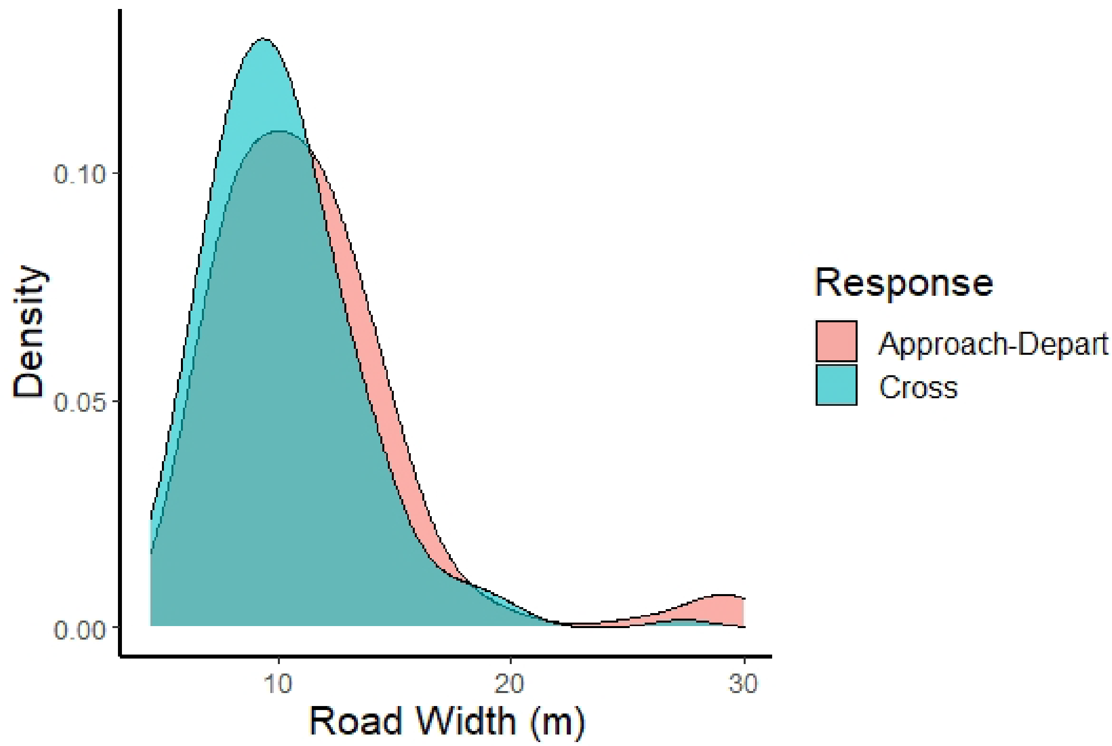

Figure 1.17 A density plot of the width of roads in southern Idaho, USA when Barn Owls cross (teal) or approach-depart (red).

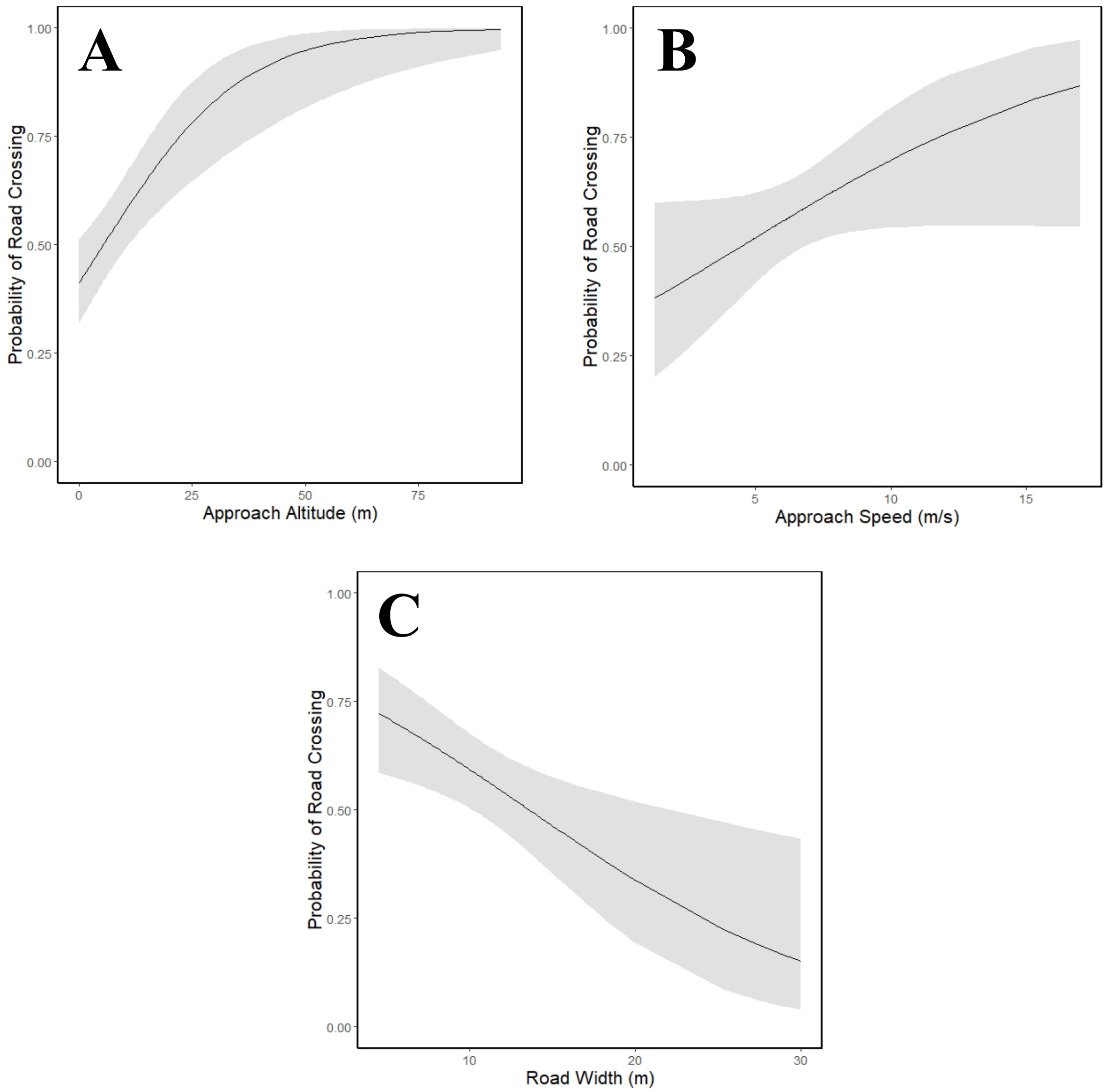

Figure 1.18 The probability of Barn Owls crossing a road when encountered in southern Idaho, USA as a function of A) approach altitude, B) approach speed, and C) road width with 95% confidence intervals. For each graph the non-plotted predictors are held at their mean.

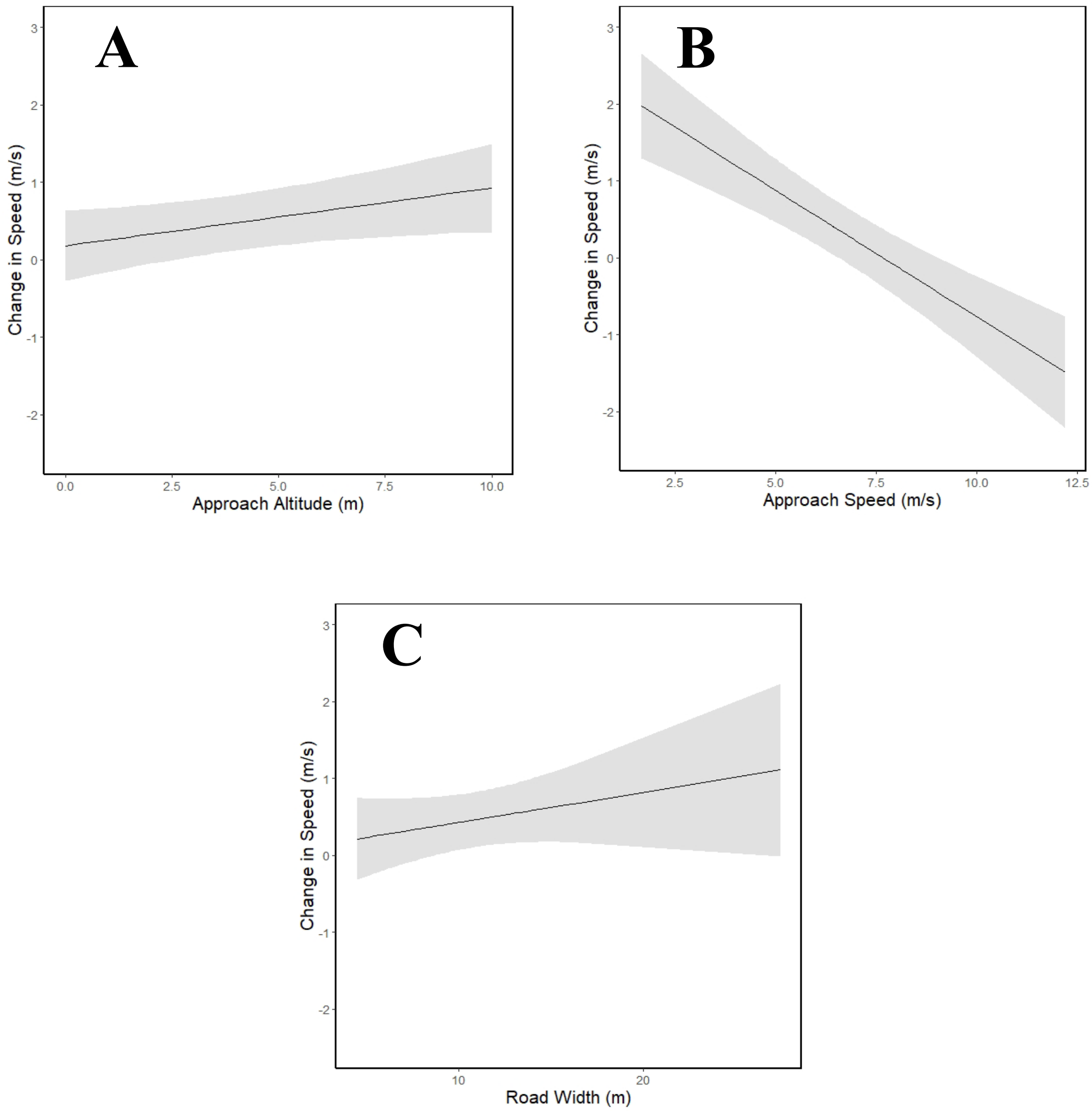

Figure 1.19 Barn Owls' change in speed when crossing roads in southern Idaho, USA as a function of A) approach altitude, B) approach speed, and C) road width with 95% confidence intervals. For each graph the non-plotted predictors are held at their mean.

