

**The effect of road density and proximity on predation attempts on the white footed mouse
(*Peromyscus leucopus*)**

By

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A thesis submitted to

The Faculty of Graduate Studies and Research

In partial fulfillment of

the requirements for the degree of

Master of Science

Department of Biology

Carleton University

Ottawa, Ontario

August 2013

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ABSTRACT

Some authors have hypothesized that observed increases in small mammal populations with increasing road density (after controlling for habitat effects) may be due to predation release. Predation, especially predation by birds, could be reduced in areas with high road density, because of negative effects of roads on predator numbers and/or hunting activity. However, there are no studies testing the relationship between road density and predation rate on small mammals. Based on the predation release hypothesis, I predicted that *Peromyscus leucopus* placed in sites with higher surrounding paved road density and/or closer to a paved road would experience fewer predation attempts than *P. leucopus* placed in sites with lower surrounding paved road density and/or farther from a paved road. Considering all predators, there was no evidence of any decrease in predation attempts in relation to paved road density, but the credible interval was wide, and the possibility of a biologically relevant increase could not be ruled out. Considering only raptorial birds there was evidence of a decrease in predation attempts with paved road density, and an increase with increasing distance from the road, as predicted. However, the number of raptors was small and this change was not observed for the more numerous specialist mammalian predators. Overall, these results provide at best weak support for the hypothesis that reduced predation, specifically by birds, causes the positive relationship between road density and small mammal abundance.

ACKNOWLEDGEMENTS

I would like to start by thanking my supervisor Dr. Lenore Fahrig, for her support, guidance and most importantly patience throughout the course of my project. Your knowledge and expertise enabled me to excel at all tasks and kept me encouraged throughout. Thank you for the time and funding that you have put into my project, being part of your lab has been an incredible experience.

I would also like to extend my appreciation and thanks to my advisory committee members, Dr. David Currie and Dr. Stephen Cooke for your feedback during our meetings. I would like to thank Dr. Charles Francis and Dr. Adam Smith of the National Wildlife Research Center, for your assistance with some of the advanced statistics. I would like to thank Dan Bert for his technical support both in the lab and the field. Thank you to Dave Omond for sharing your knowledge and time during the design and construction phases of the enclosures. Lastly, I would like to thank Trina Rytwinski for all your help throughout my project. Your expertise and knowledge on small mammals and guidance enabled me to remain on track.

A special thank you goes out to NSERC student Victoria Gerber and volunteer Oda Waldeland, who provided assistance in the field. I enjoyed working with you and wish you both the best in the future. I realize that some days were long and less than perfect, but your dedication to helping me succeed is sincerely appreciated.

Thanks to all members of the Geomatics and Landscape Ecology Laboratory for your help and suggestions during the analysis and writing. Special thanks to Sara, Sandra, Pauline and Paratsu for your occasional tutorials and chats! It was encouraging to know that I was not alone through this whole process.

I would also like to extend my love and thanks to my friends and especially my family. I am forever grateful for your love and support. Colleen, thank you for helping me in the field and for your visits throughout my time in Ottawa. Mom, Dad and Michelle, thank you for all the long talks and words of encouragement. Lastly, I would like to thank Taylor Curley for always being there for me. I would never have gotten through some difficult days without you. You were all so supportive and provided a needed distraction from my thesis. Thank You.

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INTRODUCTION

A literature review on the effect of roads on animal population abundance and distribution discovered that most (approx. 59%) populations show negative effects of roads (Fahrig and Rytwinski 2009). Negative effects of roads on populations are thought to result from increased mortality (Forman and Alexander 1998; Kocielek et al. 2011), population fragmentation (Forman and Alexander 1998, Trombulak and Frissell 2000) and traffic disturbance (Forman and Alexander 1998; Lode 2000). Species that are most negatively affected by roads include birds which mainly show negative effects (Findlay and Houlahan 1997; Findlay and Bourdages 2000), midsized mammals which generally show either negative or no effect (Altrichter and Boagilo 2004; Mowat 2006; Roedenbeck and Voser 2008), and large mammals which show predominantly negative effects (Newmark et al. 1996; Fahrig and Rytwinski 2009, Rytwinski and Fahrig 2011).

Although most effects of roads on population abundance and distribution are negative, the literature review by Fahrig and Rytwinski (2009) found that around 29% of populations are unaffected and that roughly 12% of populations are positively affected by roads. Small mammals generally show either positive or no effect. It has been suggested that species that avoid going onto roads, have small territories, high reproductive rates and a high tolerance for road disturbance, should show no effect of roads on population persistence (McGregor et al. 2008). Road avoidance reduces road mortality, and species with small territories and high reproductive rates are able to sustain populations within road-bounded areas (Jaeger et al. 2005). Positive effects of roads may occur for species for which roads provide food (Knight and Kawashima 1993; Meunier et al. 2000; Lambertucci et al. 2009), nesting sites (Haxton 2000; Steen et al. 2006) or basking sites (Rosen and Lowe 1994). Roads may also indirectly cause increases in

abundances of animals whose predators are negatively affected by roads, the predation release hypothesis (Johnson and Collinge 2004; Rytwinski and Fahrig 2007; Fahrig and Rytwinski 2009).

A possible example of predation release occurs in *Peromyscus leucopus*, the white-footed mouse. Rytwinski and Fahrig (2007) found higher population abundances of *P. leucopus* in forest sites situated in landscapes with higher road density than in sites in landscapes with lower road density. Rytwinski and Fahrig (2007) observed a 56% increase in mouse relative abundance with an increase of 1 km/km² in road density. They tested various possible explanations, involving habitat or food availability, for this unexpected result. None was supported and they concluded that the positive effect of roads on mice may be explained by a predation release effect, as predator populations may be more susceptible than small mammal populations to road effects, or their hunting activity may be disturbed by traffic. Predation release has been proposed several times as a possible explanation for the positive effects of roads on small mammal species (Johnson and Collinge 2004; Rytwinski and Fahrig 2007; Bissonette and Rosa 2009; Fahrig and Rytwinski 2009), as well as the white tailed deer (*Odocoileus virginianus*) (Munro et al. 2012).

While the predation release hypothesis has not been directly tested, it seems to be supported in studies demonstrating stronger negative effects of roads on large mammals than on small mammals (Rytwinski and Fahrig 2011, 2012). Since larger species are often the predators of smaller species, it is possible that the negative effects of roads on larger mammals could lead to reduced predation in areas of high road density. Strong negative effects of roads on predatory birds have also been demonstrated (Newton et al. 1991; Trombulak and Frissel 2000; Bautista et al. 2004), with the exception of carrion feeders, such as ravens and some raptor species (Colman and Fraser 1989). With small mammal populations being highly influenced by predatory birds

(Sinclair et al. 1990; Cheveau et al. 2004; Paz et al. 2013), it is possible that negative effects of roads on avian predator populations could lead to reduced predation and higher abundance of small mammals in areas of high road density.

The objective of this study was to determine whether the positive effect of road density on population abundance of *P. leucopus* reported by Rytwinski and Fahrig (2007) could be caused by predation release. I tested this hypothesis by placing individual *P. leucopus* in wire mesh enclosures within forest patches selected to represent a range of road densities in the surrounding landscapes. I recorded predation attempts on the *P. leucopus* in the enclosures using motion triggered cameras. I predicted a decrease in predation attempts with increasing road density, if the predation release hypothesis explains the positive effect of roads on *P. leucopus* abundance.

Life History and Predators of *Peromyscus leucopus*

Peromyscus leucopus is a semi-arboreal, nocturnal mammal that prefers deciduous forest habitat with dense cover and features such as logs, stumps and rocks (Barry and Franq 1980). The travel routes of *P. leucopus* include coarse woody debris (CWD) such as fallen logs, branches, stumps and snags (Dueser and Shugart 1978; Barnum et al. 1992; Panz and Kirkland 1992) and it is thought that CWD is used as navigational aids and foraging sites (Wolff and Hurlbutt 1982; Drickamer and Stuart 1984). It has been suggested that CWD reduces the risk of predation, since it makes detection by auditory predators more difficult (Fitzgerald and Wolff 1988; Barnum et al. 1992; Roche et al. 1999). The diet of *P. leucopus* is diverse and changes seasonally. Insects, seeds, fruit and vegetation are the primary foods. The breeding season

extends from March to October with peaks in spring and late summer. Postnatal growth is completed within 2 months of birth. The range of *P. leucopus* extends from Southeastern Canada and Eastern US to Southern Saskatchewan and Montana, south to Arizona.

As a prey source, small mammals, including *P. leucopus*, compose part of the diet of many species including both specialist and generalist predators (Korpimaki and Krebs 1996; Salo et al. 2010). Specialist predators, such as weasels (*Mustelidae*) and owls (*Strigiformes*) are well adapted to killing and hunting rodents, which serve as their main source of food (Watson 1957; Erlinge et al. 1974; Erlinge 1975). Generalist predators exploit a wide range of food items and feed on small mammals when they are easily available (Anderson and Erlinge 1977). These predators include foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*), among others (Englund 1965; Ryszkowski et al. 1973). However, generalist predators do not necessarily rely on small mammals for a large proportion of their diet. For example, small mammals make up only about 1% of the diet of raccoons (Schoonover and Marshall 1950; Rivest and Bergeron 1980).