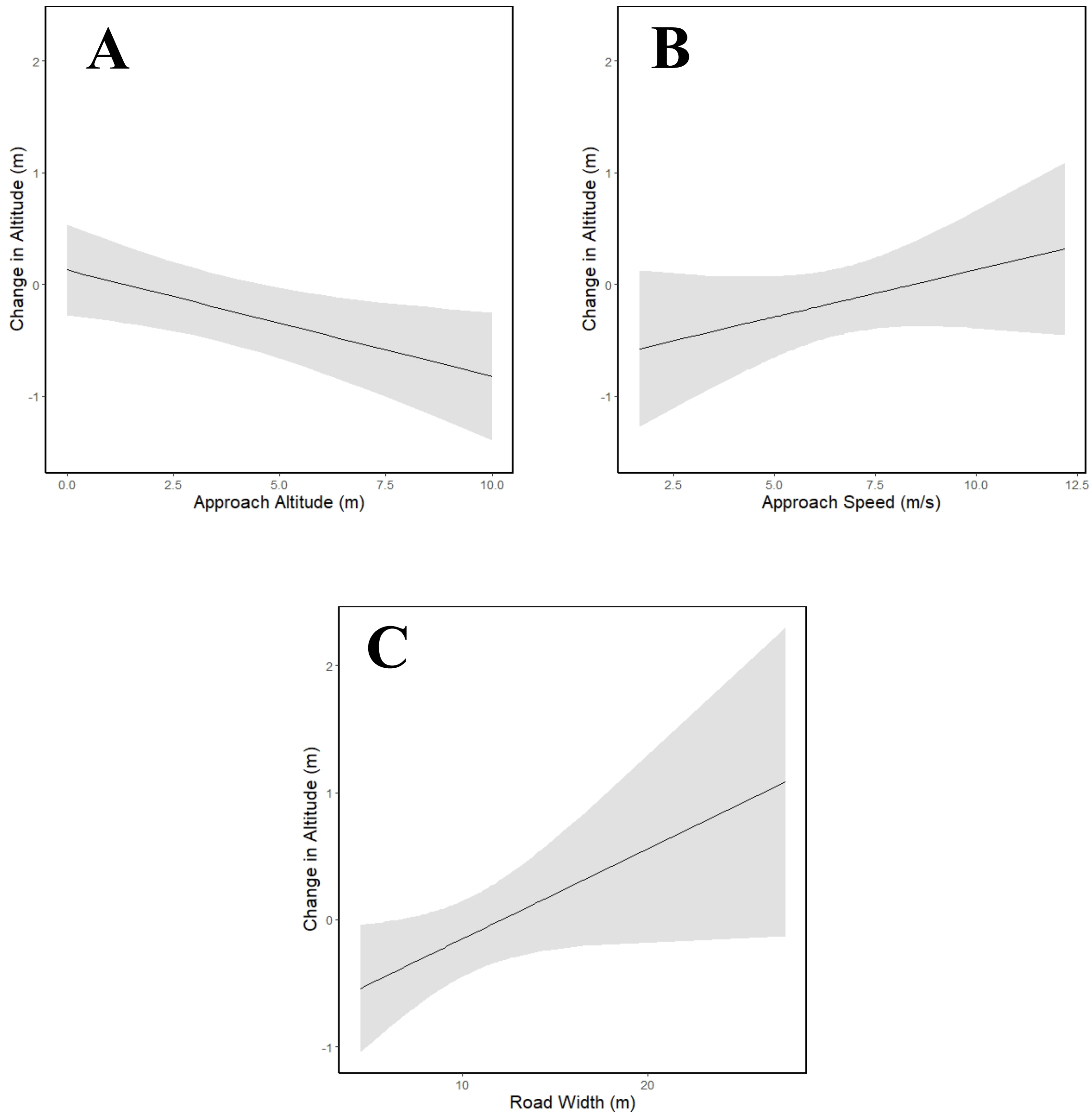

Figure 1.20 Barn Owls' change in altitude when crossing roads in southern Idaho, USA as a function of A) approach altitude, B) approach speed, and C) road width with 95% confidence intervals. For each graph the non-plotted predictors are held at their mean.

CHAPTER TWO: THE EFFECTS OF ROADS ON BARN OWL BREEDING OCCUPANCY AND PRODUCTIVITY IN SOUTHERN IDAHO

Abstract

Barn Owls (*Tyto alba*) are a species of conservation concern in many portions of their cosmopolitan range. One important factor contributing to population declines and sometimes local extirpations is roads, which cause direct mortality through Barn Owl-vehicle collisions, fragment habitat, limit dispersal and movement, and imperil long-term population viability in some cases. My aim was to examine the potential effects of roads on Barn Owl breeding occupancy and productivity within a population of owls in southern Idaho, USA which has some of the highest reported rates of roadway mortality. I monitored a nest box population of Barn Owls between 2019 and 2022 to record breeding occupancy and productivity (number of fledglings). I assessed occupancy in an average of 276 nest boxes per year and found that occupancy was 66%. Nests produced an average of 3.7 fledglings over both years (n = 225 nests). Both breeding occupancy and productivity decreased with proximity to roads. These results suggest that roads have the potential to influence owl populations not only through wildlife-vehicle collisions but indirectly through reductions in occupancy and productivity.

Introduction

There are currently more than 750 million vehicles traveling on over 64 million km of road on Earth, with 25 million more km of road anticipated by 2050 (van der Ree et al. 2011, CIA 2013, Laurance et al. 2014). Although roads are crucial to human transportation needs, their effects on wildlife can be far-ranging. Roads cause habitat loss, degradation, and fragmentation; light and noise pollution; spread of exotic species; and direct mortality of animals (Trombulak and Frissell 2000, van der Ree et al. 2015). Avian populations are harmed by roads through direct mortality (Loss et al. 2015, Husby 2016, Ceia-Hasse et al. 2018), significant demographic changes (Mumme et al. 2000, Freire et al. 2020), limitations on movements and dispersal (Develey and Stouffer 2001, Kociolek et al. 2011), and reduced long-term population viability (Borda-de-Água et al. 2014).

Some species of birds are less likely to nest near roads despite the availability of suitable habitat (Bollinger and Gavin 2004, Margalida et al. 2008). In others, reproductive output is diminished when nesting near roads. For instance, smaller clutch and brood sizes occur in urban areas with numerous roads compared to rural areas (Chamberlain et al. 2009) or in the presence of road noise (Halfwerk et al. 2011, Kight et al. 2012). Roads can also have marked effects on productivity, with fewer offspring fledging near roads and in urban areas (Kuitunen et al. 2003, Holm and Laursen 2011, Seress et al. 2012, Ng et al. 2019). Moreover, roads alter post-fledging survival, with juvenile birds exhibiting lower survival if they encounter roads following fledging (Streby and Andersen 2013, Adalsteinsson et al. 2018). Thus, irrespective of the stage of reproduction, roads and vehicular traffic have the potential to reduce numbers of nesting pairs, nesting success, productivity, and survival in birds (Mumme et al. 2000, Kuitunen et al. 2003, Margalida et al. 2008, Yoo and Koper 2017, Ng et al. 2019).

In many portions of their cosmopolitan range, Barn Owls (*Tyto alba*) are notable among birds of prey for high rates of road mortality (Moore and Mangel 1996, Ramsden

2003, Baudvin 2004, Gomes et al. 2009, Boves and Belthoff 2012, Payan et al. 2013, Belthoff et al. 2015, Pande et al. 2018). Indeed, along one interstate highway in southern Idaho, USA, thousands are estimated to be killed by wildlife-vehicle collisions annually (Boves and Belthoff 2012). Although wildlife-collisions involving Barn Owls have contributed to population declines, extirpation near roads, and reduced forecasts for long-term population viability (Ramsden 2003, Martínez and Zuberogoitia 2004, Borda-de-Água et al. 2014), their effects on owl reproduction are less clear. Decreased distance to roads and increased length of roads around nests reduces occupancy of breeding pairs of Barn Owls in Spain, Israel, Canada, and Poland (Martínez and Zuberogoitia 2004, Charter et al. 2012, Hindmarch et al. 2012, Żmihorski et al. 2020), but Regan et al. (2018) found no effect of either on occupancy during winter and spring in southern Idaho. In some cases, there is no discernible effect of roads on productivity (Bond et al. 2004, Frey et al. 2011, Charter et al. 2012, Hindmarch et al. 2014), but in others roads reduce daily nest survival (Martin et al. 2010) or even increase fledging rates (Meek et al. 2009).

My objective was to assess the potential effects of roads on patterns of Barn Owl occupancy and reproduction in a population of owls in southern Idaho, USA. This population is of interest because it experiences some of the highest reported worldwide rates of roadway mortality (Boves and Belthoff 2012, Grilo et al. 2012, Belthoff et al. 2015, Arnold et al. 2019). Specifically, I investigated how distance to roads, and total length of roads around nest boxes, affected Barn Owl breeding occupancy and productivity.

Methods

Study Area

I studied Barn Owls using nest boxes in southwestern Idaho (43.6° N, 116.7° W), primarily in Ada, Canyon, Gem, and Owyhee counties. The study area spanned roughly 3,000 km^2 and was comprised mostly of agriculture (50%) and grasslands/pasture (30%) with a small amount of developed areas (10%), shrub/scrub (8%), and other land cover classes in low proportions. Nest boxes numbered > 300 per year (Figure 2.1) and were built and installed by Canyon County Weed and Pest Control in 2011 - 2021 as part of an integrated pest management program aimed at reducing gophers (*Thomomys* spp.) and other rodents. Boxes were of identical design, constructed of plywood, mounted ~ 4 m high on steel poles, and with the entrance hole facing northeast (Figure 2.2). They occurred along irrigation ditches and canals, within vineyards and orchards, on the borders of row crop fields and pastures, and occasionally in more residential and suburban areas.

Occupancy and Productivity

I monitored nest boxes from October 2019 to January 2022 to assess breeding occupancy and productivity during two breeding seasons (2020 and 2021). If owls were present during a visit I captured them by hand and marked them with uniquely numbered US Geological Survey metal leg bands (size 6 or 7A lock-on bands). During the breeding season (primarily April through July), I visited each nest box one or more times to assess breeding occupancy and count and band nestlings (Figure 2.3). Boxes were considered occupied for breeding if a nesting attempt occurred, which was defined as the laying of at least one egg. Because of the multiple visits to each nest box during and after the breeding season, I assumed detection for breeding occupancy was essentially perfect. If nestlings were too young to band upon any visit to a nest, I revisited at an appropriate time to band them before they reached an age characteristic of fledging. Because not all banded nestlings survived to fledge (pers. observ.), I revisited each nest box in the autumn (October through December) after the breeding season to count the number of nestlings that died between banding and fledging and thus remained in the nest box. Consumption of dead Barn Owl nestlings by siblings is uncommon and unlikely to occur in owls large enough to be banded (Hawbecker 1945, Lee 1998), thus I assumed cannibalism to be zero. During autumn follow-up visits to boxes I also 1) confirmed that nest boxes earlier assessed as unoccupied remained unoccupied for the duration of the breeding season or otherwise were occupied by a nesting pair, and 2) cleaned debris composed of trampled regurgitated pellets and prey remains typical of Barn Owl nests. I calculated productivity (number of fledglings) for each nest as the number of nestlings I counted in the breeding season minus the number of dead nestlings found in the nest box during the subsequent autumn. Additionally, I only included boxes in the productivity analysis that had reliable nestling counts, i.e., no evidence that fledging of some individuals could have already occurred before my first visit.

Statistical Analyses

To assess how breeding occupancy and productivity potentially varied as a function of roads, I used publicly available road data (U.S. Census Bureau 2016) to create four independent variables for each nest box. These variables were: 1) distance to the nearest road of any size, 2) distance to the nearest major road (interstates and U.S. and state highways), 3) total length of all roads within a 1-km radius, and 4) a binary variable indicating the presence or absence of major roads within a 1-km radius (Table 2.1). I also assessed several land cover composition variables that had previously been identified as important to Barn Owl reproduction (Leech et al. 2009, Wright 2018, Żmihorski et al. 2020, Huysman and Johnson 2021) using the National Land Cover Database (NLCD; Yang et al. 2018). These included proportions of 1) developed land, 2) shrub and scrub, 3) grassland and herbaceous, 4) pasture and hay fields, and 5) cultivated crops, all measured within a 1-km radius buffer similar to the road variables. I used a 1-km radius for calculating road and land cover variables based on Barn Owl reproductive studies by Frey et al. (2011) and Wendt and Johnson (2017) among others, and because it approximated a common home range size observed in the species (Arlettaz et al. 2010, Hindmarch et al. 2017). Lastly, I incorporated three temporal variables: 1) years since nest box installation, because Barn Owls may be more likely to occupy nest boxes the longer they have been established (Meyrom et al. 2009); 2) a categorical variable for year, given that breeding occupancy and productivity were assessed in both 2020 and 2021; and 3) nest initiation date in ordinal days, which was only relevant for the productivity analysis. Nest initiation date was the day that the first egg was laid, and was calculated by subtracting the estimated age of the oldest nestling plus 30 days incubation time from the visit date (Marti et al. 2005). Before analyzing data with models, I checked all continuous explanatory variables for correlation, but none exceeded the threshold of $|r| > 0.7$ (Dormann et al. 2013). All variables used in the models and their abbreviations are summarized in Table 2.1.

To assess factors that potentially affected Barn Owl breeding occupancy I used a generalized linear mixed model (GLMM) within a Bayesian framework with the *brms* package in R (Bürkner 2018). Given the binary nature of the response variable I used a Bernoulli distribution with a logit link. I assessed breeding occupancy (occupancy = 1) as a function of the distance to nearest road, distance to nearest major road, length of all roads, presence of major roads, developed land, shrub/scrub, grassland/herbaceous, pasture/hay, cultivated crops, years since installation, and year as fixed effects and nest box ID as a random intercept. All continuous variables were scaled for analysis. I used 1,000 warm-up iterations and 1,000 sampling iterations over four MCMC (Markov chain Monte Carlo) chains. I used weak priors for the fixed effects, using a normal distribution with a mean of 0 and a standard deviation of 2.5. For the fixed and random intercepts I used the default improper flat priors provided by *brms*.

I assessed factors that potentially affected Barn Owl productivity using another Bayesian GLMM. Because the variance of the response variable was equal to the mean I used a Poisson distribution and a log link. I used number of fledglings as the response variable with distance to nearest road, distance to nearest major road, length of all roads, presence of major roads, developed land, shrub/scrub, grassland/herbaceous, pasture/hay, cultivated crops, years since installation, year, and nest initiation date as fixed effects and nest box ID as a random intercept. I ran the model with identical scaling of variables, warm-up and sampling iterations, chains, and priors as in the model that assessed occupancy (see above).

To evaluate whether the models sampled the parameter space effectively I checked for convergence of the chains and verified that the potential scale reduction factors on split chains (Rhat) were < 1.01 (Gelman et al. 2013). I considered random effects warranted if the variance was greater than 0.05 (Shipley et al. 2020) and considered predictor variables to have a meaningful effect if their 90% credible interval failed to overlap zero. I assessed the fit of both models by first calculating a Bayesian approximation of the coefficient of determination (Bayesian R^2; Gelman et al. 2019). For the breeding occupancy model I additionally determined the correct classification rate (CCR) and calculated area under curve (AUC; Robin et al. 2011). An AUC value greater than 0.75 is considered good model fit whereas a value closer to 1 is considered excellent (Williamson et al. 2020). For the productivity model I also calculated root mean square error (RMSE). Although the variance of the random intercept in the occupancy model was high enough to warrant inclusion, it was well below 0.05 in the productivity model. Thus, I ran and present the results of the productivity model without the random intercept for nest box ID included. With a high AUC and CCR value and an acceptable Bayesian R^2 value, the model assessing occupancy as a function of road and land cover variables showed good fit, but the productivity model had a relatively low Bayesian R^2 value and only moderate RMSE. All analyses were run in R (R Core Team 2021). For descriptive statistics, I present all means in the results with ± one standard deviation.

Results

Occupancy, Productivity, and Timing of Nesting

Between October 2019 and January 2022, I visited 321 different nest boxes a total of 1,611 times. I banded 1,457 Barn Owls, recaptured 476 owls, and recovered 245 dead owls (primarily nestlings that did not survive to fledge). Breeding owls occupied 142 of 246 (58%) nest boxes and 224 of 306 (73%) nest boxes in the 2020 and 2021 breeding seasons, respectively. Occupancy was 66% when considering both years combined. Of the 245 individual boxes that I assessed both in 2020 and 2021, 71% remained in the same occupancy state from year to year (n = 128 boxes occupied in both years, n = 45 boxes unoccupied in both years), 24% went from unoccupied to occupied, and 5% went from occupied to unoccupied. Nests averaged 4.0 ± 2.2 fledglings (range: 0 – 8, n = 110 nests) and 3.5 ± 1.7 fledglings (range: 0 – 8, n = 115 nests) in 2020 and 2021, respectively, totaling 3.7 ± 2.0 fledglings (range: 0 – 8, n = 225 nests) across both breeding seasons (Figure 2.4). In 2020 and 2021, respectively, Barn Owls initiated nesting on 16 March ± 14 days (range: 18 February – 13 May, n = 110 nests) and 14 March ± 9 days (range: 17 February – 5 April, n = 115 nests; Figure 2.5).

Breeding Occupancy

Barn Owl breeding occupancy varied with the distance of the nest box to the nearest road of any size, the number of years since nest box installation, and the year monitored (Table 2.2). Specifically, when boxes were within 100 m of a road, probability of breeding occupancy was < 0.5, but probability of occupancy was > 0.9 as distance increased to > 500 m (Figure 2.6). When boxes were recently installed, probability of occupancy was around 0.3, but if they had been available for a decade probability of occupancy was ~ 0.8 (Figure 2.7). Occupancy was also lower in 2020 than in 2021 (Figure 2.8). The other variables that I examined had no meaningful effects on breeding occupancy (Figure 2.9).

Productivity

Barn Owl productivity was related to the distance of the nest box to the nearest road of any size, nest initiation date, and the year monitored (Table 2.3). When boxes were within 100 m of a road, Barn Owls produced around 3.5 fledglings but, as distance increased to > 500 m, number of fledglings increased to ~ 5 (Figure 2.10). Although distance had a reasonably low effect size, the approximately 40% increase in productivity across the entire range of distances is likely biologically meaningful. Barn Owls that initiated nests earlier in the breeding season were more productive; for example, nests initiated in February produced around 6 fledglings, whereas those in late April only averaged ~ 2 (Figure 2.11). Productivity was greater in 2020 than in 2021 (Figure 2.12). No other variables that I investigated had meaningful effects on productivity (Figure 2.13).

Discussion

Wildlife-vehicle collisions are perhaps the most readily observable negative effect of roads because animal carcasses sometimes persist for weeks for motorists to observe (Boves and Belthoff 2012). However, the less visible indirect effects of roads may still have significant consequences for avian populations. Notably, roads can affect reproduction, from lowering the probability that individuals may nest near roads to reducing post-fledging survival. For Barn Owls, roads and road mortality have been linked to population declines and local extirpation (Ramsden 2003), but effects on reproduction are less clear. My goal was to assess if and how the distance to the nearest roads (both major roads and those of any size), and their length and presence around nest boxes, affected Barn Owl breeding occupancy and productivity in southern Idaho, where owls are known to experience substantial roadway mortality. I found that as distance to the nearest road decreased, so did breeding occupancy and the number of fledglings produced.

Breeding Occupancy

In my study area in southern Idaho, USA, the probability of Barn Owl breeding occupancy more than doubled when comparing nest boxes adjacent to roads versus those a half kilometer away. Given that otherwise suitable nesting structures were available near roads, I believe that this is strong evidence that proximity to roads reduced the likelihood of owls initiating nesting. With similar results reported in Israel, where nest boxes are more likely to be occupied at farther distances from roads (Charter et al. 2012), and in Portugal, where Barn Owl occurrence is negatively associated with distance to major roads (Grilo et al. 2014), this relationship is not unique to southern Idaho. In contrast to my results, Regan et al. (2018) found that distance to road has no effect on occupancy during winter and spring in other locations in southern Idaho. However, there is also evidence that Barn Owls may be attracted to roadside verges (Hindmarch et al. 2017, Arnold et al. 2019), presumably for foraging, so it is possible that owls Regan et al. (2018) detected were not at their nesting location and rather hunting or traveling within their home range.

When assessing the potential impacts of roads on Barn Owl occupancy, the total length of road surrounding nesting sites has been important in several previous Barn Owl studies. For instance, in Canada, occupied breeding sites contain lower total lengths of roads (both highways and secondary roads) than unoccupied sites (Hindmarch et al. 2012), and similar patterns have been reported in Spain (Martínez and Zuberogoitia 2004), Switzerland (Frey et al. 2011), and Poland (Żmihorski et al. 2020). However, total length of road was not related to breeding occupancy in my study area. One potential factor was that my ability to detect a relationship could have been affected by the fact that total length of road was not substantially heterogenous across nest box sites in my study, especially when compared to variation in distance to nearest road. Indeed, Frey et al. (2011) attribute a lack of correlation between land cover characteristics and Barn Owl occupancy to relative homogeneity in their study area, and Hindmarch et al. (2012) suggest it may be because of overall high occupancy rates, both of which may have factored into my ability to detect a pattern between cumulative road length and owl occupancy.