Predatory birds are likely one of the main predators of small mammals. Many studies have found that small mammals make up the majority of prey biomass in the diet of predatory birds (Korschgen and Stuart 1972; Korpimaki and Norrdahl 1991). However, whether this predation is sufficient to drive small mammal abundances depends on whether bird predation is a large part of mortality of small mammal populations. Studies examining the effects of avian predators on small mammal populations have produced mixed results (Erlinge 1987; Desy and Batzli 1989; Ylonen et al. 1991; Norrdahl and Korpimaki 1995). Erlinge (1987) and Desy and Batzil (1989) found an impact of avian predators on small mammal populations while Yolen et al

(1991) and Norrdahl and Korpimaki (1995) concluded that predatory birds alone are not likely to regulate prey populations in the long term but may cause short term changes in their population dynamics.

METHODS

Site Selection

This study was conducted in Eastern Ontario, Canada, between May 8th and August 18th 2012, using a subset of 28 of the 36 focal forest patches surveyed for *P. leucopus* abundance by Rytwinski and Fahrig (2007, 2009). The focal patches were located within rural landscapes that varied widely in paved road density (0.27-1.69 km/km²). Each landscape was defined as the area within a 2-km radius from the center of each focal patch (Figure 1). This size of landscape was based on reports of individual *Peromyscus sp.* traveling more than 1 km (Diffendorfer and Slade 2002; Howard 1960, Bowman et al. 1999).

The sites were selected to maximize the variation of paved road density among the surrounding landscapes while controlling for variables other than paved road density that might affect abundance of *P. leucopus* (Rytwinski and Fahrig 2007, 2011). Selected landscapes contained 25-35% forest, no water (i.e., no rivers or lakes) and no railways. Focal patches were all larger than 1 ha and of similar forest type (deciduous or mixed deciduous). Landscapes with lower and higher paved road densities were distributed across the Ottawa region and Eastern Ontario as much as possible to avoid any effects of regional trends (Figure 2). In addition I measured the distance from the experimental sites within the focal patches to the nearest paved road. The correlation between the paved road density in the surrounding 2-km radius landscapes and the distance to the nearest paved road was -0.381.

Trapping of Mice

The *P. leucopus* individuals used in the predation experiment (see below) within a given focal patch were obtained by trapping mice in that patch immediately preceding the experimental two-day period for that patch. Traps were placed in the focal patch the night prior to the experimental period and left for approximately 24 hours. If three mice were not obtained, trapping continued for a second night and the start of the experimental period was delayed by one day. I used 30 (20.32 x 7.62 x 10.16 cm) Sherman traps, placed against a fallen log or a stump, and baited with one teaspoon of peanut butter on a 5 x 5 cm piece of waxed paper. A slice of apple (3 x 3 cm) was also placed in the trap and cotton batting was added for warmth and shelter. Trapped mice that were pregnant or lactating were not used in the predation experiment.

Predation Attempts

To estimate the number of predation attempts at each site I placed each of the three trapped mice (above) from the site in one of three wire mesh enclosures. A fourth enclosure was included as a control to ensure that predators were attracted to the mouse rather than the enclosure itself. The four enclosures were placed a minimum of 40 m and a maximum of 200 m from each other and from the edge of the forest. Mice were left in the enclosures for 48 hours while two video cameras recorded predation attempts. Given that I had 28 sites to ensure an adequate gradient in road density, I was only able to sample predation attempts for one 48-hour period at each site. I randomized the order in which sites were visited, to avoid any potential correlation between road density and seasonal trends in predation attempts. After the experimental 48 hour period, the mice were released at their location of capture.

The enclosures were built to allow predators to detect the mouse visually or by olfaction. The enclosures were 38.1 x 30.48 x 30.48 cm, mounted on a 1.22 x 1.22 m piece of plywood.

The top and sides were covered with 12.7 mm steel mesh (Figure 3). The top was hinged at the halfway point to allow for the addition of the mouse, food and new bedding as needed. All metal, with the exclusion of the steel mesh, was painted black using an odorless outdoor paint (BEHR Premium Plus) to limit light reflection. Inside each enclosure I covered the floor with substrate from the surrounding forest including leaves, twigs and grasses, and I placed a fist sized ball of cotton batting in the enclosure. Half a cup of black oil sunflower seeds was also added for food. I checked on the enclosures daily for structural damage and to provide *P. leucopus* with additional seeds, vegetation and cotton as needed. The control enclosure was treated identically to experimental enclosures, except for the absence of a mouse. The control enclosure was rotated, such that each enclosure served as the control enclosure at seven of the 28 sites.

To monitor predation attempts on the mice, I used Moultrie I40XT Game Spy Digital infrared-triggered game cameras, which provided both still shots and video footage (Cutler and Swann, 1999; Swann et al., 2004). The motion triggered cameras detect the difference between the ambient background temperature and heat energy caused by a moving animal. Two cameras were directed at each enclosure. The cameras were mounted on trees at a 90° angle from each other at a height of 40 cm above the ground and at an approximate distance of 2 m from the enclosure (Swann et al., 2004). Each camera was leveled and focused on the enclosure and the surrounding approx. 50 m² area. The sensitivity of the cameras was set to high, the video duration to 20 seconds and the video delay for the re-set of the camera to 60 seconds.

Potential Confounding Variables

In addition to paved road density and distance to the nearest paved road, several potential confounding variables were measured to control for their effects. These included site characteristics (number of woody tree species, percent cover of coarse woody debris (CWD), and

mean tree diameter at breast height (DBH)), focal forest patch size, percent forest in the landscape, and Julian date. The site characteristics were taken from Rytwinski and Fahrig (2007, 2011) (Appendix 1); see Rytwinski and Fahrig (2007, 2011) for vegetation survey methods. Although our experiment was conducted 3-5 years following these measurements, I assumed they would have changed slowly enough to be still representative of relative differences among the sites. Paved road density, size of the focal patch and percent forest in the landscape were taken from Ontario Ministry of Natural Resources thematic data (Forest cover: Ontario Ministry of Natural Resources 2010, Road density: Ontario Ministry of Natural Resources, Ontario Road Network 2012), and quantified using ESRI ArcView 10 (Environmental Systems Research Institute, Redlands California). Paved road density was the total length of paved roads within each 2 km radius landscape, divided by the total area of the landscape (km/km^2). I also calculated total road density (including paved, gravel and dirt roads). Below I report results for paved road density only; results using total road density were qualitatively identical to the results for paved road density.

Data Analysis

Three response variables were examined: the total number of predation attempts by all species, the number of predation attempts by specialist predators (i.e., excluding raccoons and skunks), and the number of predation attempts by raptorial birds. Data for the three enclosures containing a mouse in each focal patch were combined, producing one value for each response variable for each focal patch. The "raw" number of video clips could not be used to represent the number of predation attempts because occasionally the camera recorded the mouse moving with no predator present, or it recorded a passing non-predator animal (e.g. a deer). Therefore, all video clips were filtered to ensure that they contained a predator on or approaching the

experimental enclosure. In addition, a difficulty in quantifying the number of predation attempts from the video footage was that the same predation attempt by the same individual predator could be recorded in subsequent video clips if the individual remained at the enclosure for more than the 60 second video delay period. I was concerned that this might inflate the apparent number of predation attempts at sites containing a very persistent individual predator. Since predators were not marked, I could not identify individuals. However, I reasoned that a large time gap between video clips of the same species of predator indicated either that the predator went away and then returned later to make another predation attempt or that a different individual predator of the same species made the second attempt. I therefore reduced the number of sequential same-species predation attempts by applying a minimum time gap between same-species predation attempts. I tried different minimum time gaps (5, 10, 20, 60, 120 minutes between video clips of the same species). The estimates using different time gaps were highly correlated (Table 1), and using different minimum time gaps did not qualitatively change our results. Therefore I present only the analyses using the 20 minute minimum time gap.

The numbers of predation attempts by each of the three species groups were analysed using an over-dispersed Poisson regression with a log-link on the predictor variable. The model was implemented in a hierarchical Bayes framework using WinBUGS and the R2WinBugs interface. An uninformative (uniform) prior was placed on all parameters including the regression coefficients. To determine an expected change in predators under the predation release hypothesis, the slope of the relationship between mouse numbers and the predictor variable (paved road density or log-transformed distance to nearest paved road) was estimated from the mouse data in Rytwinski and Fahrig (2007, 2011) for the sites used in this study, using an over-dispersed Poisson model with a log-link. For paved roads, the slope on a log scale was

estimated at 0.41 (which corresponds to a 1.5x increase ($e^{0.41}$) in mouse populations for every 1 km / km² increase in road density). For log distance to nearest road, the slope was -0.21. It was assumed that a similar or greater proportional change in predation attempts in the opposite direction (i.e., on a log scale, a -0.41 slope in relation to paved road density, or a +0.21 slope or greater in relation to log distance from road) would be sufficient to result in a predator release effect.

I calculated the correlations between the potential confounding variables - percentage CWD, number of tree species, mean tree DBH, size of the focal patch, amount of forest in the surrounding landscape, and Julian date - and paved road density and distance to the nearest paved road to determine which of these might explain some variation in predation attempts, thus potentially masking an effect of paved road density or distance to the nearest paved road.

– I performed the statistical analyses using SPSS version 19.0 and WinBUGS 1.4.