My study joins others in suggesting that the presence of roads reduces breeding occupancy in Barn Owls. This effect may be mediated through Barn Owls avoiding nesting near roads because of traffic noise and its associated effects on foraging ability, increased mortality in owls using nest boxes near roads, or a combination of the two. Anthropogenic noise negatively affects nest site selection in other cavity-nesting birds (Halfwerk et al. 2016, Kleist et al. 2017), and Hindmarch et al. (2012) found that Barn Owls are less likely to occupy sites with increased traffic exposure. It is also possible that owls are avoiding the areas around roads because the associated noise negatively influences foraging; however, despite traffic and other anthropogenic noise reducing foraging efficiency in owls (Mason et al. 2016, Senzaki et al. 2016), Barn Owls can still be attracted to habitat along roads (Hindmarch et al. 2017) and rodent densities are not necessarily reduced in such habitat (McGregor et al. 2008, Arnold et al. 2019). Lastly, high rates of road mortality prevalent in Barn Owls (Belthoff et al. 2015), and especially in and near my study area in southern Idaho (Boves and Belthoff 2012), possibly reduced breeding occupancy near roads. For instance, Barn Owl pairs often roosted together in their respective nest boxes in the months prior to nest initiation (pers. observ.), so a road mortality in one or both members of the roosting pair over the winter could potentially reduce breeding occupancy in the subsequent spring if individuals were not able to repair or otherwise moved to different breeding locations after mortality of their mates.

Barn Owls in my study area were over twice as likely to occupy boxes that had been standing for eight or more years than those that had been installed prior to the breeding season they were monitored in. Thus, breeding occupancy in a particular nest box was affected by the number of years the nest box had been available. This finding mirrors other Barn Owl studies (Meyrom et al. 2009, Frey et al. 2011, Wendt and Johnson 2017), and perhaps reflects the time it takes for owls to discover and colonize newer boxes. Barn Owl breeding occupancy was also much higher in 2021 than in 2020. Boves and Belthoff (2012) reported significant inter-annual variation in the rates of Barn Owl road mortality in southern Idaho and postulated that this could reflect differences in breeding occupancy or success in the year preceding winter road mortality. My results confirm that annual breeding occupancy can vary substantially, and thus may contribute to variation in number of wildlife-vehicle collisions involving Barn Owls each year. These yearly differences in occupancy may be caused in part by changes in winter weather severity, which can reduce breeding attempts in the subsequent spring and decrease survival in Barn Owls (Marti 1994), or potentially by changes in the availability of unmonitored natural nesting sites (McClure et al. 2017).

Although I found that road proximity, installation date, and study year all influenced breeding occupancy in Barn Owls, there was no relationship with land cover surrounding nest boxes. Negative effects of developed land and scrub, and positive relationships with grasslands and agriculture are previously reported (Salvati et al. 2002, Martínez and Zuberogoitia 2004, Charter et al. 2012, Wendt and Johnson 2017, Regan et al. 2018, Żmihorski et al. 2020, Huysman and Johnson 2021). However, as in my study, others have found no discernable effect of habitat composition on Barn Owl breeding occupancy (Leech et al. 2009, Frey et al. 2011, Hindmarch et al. 2012). I believe the lack of a relationship between land cover and occupancy in my study may have been related to the high rates of occupancy and relatively low variability in landscape composition among nest boxes. It is also possible that more nuanced factors such as prey availability, microhabitat, or configuration/combination of land cover types play a role in breeding occupancy and could not be detected at the lower resolution of land cover composition.

Productivity

The productivity of Barn Owls decreased by approximately 1.5 fledglings when comparing nest boxes over a half kilometer away from the nearest road to those adjacent to roads. To my knowledge, this is the first study where roads have been correlated with decreased productivity in Barn Owls. In Florida, Martin et al. (2010) reported decreasing daily survival rates in nestling Barn Owls with major roads present within a 1,500 m radius, but the trend was not statistically significant. Counterintuitively, Meek et al. (2009) found that Barn Owl fledging rates actually increase with more roads present around nests, however, they suggest their findings may be spurious. Many previous studies have simply found no correlation between roads and productivity (Bond et al. 2004, Frey et al. 2011, Charter et al. 2012, Hindmarch et al. 2014). Although the factors responsible for variability in results are unclear, the especially high rates of road mortality observed near my study area may account for my unique results. It is also possible that lower rates of occupancy in other areas results in fewer owls nesting in marginal habitat near roads, leading to less pronounced differences in productivity.

There are several possible explanations for the negative relationship between road proximity and Barn Owl productivity that I observed: road mortality of parents may serve as a secondary source of nest decline or failure; nest sites closer to roads may be less desirable for owls and therefore relegated to younger, less experienced parents; or traffic and anthropogenic noise may reduce the ability of parents to attend to needs of their brood. Of the few occasions where I was able to confirm that a nest lost a parent during the breeding season in my study, none were able to fledge their full brood, and similar anecdotal evidence has been reported before in this species (Martin et al. 2010, Hindmarch et al. 2014). Barn Owls also appear less likely to occupy boxes closer to roads. Therefore, younger and less experienced owls may colonize these more marginal areas, as seen in other bird species and proposed in Barn Owls (Reese and Kadlec 1985, Reijnen and Foppen 1991, Habib et al. 2007, Reitsma et al. 2008, Hindmarch et al. 2014). Given that younger birds tend to have lower reproductive output (Ruthrauff 2002, Angelier et al. 2007), including in Barn Owls (Frey et al. 2011), it is possible that the smaller number of fledglings produced in proximity to roads related to younger and less experienced owls. Lastly, traffic and other anthropogenic noise associated with roads may have influenced the ability of parents to raise offspring in those sites closest to roads. Anthropogenic noise may deter or reduce hunting success in owls and ultimately the provisioning ability of parents (Mason et al. 2016, Senzaki et al. 2016), female American Kestrels (*Falco sparverius*) are more likely to abandon nests in higher disturbance areas close to roads (Strasser and Heath 2013), and parental nest attendance, visits, and feeding decline in species nesting closer to roads or exposed to disturbances such as recreationalists and their associated off-road vehicle use (Schroeder et al. 2012, Spaul and Heath 2016, Ng et al. 2019). Any combination of these effects may ultimately explain the reduced productivity of owls nesting closer to roads that I observed.

Barn Owls in my study area were more productive when nest initiation was earlier; owls that started nesting in late February produced over twice as many fledglings as nests initiated in April and May. This pattern of decreased productivity over time has been observed in Barn Owls before and may reflect a trend of younger birds initiating nests later than older, more experienced, owls (Frey et al. 2011, Charter et al. 2012). Lastly, there was a slight decline (< 1 nestling) in productivity between the 2020 and 2021 breeding seasons. It is possible that environmental conditions associated with drought and unseasonably hot weather in the 2021 breeding season contributed to this pattern, given that nestling survival is often reduced in nest boxes experiencing intense heat (pers. observ.). Summer high temperatures may also help explain the relationship between productivity and nest initiation date, because nests initiated earlier often fledge most of their offspring before prolonged high temperatures can reduce nestling survival (pers. observ.). It is also possible that the higher rate of occupancy in 2021 versus 2020 included more birds in marginal nest boxes where productivity declined, lowering the overall fledgling counts in the second year of my study.

Lower nest success and productivity in Barn Owls has been linked with increasing suburban, urban, and grassland cover (Bond et al. 2004, Meek et al. 2009, Hindmarch et al. 2014), but increased fledgling rates have also been observed with increasing grassland (Leech et al. 2009, Wright 2018). I did not detect any effect of land cover classes on productivity for owls in my study area in southern Idaho, which is similar to findings of Frey et al. (2011), Charter et al. (2012), and Wendt and Johnson (2017) in other regions. Thus, it appears that unaccounted for spatial factors, or perhaps weather patterns, could be influencing productivity more so than land cover composition, which was relatively homogenous across my study site.

<u>Conclusions</u>

Barn Owl populations in many portions of their range suffer extensive road mortality (Belthoff et al. 2015). Unfortunately, the negative effects of roads include a suite of factors beyond a direct source of mortality. Roads may alter demography through selective pressure, limit movement through barrier effects, and even increase extirpations via ecological traps (Ramsden 2003, Boves and Belthoff 2012, Borda-de-Água et al. 2014). There is also strong evidence that roads reduce breeding occupancy in Barn Owls in many portions of their global range (Charter et al. 2012, Hindmarch et al. 2012, Żmihorski et al. 2020), but the effects of roads on owl productivity have been less clear. My study not only affirmed that roads reduced breeding occupancy in an area with high road mortality rates, but it provided the first strong evidence that roads can be related to reduced productivity in this species as well.

These findings are worrisome because Barn Owls are a species of conservation concern in parts of Europe and North America, and they have recently seen their conservation status elevated in Idaho (Colvin 1985, Ramsden 2003, Idaho Department of Fish and Game 2017). A population viability analysis of Barn Owls in Portugal found that road mortality rates as low as 5% can reduce populations by up to 50% (Borda-de-Água et al. 2014) but, alarmingly, it has been argued that population declines in farmland birds is more closely tied to lower reproductive output than reduced adult survival (Newton 2004). Given the reduced rates of occupancy and productivity tied to roads in my study area, coupled with high rates of road mortality, it is possible that the viability of the local population is in jeopardy, especially considering expanding development and road networks in the region (Canyon County 2020). In light of these concerns, I suggest that future research focus on 1) the mechanisms driving road-related reductions in occupancy and productivity in Barn Owls; 2) how the various effects of roads on owls, including direct mortality, reduced occupancy and productivity, and limits to movement, interplay to affect the demography and trajectory of populations; and 3) what measures can be taken to mitigate the negative influences of roads on this species. As efforts are made to protect Barn Owls from roads, it will be important to consider not only measures that reduce direct mortality, but also the ways in which roads lower productivity and occupancy, to more fully ensure conservation success.

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Tables

Table 2.1 A list of predictor variables, including their names, modeling codes, and definitions, used in analysis of breeding occupancy and productivity of Barn Owls in southern Idaho, USA.

Name	Code	Definition
Distance to Nearest Road	all_dist	Distance of the nest box to nearest road of any size in m
Distance to Nearest Major Road	maj_dist	Distance of the nest box to nearest major road in m
Length of All Roads	all_length	Total length of all roads within a 1-km radius of the nest box in km
Presence of Major Roads	maj_pres	Categorical variable for the presence of major roads within a 1-km radius of the nest box, either yes or no
Developed Land	prop_dev	Proportion of land with a 1-km radius of the nest box that is classified as developed by the NLCD[1], including development of open space, and low, medium, and high intensity
Shrub / Scrub	prop_scrub	Proportion of land with a 1-km radius of the nest box that is classified as shrub/scrub by the NLCD
Grassland / Herbaceous	prop_grass	Proportion of land with a 1-km radius of the nest box that is classified as grassland/herbaceous by the NLCD
Pasture / Hay	prop_past	Proportion of land with a 1-km radius of the nest box that is classified as pasture/hay by the NLCD
Cultivated Crops	prop_ag	Proportion of land with a 1-km radius of the nest box that is classified as cultivated crops by the NLCD
Years Since Installation	ysi	Number of years since the nest box was installed. Calculated as the year that of the study (2020 or 2021) minus the year the nest box was installed.
Year	year	Categorical variable for the year that breeding occupancy was assessed, either 2020 or 2021
Nest Initiation Date	ordinal	Estimate of the ordinal date the first egg was laid, thus initiating the nest
Nest Box ID	box_ID	Unique identifier for each individual nest box

[1] National Land Cover Database (see Yang et al. 2018)

Table 2.2 A summary of the model investigating breeding occupancy (occupancy = 1) by Barn Owls in southern Idaho, USA as a function of road, land cover, and temporal covariates. Coefficient estimates, 90% credible intervals, standard error, variance of random effects, and metrics of models fit are shown. All continuous variables are scaled and codes for covariates are explained in Table 2.1.

Covariate	Estimate	5%	95%	SE	Variance
Intercept	0.52	0.06	1.00	0.29	
all_dist	0.92	0.50	1.39	0.27	
maj_dist	0.20	-0.24	0.65	0.27	
all_length	0.10	-0.43	0.65	0.33	
maj_pres (Yes)	0.86	-0.18	1.94	0.65	
prop_dev	-0.49	-1.50	0.46	0.60	
prop_scrub	-0.02	-0.51	0.48	0.30	
prop_grass	0.36	-0.51	1.22	0.53	
prop_past	0.63	-0.28	1.56	0.56	
prop_ag	0.63	-0.68	1.97	0.81	
Ysi	0.86	0.51	1.26	0.23	
year (2021)	1.35	0.88	1.85	0.30	
Random Intercept					6.30
Metrics of Model Fit:	**Bayesian R^2**	**AUC**	**CCR**		
	0.50	0.98	95.11%		

Table 2.3 A summary of the model investigating productivity (number of fledglings produced) by Barn Owls in southern Idaho, USA as a function of road, land cover, and temporal covariates. Coefficient estimates, 90% credible intervals, standard error, and metrics of models fit are shown. All continuous variables are scaled and codes for covariates are explained in Table 2.1.

Covariate	Estimate	5%	95%	SE
Intercept	1.35	1.26	1.44	0.06
all_dist	0.08	0.01	0.14	0.04
maj_dist	0.07	-0.02	0.15	0.07
all_length	0.08	-0.00	0.15	0.08
maj_pres (Yes)	0.12	-0.05	0.30	0.11
prop_dev	0.04	-0.07	0.15	0.07
prop_scrub	0.06	-0.04	0.15	0.06
prop_grass	0.09	-0.09	0.28	0.11
prop_past	0.07	-0.12	0.27	0.12
prop_ag	0.11	-0.15	0.37	0.16
ysi	0.01	-0.05	0.07	0.04
ordinal	-0.21	-0.27	-0.15	0.04
year (2021)	-0.17	-0.30	-0.06	0.07
Metrics of Model Fit:	**Bayesian R^2**	**RMSE**		
	0.26	1.72		

Figures

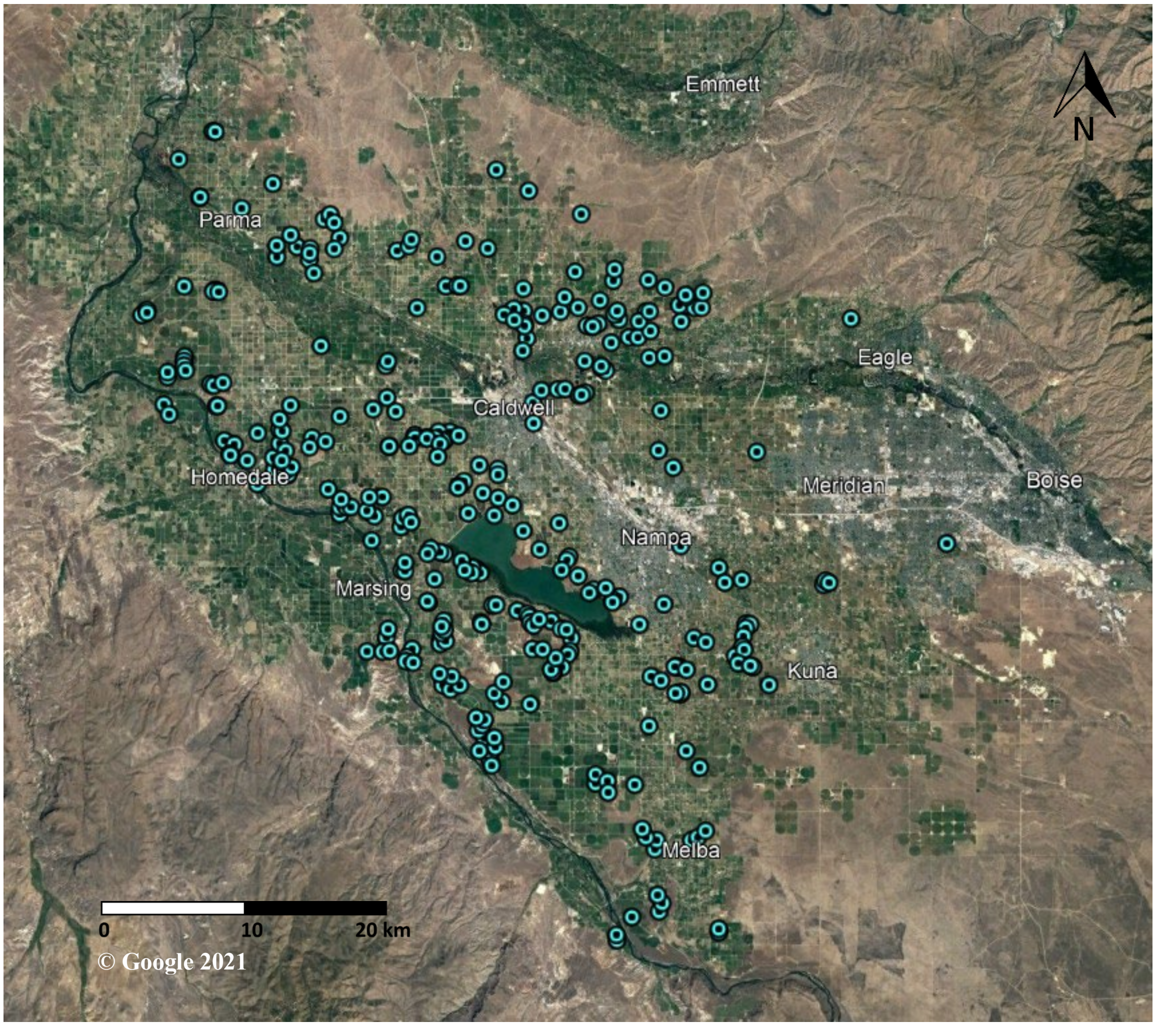

Figure 2.1 The location of Barn Owl nest boxes monitored during 2019 – 2022 to observe breeding occupancy and productivity in relation to roads in Canyon County and surrounding areas in southern Idaho, USA.

Figure 2.2 A Barn Owl nest box installed by Canyon County Weed and Pest Control adjacent to an agricultural field in southern Idaho, USA.

Figure 2.3 A view from inside a nest box containing six Barn Owl nestlings in southern Idaho, USA. Beneath the owls the typical debris (regurgitated pellets, prey remains, and owl waste) that accumulates and requires periodic removal by investigators is apparent.

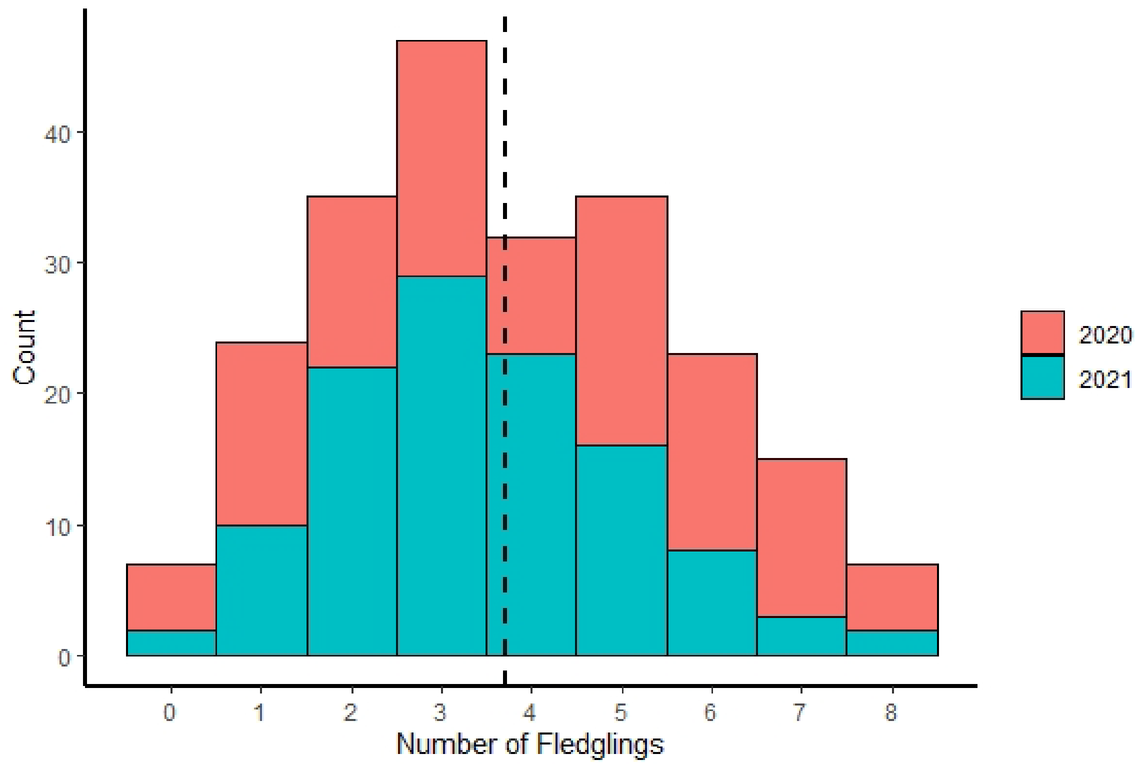

Figure 2.4 A histogram showing the number of fledglings per nest for Barn Owl nests in southern Idaho, USA in 2020 (red) and 2021 (teal). The vertical dashed line represents the mean for both years combined.