RESULTS

Altogether there were 1039 video clips showing predation attempts, at 25 of the 28 focal patches. This translated into 257 predation attempts using the minimum 20 minute minimum time gap between successive predation attempts by the same predator species. Predation attempts were converted to the number of attempts per enclosure-day at each site, to account for the fact that at three sites I was only able to trap two (rather than three) mice. I recorded predation attempts by seven predator species (Table 2; Figure 4). 98.8% of recorded predation attempts were made by mammals. Most (88% of all attempts) were made by raccoons (*Procyon lotor*). I recorded only three predation attempts by avian predators, each at a different focal patch (Table 2).

All correlations between the potential confounding variables and both paved road density and log (distance to nearest paved road) were weak (all $\leq |0.4|$; Table 3). Therefore, effects of road density or distance to nearest road on predation attempts were unlikely to have been confounded by these factors. Control enclosures were much less likely to attract predator species than enclosures containing a mouse; 6% of video clips were recorded at control enclosures.

For all predator species combined, there was no evidence of a relationship between predation attempts and paved road density (Figure 5, $\beta = 0.03$, 95% C.I. -1.1 to 1.2). However, given the imprecision of the estimate, the probability that the true slope was less than -0.41 was still 22%, thus the hypothesis of a reduction in predation attempts could not be ruled out. In contrast, the total number of predation attempts decreased with the log of the distance to nearest road (Figure 6, $\beta = -0.9$, 95% C.I. -1.6 to -0.3), contrary to the prediction of the predation release hypothesis. Given these data, the probability that the number of predation attempts increased away from roads was < 0.01 .

Considering only raptorial birds, there was evidence of a decline in number of predation attempts by birds with increasing paved road density (Figure 7, $\beta = -7.6$, 95% CI -31.9 to -0.21), as predicted under the predation release hypothesis, with strong evidence that the decline was more than -0.41 (probability 0.97). Similarly, there was evidence that the number of bird predation attempts increased with increasing distance from roads (Figure 8, $\beta = 2.4$, 95% CI -0.1 to 33.5), with a probability of 0.96 that the increase was greater than 0.21. However, only 3 raptor predation attempts were detected during the study, many fewer than for mammalian species.

Considering both mammalian and avian specialist predation attempts combined, there was more evidence in favour of an increase in predation attempts with increasing road density than the predicted decline (Figure 9, $\beta = 1.0$, 95% CI -1.7 to 3.8). Again, however, given the imprecision in the estimates, the possibility of a decline with a slope less than -0.41 was still 0.13 indicating that a reduction in predation attempts could not be ruled out. In contrast, the relationship between specialist predation attempts and log of road density was in the predicted direction with an apparent increase (Figure 10, $\beta = 0.7$, 95% CI -1.1 to 2.7), and a probability of 0.70 that the increase was greater than the 0.21 predicted. However, the credible intervals were wide and the probability of a decrease was still 0.22.

Scatter plots suggested a negative effect of Julian date and a positive effect of mean tree DBH on the total number of predation attempts (Figures 11, 12).

DISCUSSION

The purpose of this study was to test the hypothesis that the positive response of *P. leucopus* (and possibly other small mammal species) abundance to road density in the surrounding landscape (Adams and Geis 1983; Rosa and Bissionette 2007; Rytwinski and Fahrig 2007; Rytwinski and Fahrig 2011) is due to a negative effect of roads on predation on small mammals (predation release), due to a negative effect of roads on the abundance and/or activity of small mammal predators. The effects of increased road density on large mammalian predators and predatory bird populations through road mortality or disturbance are well documented (Trombulak and Frissel 2000; Gibbs and Shriver 2002; Forman et al. 2003; Bautista et al. 2004, Rytwinski and Fahrig 2009). Yet empirical evidence of the negative effect of road density on predation attempts is lacking. I examined the possibility of predation release by comparing the

number of predation attempts on *P. leucopus* in 28 focal patches situated in landscapes ranging widely in road density.

Contrary to initial predictions, I found no significant relationship between paved road density or distance to the nearest paved road on the number of predation attempts directed toward *P. leucopus* (Figure 5 and 6). There was no evidence of an overall decline in predation attempts with increasing road density and proximity to roads. However, the sampling variance was quite high, and, given the observed data, the possibility of a decline big enough to affect prey populations could not be ruled out. I suggest it is unlikely that this lack of effect was due to confounding variables. Past studies have found that road density is often highly correlated with other land cover variables including for example the percent of forest within the landscape (Houlahan and Findlay 2003). In my site selection the percent of forest in the landscape was controlled to within a relatively narrow range (18-38%), and it was weakly correlated with paved road density ($r=-0.022$) and distance to nearest paved road ($r=0.199$). Therefore, variance in landscape-scale forest cover is unlikely to have masked an effect of paved road density or distance to nearest paved road on small mammal predation attempts. There were also no significant correlations between paved road density or distance to nearest paved road and any of the other potentially confounding variables I measured – number of tree species, mean tree DBH, % CWD, focal patch area and Julian date. It is therefore unlikely that they masked an effect of paved road density or distance to the nearest paved road on the number of predation attempts directed towards *P. leucopus*.

A possible reason for the overall lack of effect of paved road density or distance to nearest paved road on predation attempts in this study is that small mammal abundances are not limited by predation by larger mammals. The vast majority of predation attempts I recorded were

by mammalian predators (98.8% of attempts). This may be an over-estimate of the actual proportion of attempts by mammals, for two reasons. First, the cameras used for my study would not detect predation attempts by snakes because they are designed to be triggered by changes in body heat and therefore cannot detect the movements of ectothermic animals. Small mammals are thought to be the primary food source of snakes, including snakes in our area such as the black rat snake (*Elaphe obsolete obsolete*); a study on the black rat snake in Eastern Ontario found mammalian prey in 64% of fecal samples (Weatherhead et al. 2003) and Fitch (1963) found that the diet of black rat snakes is 66% mammalian. However, the black rat snake is rare in our study area (Weatherhead et al. 2003), and other snakes in our area are non-forest species (Eastern Garter snake (*Thamnophis sirtalis sirtalis*), Northern Water snake (*Nerodia sipedon sipedon*), Eastern Milk snake (*Lampropeltis triangulum*)). Therefore, our conclusions would not likely change if we had been able to monitor predation attempt by snakes. The second reason the study may have over-estimated the proportion of predation attempts by mammals is that our cameras, being aimed at the enclosures containing the mice, may have missed many predation attempts by birds, which may have been attracted to the mouse but able to determine from a distance above it, e.g. perched above the enclosure, that it was inaccessible and therefore did not come down to within the view of the cameras.

Since most recorded predation attempts were by mammals and I did not find strong evidence for fewer predation attempts in landscapes with higher paved road density, my results suggest that the positive effect of roads on *P. leucopus* abundance is probably not due to release from predation by mammalian predators. In their empirical study in our region, Rytwinski and Fahrig (2011) found that negative effects of roads on abundance increase with increasing mammal body size. From this they hypothesized that the positive effects of road density on small

mammals could be due to release from predation by larger mammals. My results do not support this hypothesis. One possible explanation is that the main mammalian predators I recorded were generalist species, particularly raccoons, which were responsible for 88% of all predation attempts recorded. Since raccoons, and skunks would not normally be able to capture unrestrained full-grown mice (though they likely will eat the young), it seems likely their impact on mouse populations would be less than that of more specialized predators such as weasels, fishers and cats. Raccoons have readily adapted to human-dominated landscapes, finding abundant food and artificial den sites in them (Hadidian et al. 1991; Prange et al. 2003). Food sources such as corn and soy are likely responsible for the higher abundances of raccoons in agricultural landscapes with a mix of forest and croplands (Pedlar et al. 1997). The apparent decline in predation attempts over the season (Figure 12), at the same time that the population of raccoons would have been increasing, supports the notion that small mammals are not a critical component of their diet (Prange et al. 2003). It is also likely that the higher road mortality on raccoons in human-dominated landscapes is counter-balanced by reductions in recreational hunting and commercial trapping in these landscapes (Riley et al. 1998).

Although the overall results from my study do not support the hypothesis that predation attempts on small mammals by mammalian predators decline with increasing paved road density or proximity to nearest paved road, they do tentatively support the same notion for predation attempts by predatory birds. Raptorial birds (hawks and owls) are particularly efficient mouse predators, and did show significant evidence of a decline in numbers with increasing road density. However, we recorded only three predation attempts by raptors were detected, so this conclusion is tentative. In addition, this decline in predation attempts by raptors was more than offset by the lack of decline (or even a possible increase) in abundance of specialized

mammalian predators (weasels, fishers, cats) which are also likely to be very efficient mouse predators. The small sample size of bird predation attempts (only three recorded) resulted in low statistical power for this test. However, all three of these attempts were made at sites in landscapes with lower road density and farther from the nearest paved road (Figures 7 and 8). We therefore suggest that our results are at least consistent with the notion that the positive effect of roads on *P. leucopus* abundance is due to a reduction in abundance and/or activity of predaceous birds in landscapes with high road density (Paruk 1987; Anthony and Isaacs 1989; Martinez and Zuberogoitia 2004; Boves and Belthoff 2012; Silva et al. 2012). Silva et al. (2012) suggested that Little Owls and Tawny Owls in Portugal are less abundant or absent near roads with high traffic density. They found adverse effects of roads on owl abundance for up to 2 km away from the road. Martin (1990) suggested that, in areas with increased noise such as occurs near high-traffic roads, predatory birds rely more on vision for hunting; the headlights of passing vehicles may thus contribute to reduced hunting ability. Headlights appear to affect nocturnal species which fly low and can be stunned by the bright lights (Loos and Kerlinger 1993; Jackson 2002), and are known to disrupt foraging and breeding behaviour in birds (Hill 1992). Overall my results suggest that further study of the predation release hypothesis for the positive effects of roads on small mammal abundance should focus specifically on predation by avian predators.

Conclusion

This is the first study to test the hypothesis that the positive relationship between small mammal abundance and road density is caused by predation release in areas of higher road density. Our results do not support the hypothesis of predation release from mammalian predators in areas of high paved road density, but they are suggestive of release from predation by avian predators. Future research should be directed specifically at predation release from

avian predators as an explanation of the higher abundance of small mammals in areas of high road density.

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Table 1. Pearson correlations between number of predation attempts using different minimum time gaps between same-species recordings. n=28.

	20 Minutes	60 Minutes	120 Minutes
5 Minutes	0.916	0.873	0.876
20 Minutes		0.973	0.924
60 Minutes			0.957

Table 2. Predator species recorded making predation attempts on *P. leucopus* placed in enclosures.

Species Name		Number of Predation Attempts
Raccoon	<i>Procyon lotor</i>	227
Domestic Cat	<i>Felis catus</i>	12
Ermine Weasel	<i>Mustela erminea</i>	9
Striped Skunk	<i>Mephitis mephitis</i>	3
Fisher	<i>Martes pennanti</i>	3
Red-Tailed Hawk	<i>Buteo jamaicensis</i>	1
Eastern Screech Owl	<i>Megascops asio</i>	1
Barred Owl	<i>Strix varia</i>	1

Table 3. Pearson correlations between potentially confounding variables and paved road density and distance to the nearest paved road. n=28

	Paved Road Density	log(distance to paved road)
# Tree Species	-0.130	0.092
Mean tree DBH (cm)	-0.084	-0.401
% CWD	0.197	-0.332
% Forest in Surrounding Landscape	-0.022	0.199
Focal Patch Area	0.168	-0.196
Julian Date	0.136	-0.447

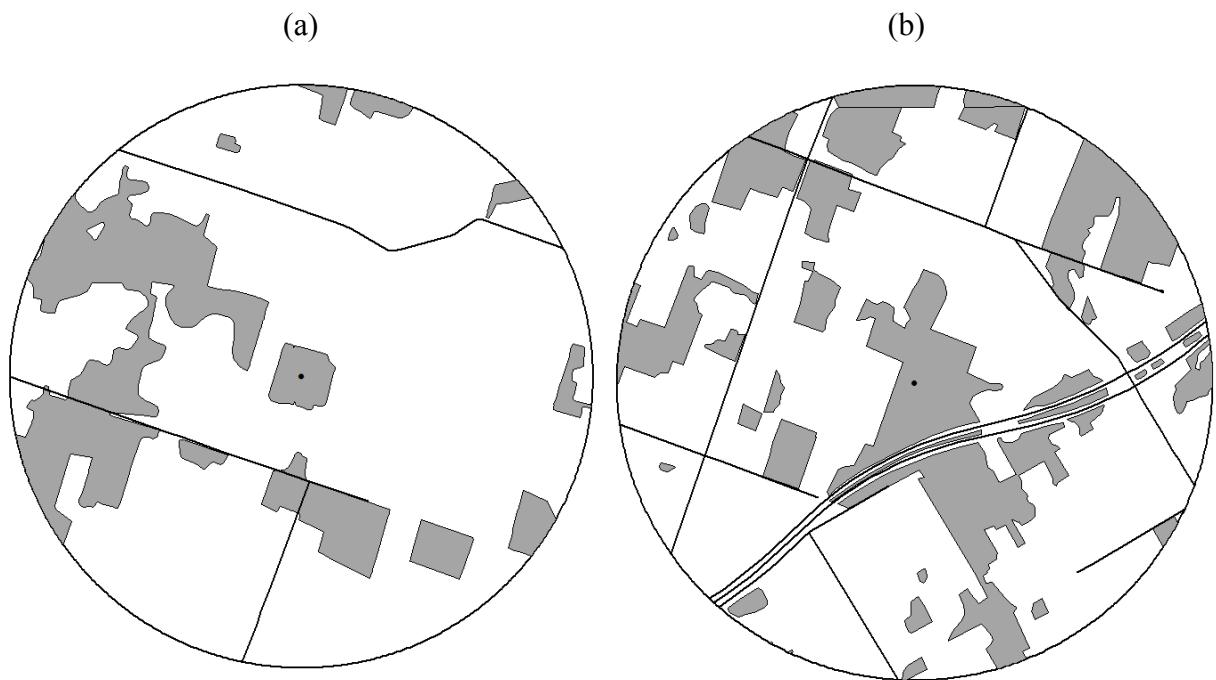


Figure 1. Examples of two of the 28, 2-km-radius landscapes surrounding experimental sites (black dots in the centers) within focal forest patches. Sites were selected to create a gradient in paved road density in the surrounding landscapes: (a) has low paved road density and (b) has high road density. Grey represents forest cover and black lines represent roads.

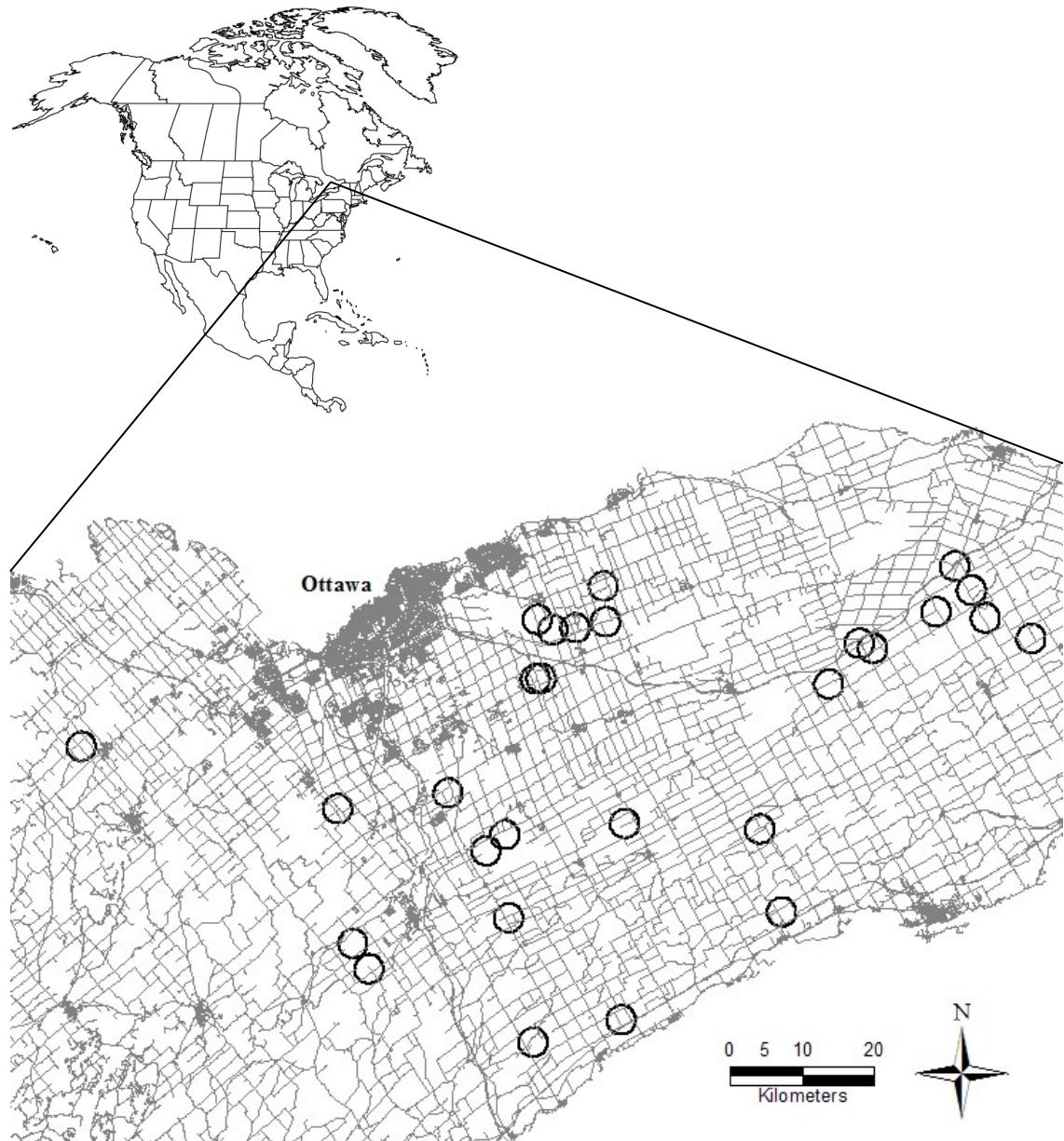


Figure 2. Distribution of 28 2-km radius circular study landscapes across the Ottawa region.