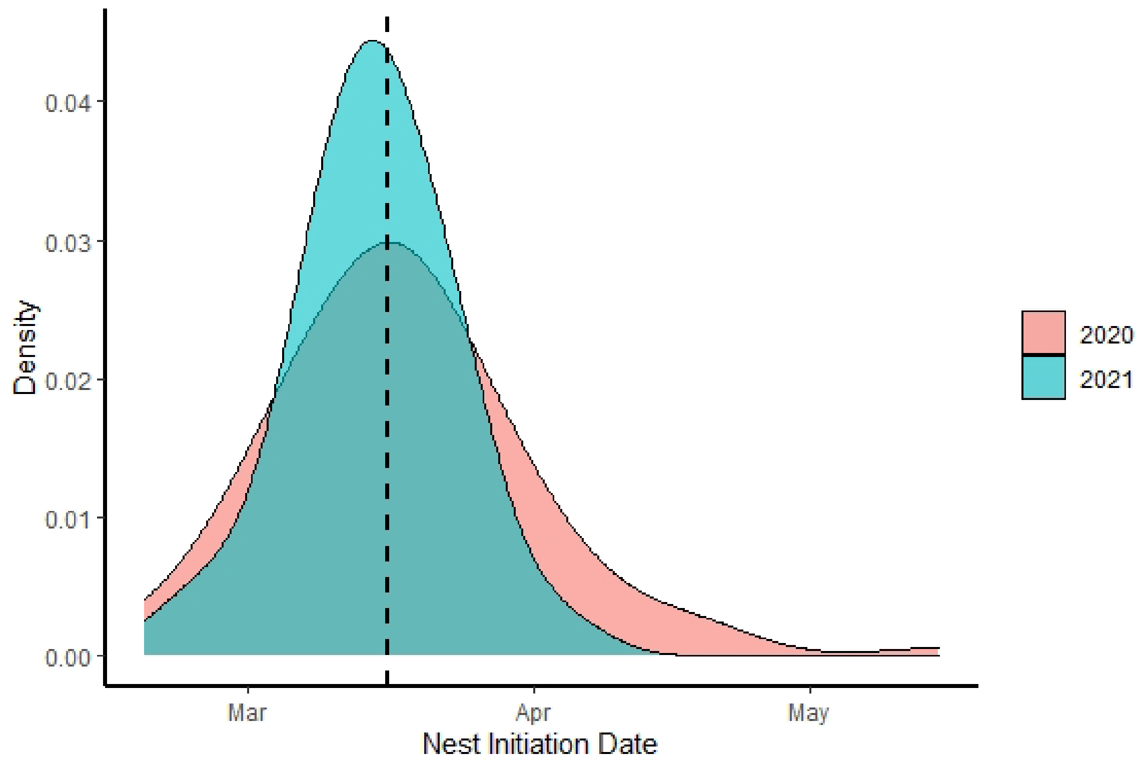

Figure 2.5 A density plot showing the nest initiation dates for Barn Owl nests in southern Idaho, USA in 2020 (red) and 2021 (teal). The vertical dashed line represents the mean for both years combined.

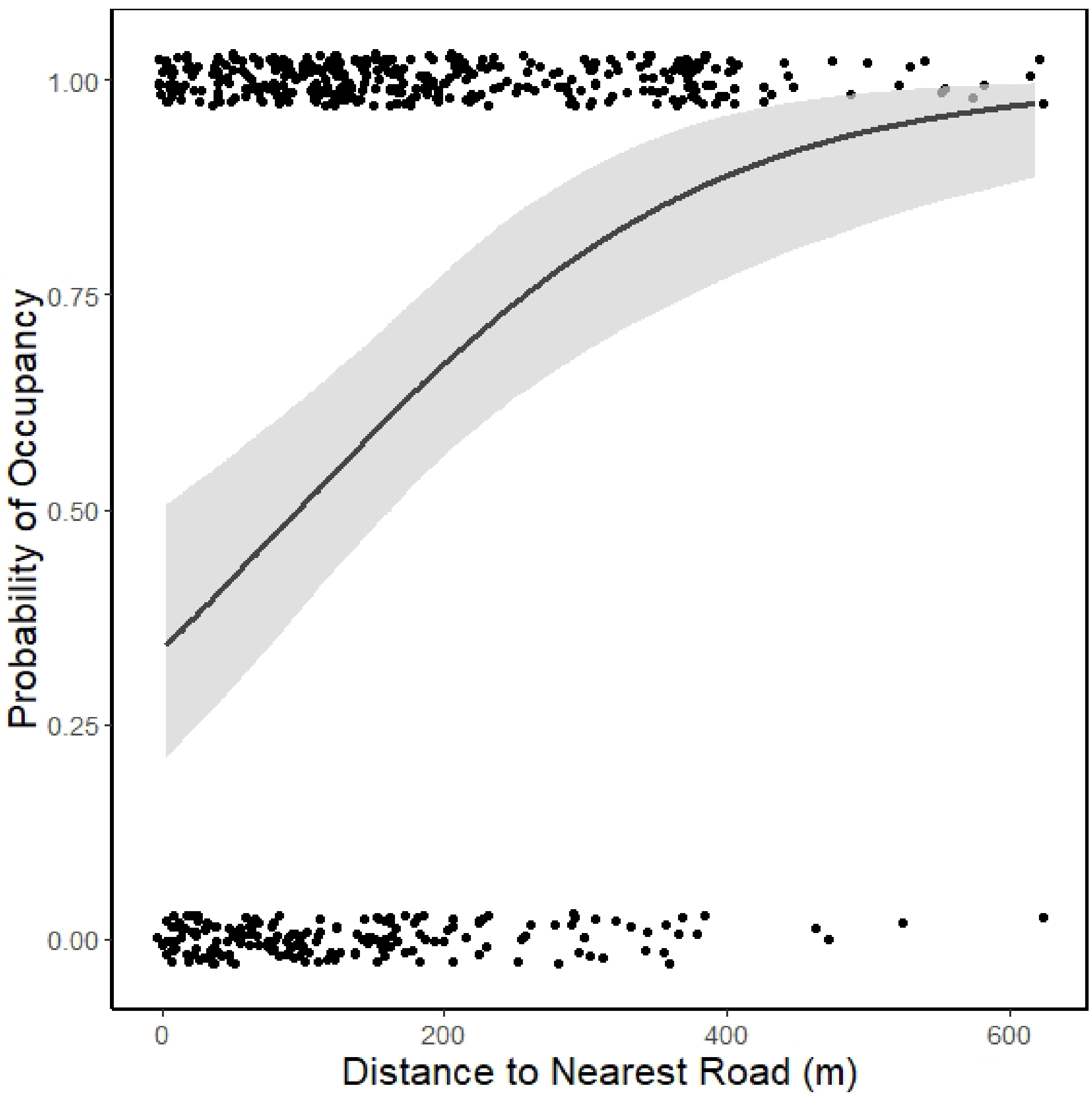

Figure 2.6 The probability of breeding occupancy in Barn Owls in southern Idaho, USA as a function of distance to nearest road with a 90% credible interval and actual data points displayed. Other continuous variables are held at their mean, presence of major roads is "No", and year is 2020 for illustration.

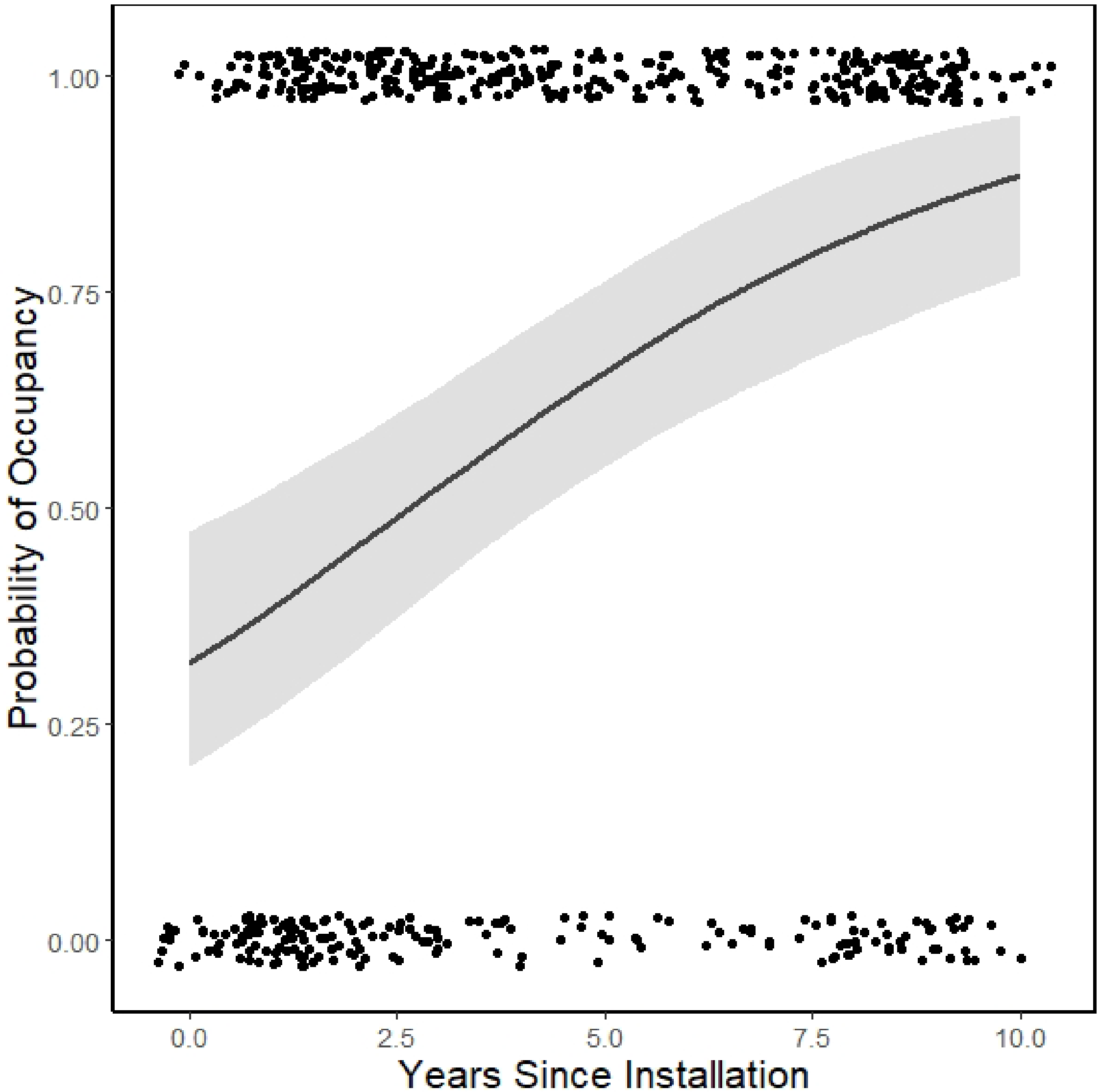

Figure 2.7 The probability of breeding occupancy in Barn Owls in southern Idaho, USA as a function of years since a nest box was installed with a 90% credible interval and actual data points displayed. Other continuous variables are held at their mean, presence of major roads is "No", and year is 2020 for illustration.