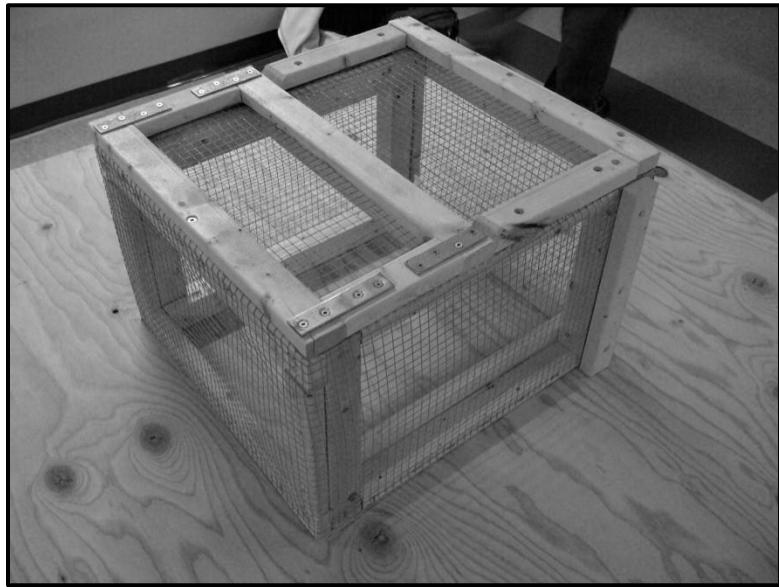


Figure 3. One of the four enclosures, showing the wire mesh on all four sites and the top. The hinged top allowed insertion and removal of a mouse, its food, and grass, litter and cotton batting.

(a)



(b)



(c)



Figure 4. Example photos of predation attempts on *Peromyscus leucopus*. (a) Raccoon (*Procyon lotor*); (b) Fisher (*Martes pennanti*); (c) Red-Tailed Hawk (*Buteo jamaicensis*)

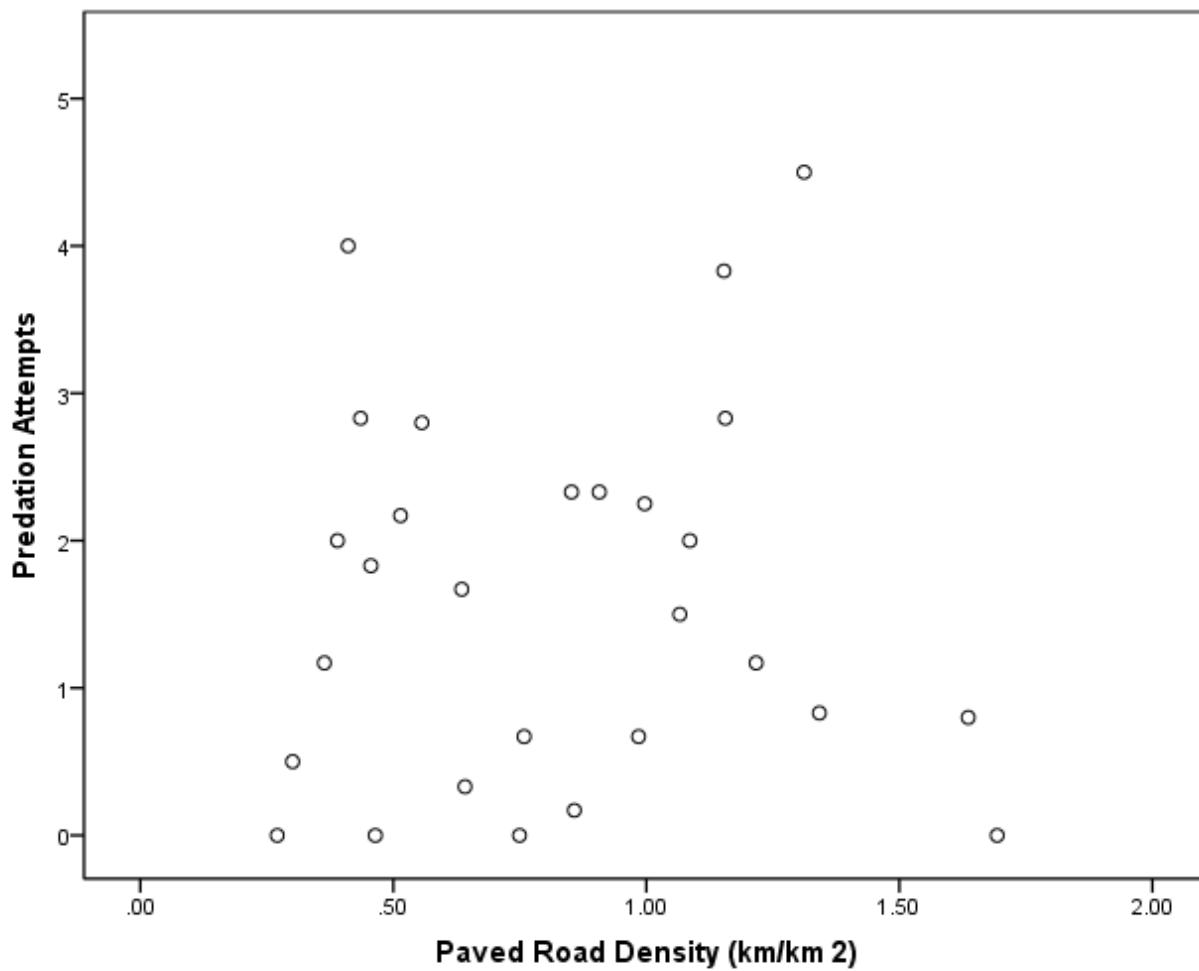


Figure 5. Number of predation attempts per enclosure-day on *Peromyscus leucopus* in experimental enclosures vs. paved road density (km/km^2) in the surrounding 2-km radius landscapes. Each point represents data from an experimental site.

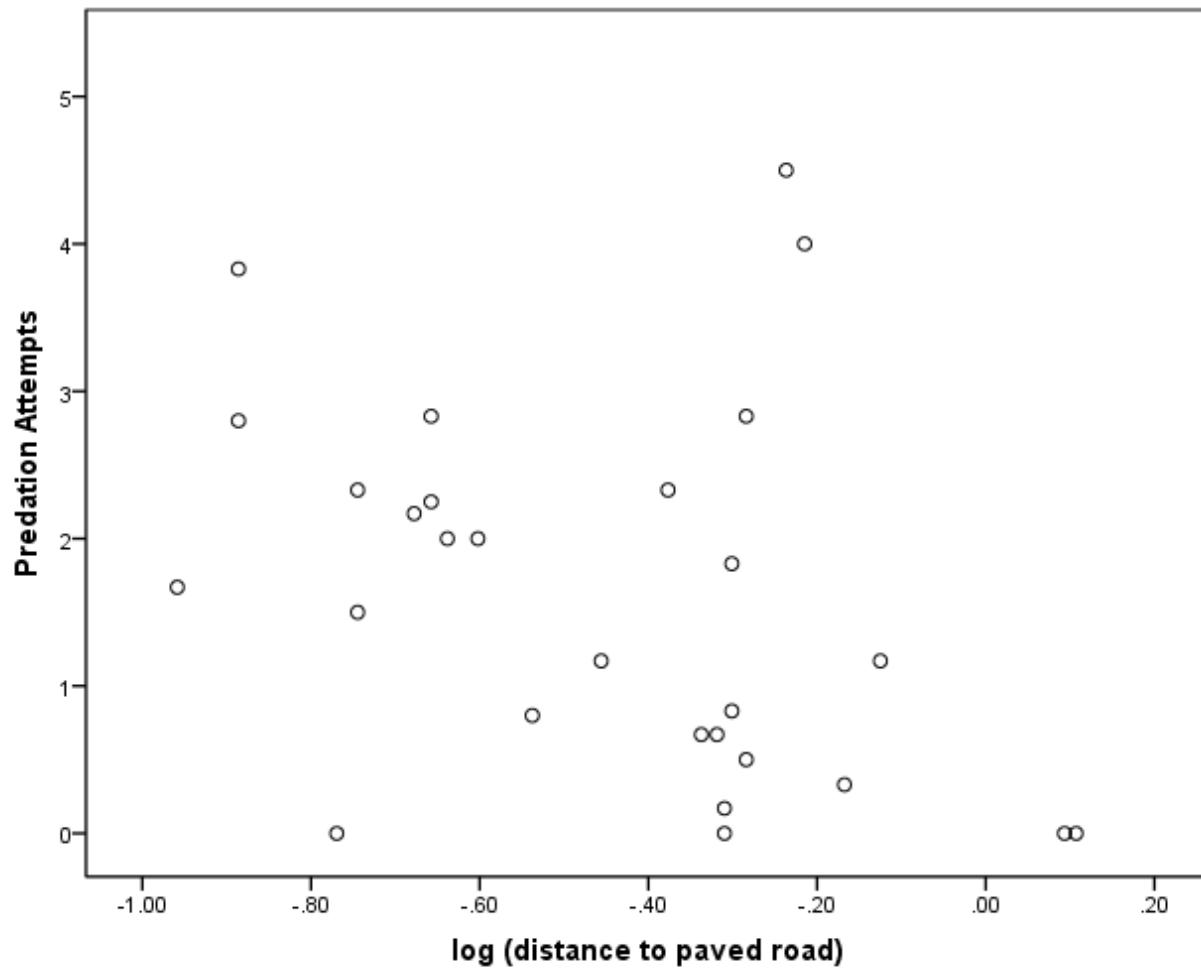


Figure 6. Number of predation attempts per enclosure-day on *Peromyscus leucopus* in experimental enclosures vs. log (distance to nearest paved road). Each point represents data from an experimental site.