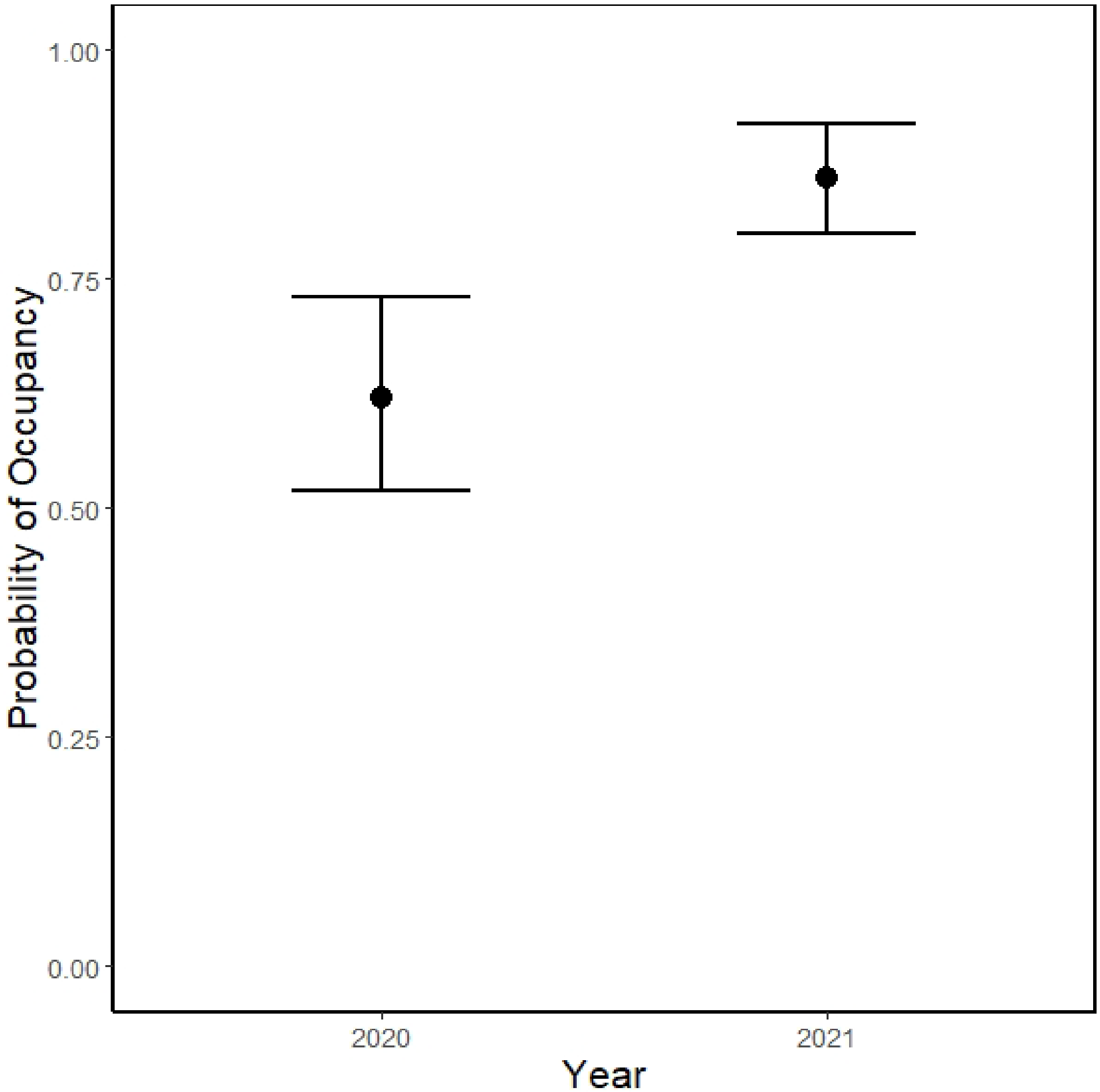

Figure 2.8 The probability of breeding occupancy in Barn Owls in two years in southern Idaho, USA with 90% credible intervals. Continuous variables are held at their mean and presence of major roads is "No" for illustration.

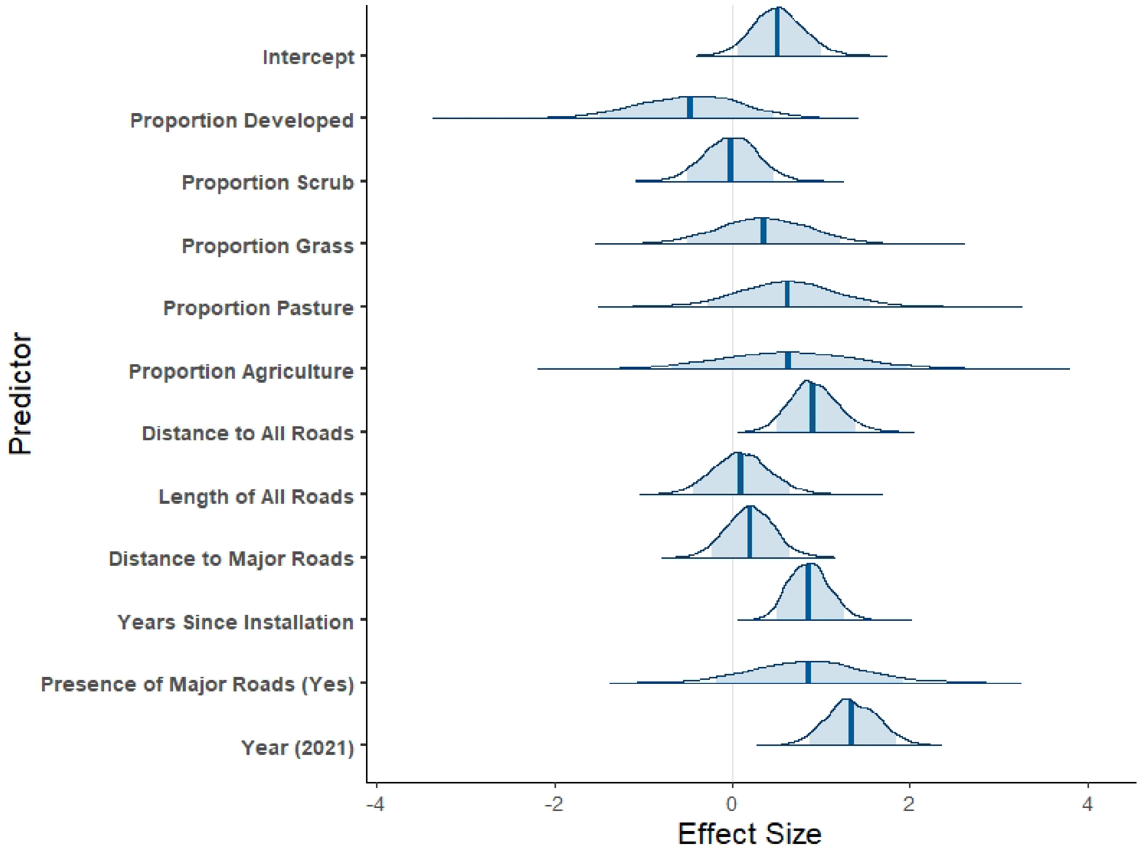

Figure 2.9 A plot of the parameter estimate distributions for the variables of the breeding occupancy model. Dark blue lines indicate the mean estimates, and the shaded blue areas represent values within the 90% credible intervals.

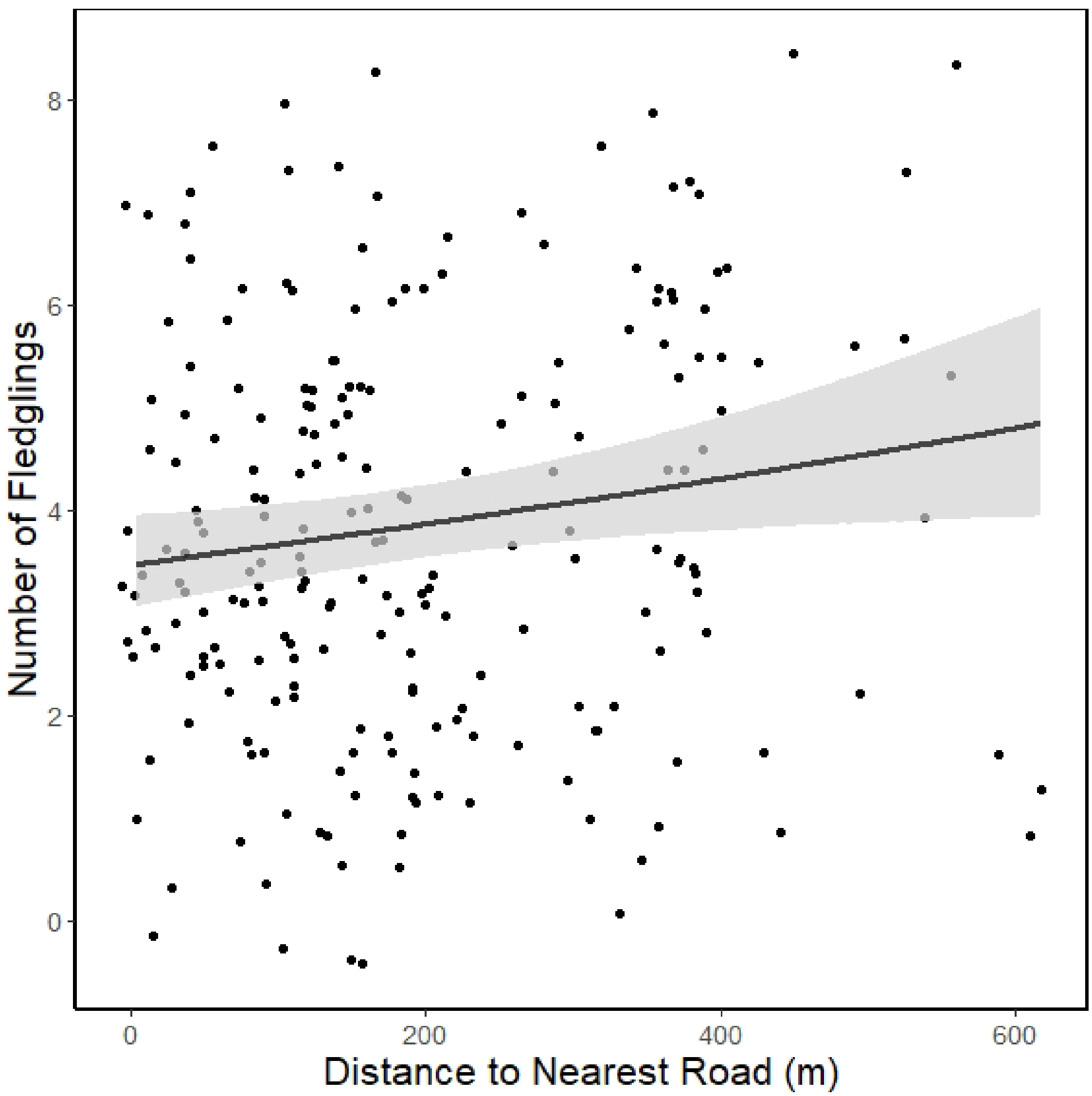

Figure 2.10 Barn Owl productivity (number of fledglings) as a function of distance to nearest road in southern Idaho, USA with a 90% credible interval and actual data points displayed. Other continuous variables are held at their mean, presence of major roads is "No", and year is 2020 for illustration.