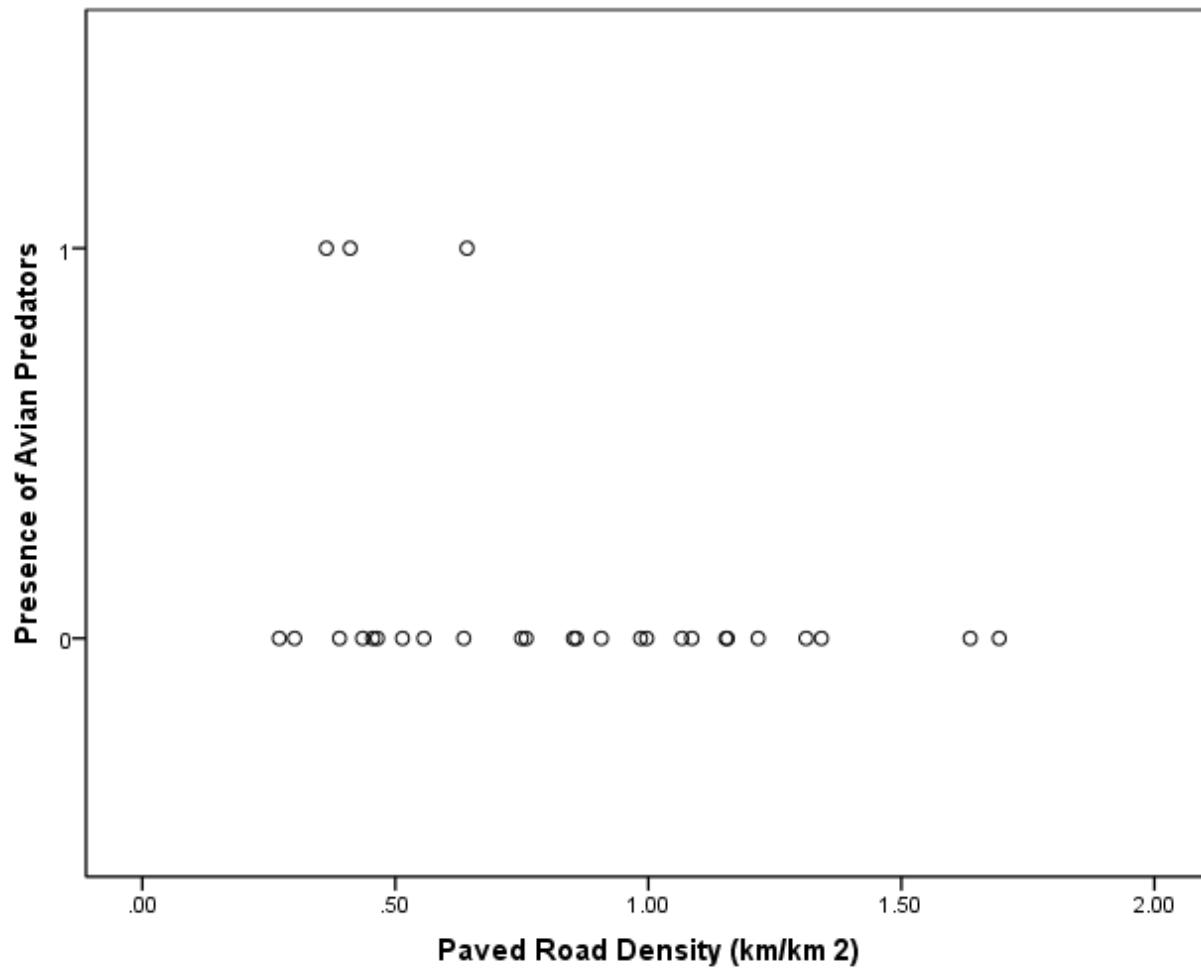


Figure 7. Presence of avian predators vs. paved road density in the surrounding 2-km radius landscapes. Each point represents data from an experimental site.

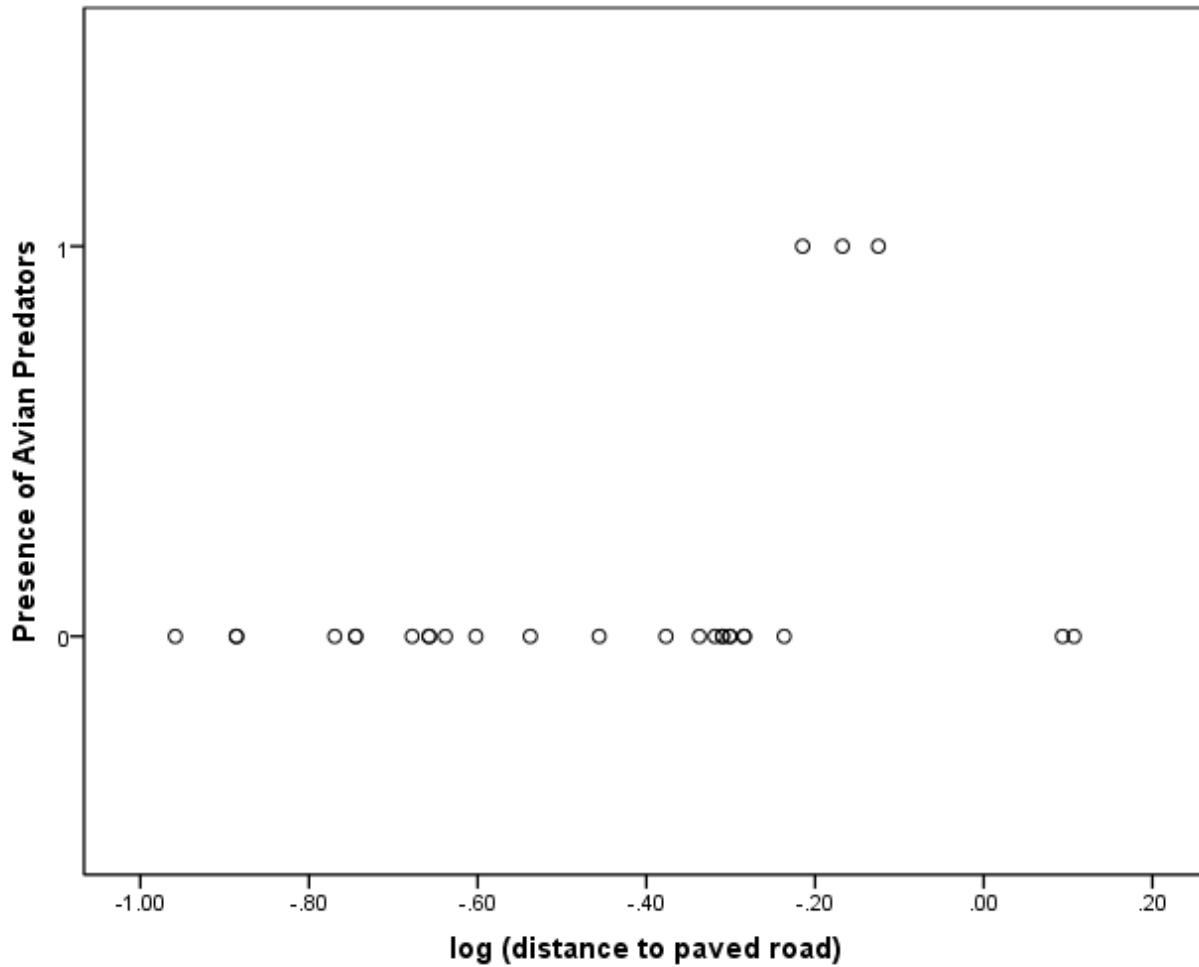


Figure 8. Presence of avian predators vs. log (distance to nearest paved road). Each point represents data from an experimental site.