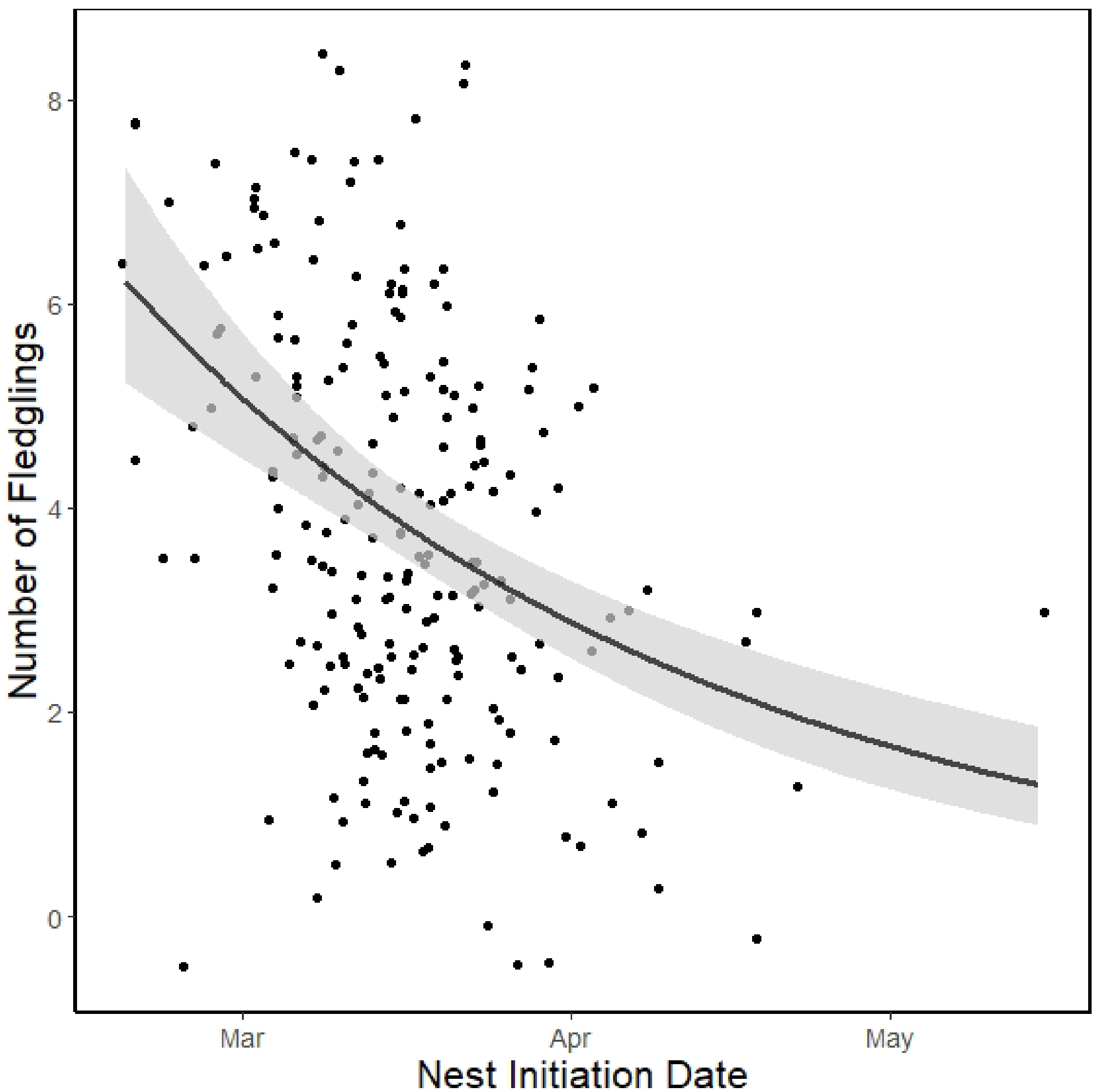

Figure 2.11 Barn Owl productivity (number of fledglings) as a function of nest initiation date (date of first egg) in southern Idaho, USA with a 90% credible interval and actual data points displayed. Other continuous variables are held at their mean, presence of major roads is “No”, and year is 2020 for illustration.

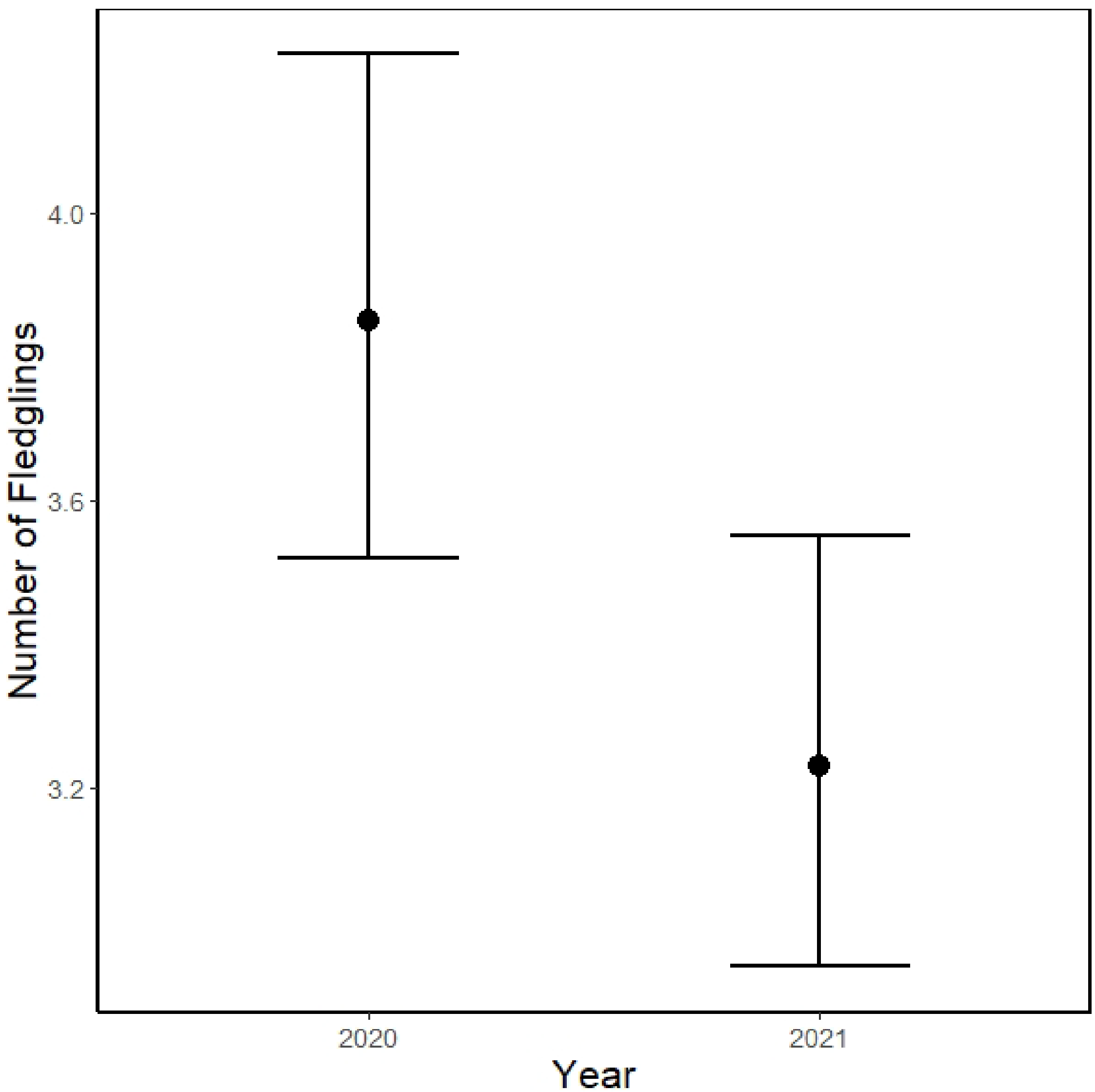

Figure 2.12 Barn Owl productivity (number of fledglings) in two years in Barn Owls in southern Idaho, USA with 90% credible intervals. Continuous variables are held at their mean and presence of major roads is "No" for illustration.

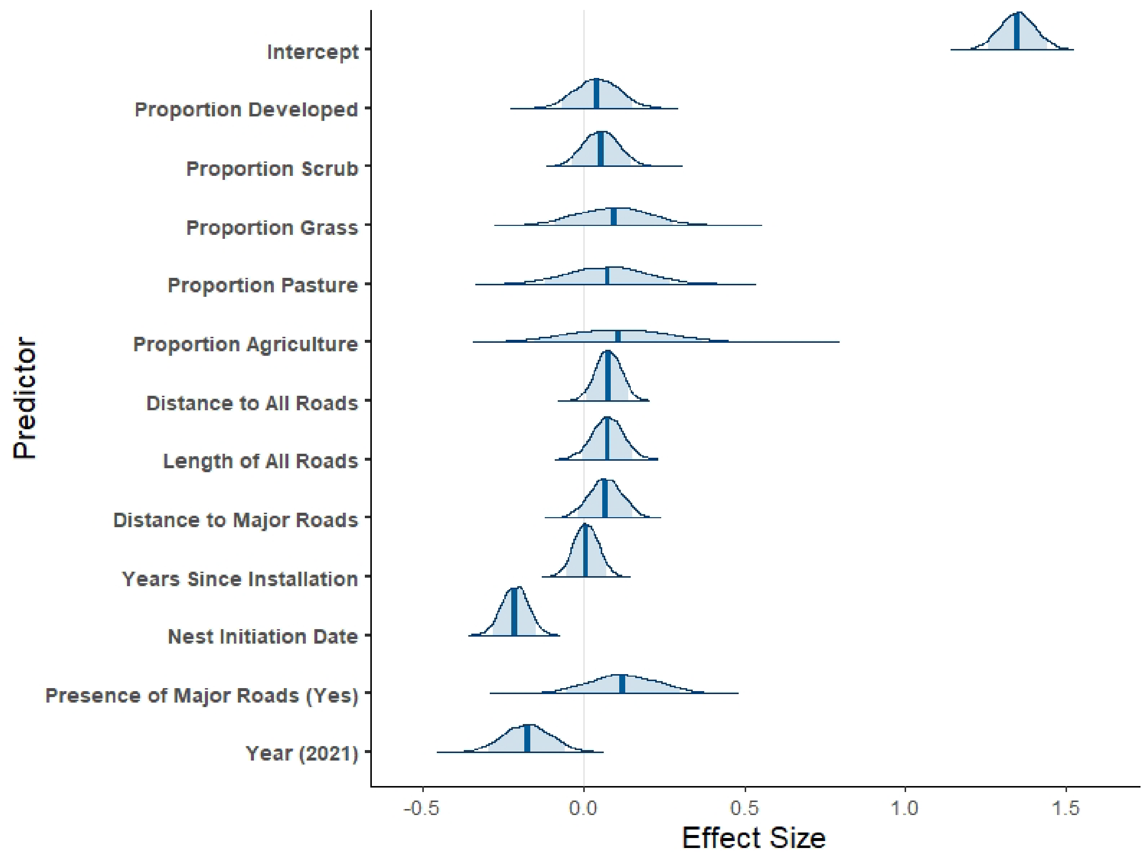

Figure 2.13 A plot of the parameter estimate distributions for the variables of the productivity model. Dark blue lines indicate the mean estimates, and the shaded blue areas represent values within the 90% credible intervals.