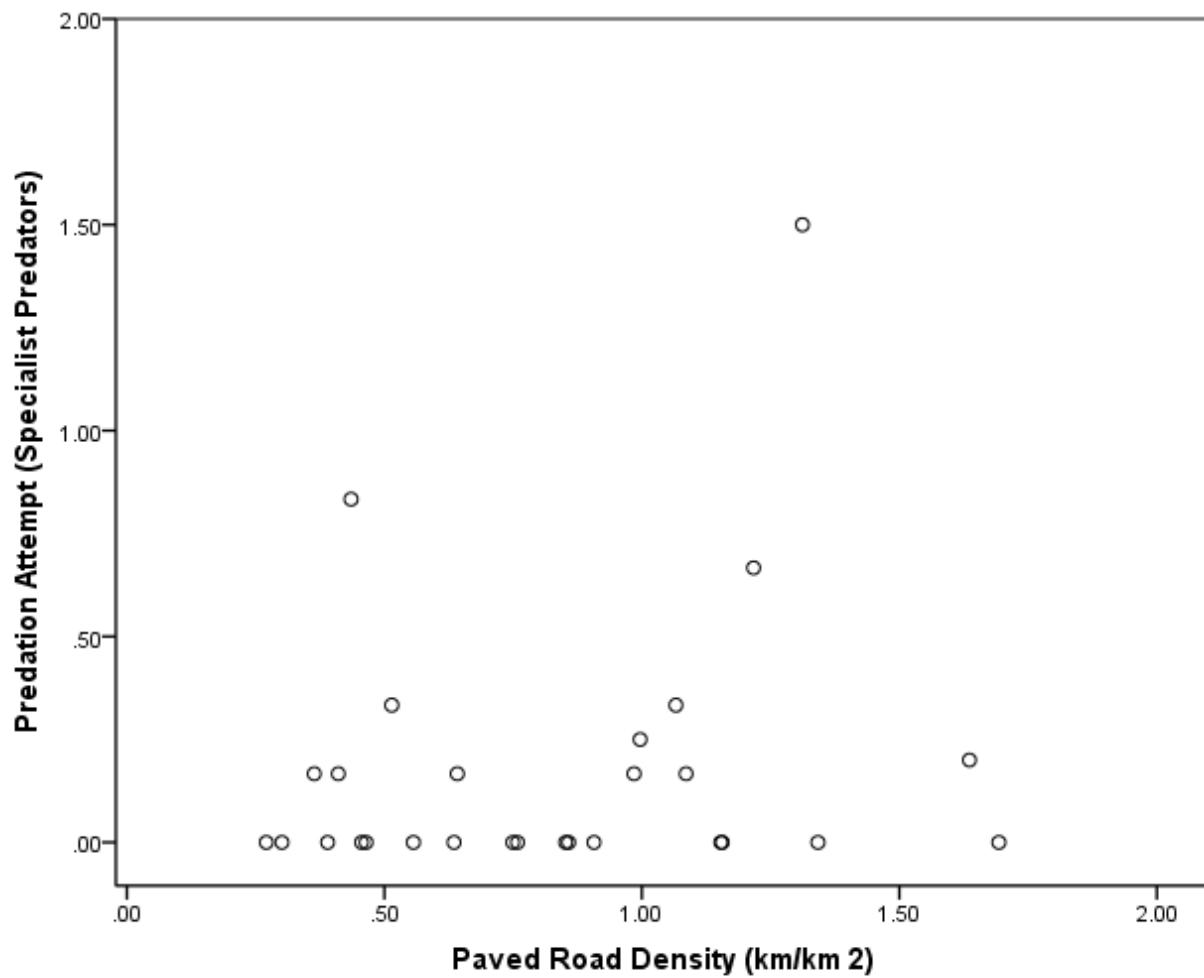


Figure 9. Number of predation attempts by specialist (non-raccoon/skunk) predators per enclosure-day on *Peromyscus leucopus* in experimental enclosures vs. paved road density (km/km²) in the surrounding 2-km radius landscapes. Each point represents data from an experimental site.

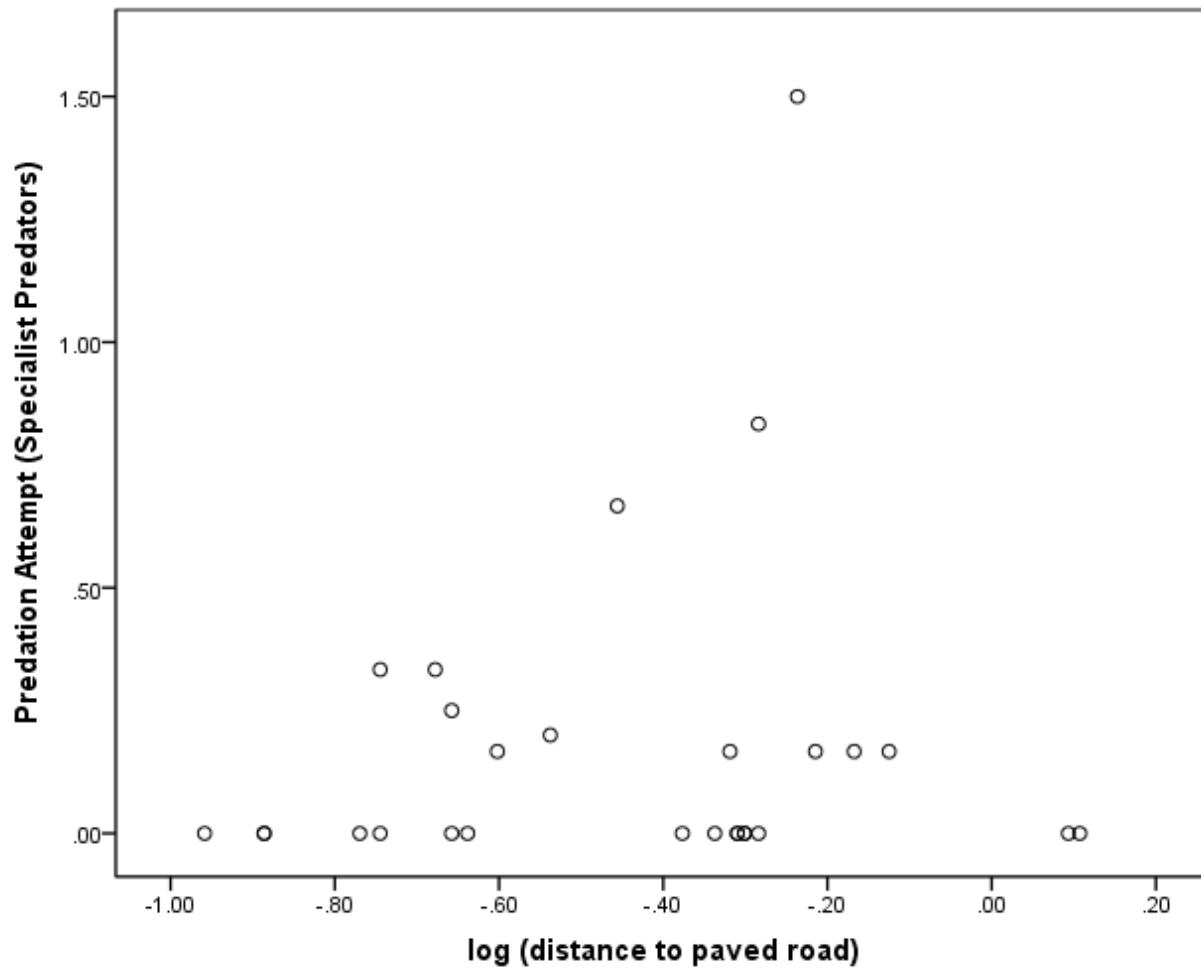


Figure 10. Number of predation attempts by specialist (non-raccoon/skunk) predators per enclosure-day on *Peromyscus leucopus* in experimental enclosures vs. log (distance to nearest paved road). Each point represents data from an experimental site.

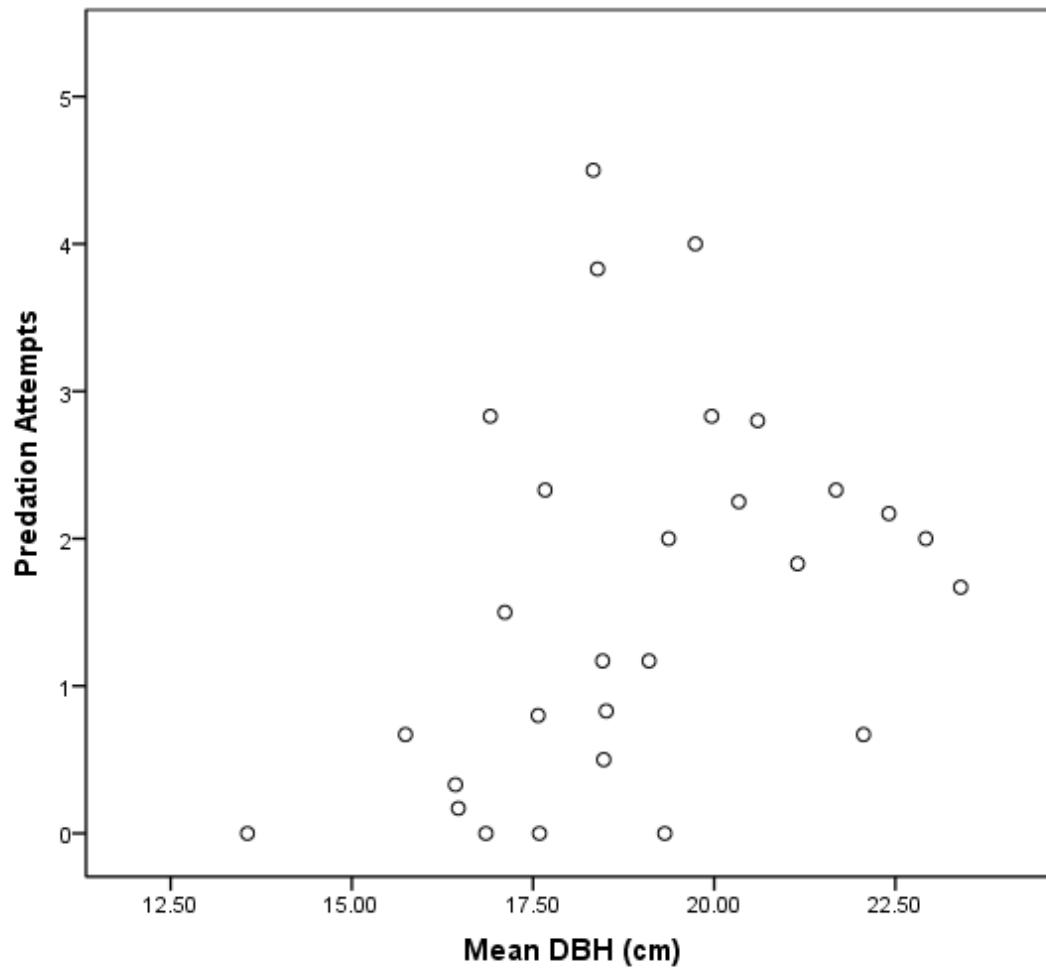


Figure 11. Number of predation attempts per enclosure-day on *Peromyscus leucopus* vs. mean tree DBH (cm) (diameter at breast height) at the experimental sites.

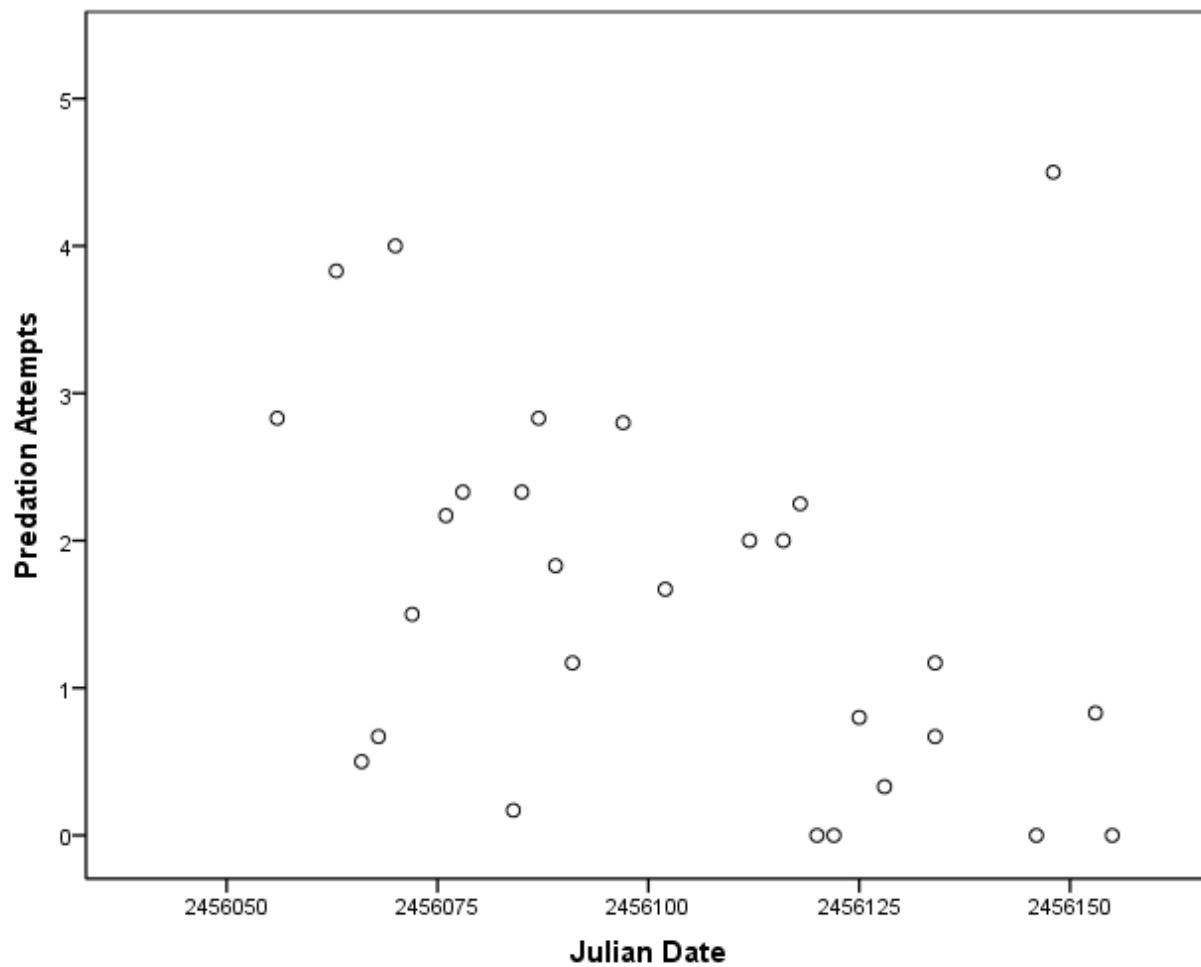


Figure 12. Number of predation attempts per enclosure-day on *Peromyscus leucopus* vs. Julian date.

Appendix A. Predictor and response data at the 28 experimental sites. Julian Date represents the first experimental day at each site; road density is the total length of road divided by 2 km; paved road density is the length of paved roads divided by 2 km; % forest is the amount of forest in the 2 km landscape; # tree species is the total number of different species of trees in the focal patch; % CWD is the percentage of coarse woody debris on the ground; total predation attempts is the total number of predation attempts by all predators at the site; birds, raccoon, skunk, fisher, weasel and cat represent the number of predation attempts by each individual predator species at each site.

Site	Julian Date	Road Density (km/km ²)	Paved Road Density (km/km ²)	Distance to Paved Road (km)	% Forest Cover	# Tree Species	Mean DBH (cm)	% CWD Cover	Focal Patch Area (km ²)	Total Predation Attempts	Birds	Raccoon	Skunk	Fisher	Weasel	Cat
10	2456146	0.76	0.270541401	1.28	18	6	13.56	4.28	2.58	0	0	0	0	0	0	0
24	2456134	0.42	0.363773885	0.75	36	2	19.1	3.95	3.41	6	1	5	0	0	0	0
27	2456056	1.24	1.156130573	0.22	18	3	19.97	6.58	3.04	17	0	17	0	0	0	0
31	2456063	1.32	1.153343949	0.13	20	5	18.39	10.72	27.46	23	0	23	0	0	0	0
33	2456148	1.45	1.311703822	0.58	38	3	18.33	3.12	6.03	21	0	12	0	0	0	9
35	2456072	1.42	1.066082803	0.18	27	4	17.11	9.46	4.29	9	0	7	2	0	0	0
36	2456085	1.25	0.852070064	0.18	28	5	21.68	12.64	10.83	15	0	15	0	0	0	0
43	2456078	1.62	0.906926752	0.42	20	4	17.67	1.16	2.24	14	0	14	0	0	0	0
47	2456122	0.46	0.464299363	1.24	26	6	19.32	3.5	21.12	0	0	0	0	0	0	0
275	2456116	0.41	0.389570064	0.23	27	6	19.37	2.85	16.3	12	0	12	0	0	0	0
290	2456076	0.75	0.514251592	0.21	21.5	7	22.41	6.04	27.5	13	0	11	0	0	2	0
294	2456087	0.74	0.435350318	0.52	21.3	8	16.91	8.68	27	14	0	9	0	0	5	0
308	2456120	1.75	1.693232484	0.17	22.9	5	17.59	5.05	22.6	0	0	0	0	0	0	0
314	2456089	0.46	0.465605096	0.5	29.7	7	21.15	9.07	21.1	11	0	11	0	0	0	0
321	2456134	1.59	0.984713376	0.48	26.5	4	15.74	5.3	16.02	5	0	4	1	0	0	0
403	2456128	0.8	0.641640127	0.68	21.7	7	16.43	6.58	10.9	2	1	1	0	0	0	0
1481	2456125	1.64	1.646098726	0.29	27.2	6	17.57	14.53	20.8	5	0	3	0	2	0	0
1500	2456155	0.76	0.749363057	0.49	29.5	7	16.85	8.18	17.6	0	0	0	0	0	0	0
1767	2456091	1.45	1.216878981	0.35	20.4	3	18.46	13.65	22.5	6	0	2	0	0	1	3
1775	2456112	1.34	1.085828025	0.25	21.8	8	22.92	19.53	24.6	12	0	11	0	1	0	0
1901	2456084	1.36	0.857643312	0.49	22.2	4	16.47	6.28	7.2	2	0	2	0	0	0	0
1966	2456066	0.3	0.300955414	0.52	23.7	4	18.48	8.76	9.05	5	0	5	0	0	0	0

2679	2456118	1.27	0.996576433	0.22	25.3	6	20.34	17.75	13.9	10	0	9	0	0	1	0
3085	2456097	0.66	0.556289809	0.13	21.3	6	20.6	8.4	13.4	14	0	14	0	0	0	0
3274	2456102	0.85	0.635191083	0.11	29.1	4	23.4	9.63	6	10	0	10	0	0	0	0
4702	2456070	0.59	0.410589172	0.61	30	5	19.74	14.81	6.5	22	1	21	0	0	0	0
4892	2456068	0.76	0.758359873	0.46	23.3	7	22.06	12.8	26.6	4	0	4	0	0	0	0
6207	2456153	1.72	1.341958599	0.5	27.4	8	18.51	5.63	14.6	5	0	5	0	0	0	0

