

TRAFFIC NOISE DECREASES BODY CONDITION
AND STOPOVER EFFICIENCY OF MIGRATING SONGBIRDS

by

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ABSTRACT

Numerous studies document impacts of roads on wildlife, and suggest traffic noise as a primary cause of population declines near roads. For migratory birds faced with increasingly human-altered habitats, noise may pose a serious threat. Using an array of speakers, we applied traffic noise to a roadless landscape, directly testing the effect of noise alone on an entire songbird community. Focusing on individuals that stayed despite the noise, we demonstrate that songbirds show a near halving of ability to gain body condition when exposed to traffic noise during migratory stopover. This marked degradation in stopover efficiency may help explain dramatic declines in migratory songbirds worldwide. We conducted complementary laboratory experiments that implicate foraging-vigilance behavior as one mechanism driving this pattern. Our results suggest that noise pollution degrades habitat that is otherwise suitable, and that a species' presence does not indicate the absence of impact.

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LIST OF ABBREVIATIONS

BCI	Body Condition Index
dB	Decibels

CHAPTER ONE

Preface

As the prevalence and intensity of anthropogenic noise has increased globally, the scientific community has shown concern regarding if and how changes to the sensory environment might impact organisms and ecosystems (Barber *et al.* 2011). There is now substantial evidence that anthropogenic noise has detrimental impacts on a variety of species (Barber *et al.* 2011; Siemers and Schaub 2010; Kight and Swaddle 2011; Francis and Barber 2013). Early work has shown significant negative effects of roads on songbird density and nesting success, and correlations between observed impacts and traffic noise (e.g., Mockford and Marshall 2009; Goodwin and Shriver 2010; Crino *et al.* 2011; Halfwerk *et al.* 2011a). Work with oil and gas development has demonstrated that gas compressor station noise alone impacts songbird breeding distribution and community species richness (Habib *et al.* 2007; Bayne *et al.* 2008; Francis *et al.* 2009). Though never tested with road noise specifically, artificial, white noise is known to alter songbird foraging and vigilance, highlighting these behaviors as a productive target for research in the context of road ecology (Quinn *et al.* 2006).

Foraging behavior is an important part of the life history of all animals because it has direct tradeoffs with vigilance behavior—and therefore survival—especially for prey species (Gavin and Komers 2006). In particular, foraging and vigilance play an important role for songbirds during migration when energy demands are high and birds are in

communities with unknown predator densities (Schmidt *et al.* 2010). Migrating birds travel long distances during nocturnal flights, fueled by fat reserves (Berthold 1996). In order to replenish these reserves, birds must rest and regain fat stores; this is known as “stopover” (Berthold 1996). During this time, birds undergo hyperphagy, when they must increase foraging to put on fat. This rise in food intake is necessary to meet amplified energy needs during migration (Hedenstrom 2008).

Not only are energy demands high during migratory flight, but migration has also been shown to account for more than 85% of all mortality in some songbird species (Silllett and Holmes 2002). Therefore, understanding what factors might increase risk of mortality during migration—and whether human influence is changing these dynamics—is important for conservation. Migrating birds are in decline across the world (Robbins *et al.* 1989; Sanderson *et al.* 2006), and as stopover habitat is lost or becomes increasingly human-altered, migrants will face even greater obstacles (Carlisle *et al.* 2009). Because mortality during migration is so high, and birds are facing one of the most energetically challenging tasks in their lives, it is critical that we consider migration and stopover as we work to preserve these species. Although many studies have investigated some aspect of birds and roads (Fahrig and Rytwinski 2009; Benítez-López *et al.* 2010; Reijnen and Foppen 2006; Halfwerk *et al.* 2011a; Goodwin and Shriver 2010), no study has yet investigated the effects of noise alone on birds during migration. Most studies have also focused only on distributional changes (e.g., Summers *et al.* 2011, but see Crino *et al.* 2011 and Halfwerk *et al.* 2011a), leaving the consequences for individuals that stayed behind in noise exposed areas open to study.

Historical noise research has provided a base of knowledge on the impacts of noise on songbirds, but much remains to be discovered relating to birds and anthropogenic noise pollution. While Quinn and colleagues (2006) clearly demonstrated an impact of white noise on foraging and vigilance, white noise has sound energy equally distributed across frequency and does not occur in nature. The influence of anthropogenic noise (which has energy concentrated primarily below 2 kHz) on the foraging and vigilance behavior of songbirds has yet to be studied (see Schmidt *et al.* 2010). Additionally, previous research has focused primarily on the effects of roads on breeding birds. These studies hypothesized that noise was a causal mechanism underlying their findings, but did not experimentally parse traffic noise from other influential factors such as increased predator density (i.e., edge effects), pollution, or lighting near roads (Forman & Deblinger 2000; Pescador & Peris 2004). In addition, the impacts of noise on *migratory* songbirds have never been investigated. To test this, we created a “Phantom Road,” testing the impacts of road noise apart from other aspects of actual roads by playing road noise in a roadless area.

This Phantom Road project was a two-year, large-scale field study accomplished through the efforts of my co-authors Dr. McClure, Dr. Carlisle, Dr. Barber, and myself, along with many field technicians. Thanks to cooperation and shared technicians from the Intermountain Bird Observatory (formerly Idaho Bird Observatory) we established two field stations: one at our control site and one at our phantom road site. Because of the difficulty of implementing a study of this magnitude and the unlikelihood that a study of this scale would be replicated, both Dr. McClure (a Postdoctoral Research Associate at the time in the Barber Lab) and I conducted concurrent, complementary and collaborative

studies at the site during fall migration. Based on Dr. Chris McClure's work at the site, the Phantom Road project has already seen one publication, in the *Proceedings of the Royal Society Series B* (see McClure *et al.* 2013). Dr. McClure conducted point count surveys at the site, studying the impacts of the phantom road on bird distributions.

Through this research and analysis, we discovered a one-quarter decline in bird numbers at the site overall and found that 13 of the species studied left the site while the noise was broadcast. Our first manuscript focused on what species were temporally expatriated from the site due to noise exposure. Here, I concentrate on the other side of the picture, bringing into focus the effects on birds that stayed behind in elevated background sound levels.

Introduction to the Field Experiment

When examining the value of stopover habitat to migrants, an important consideration is the amount of mass migrants are able to gain at a site (Carlisle *et al.* 2005). Migrants in stopover habitat with high quality habitat will gain mass faster than those in poor quality habitat (Dunn 2001). Traditionally, capturing birds in mist nets has provided the most common avenue for studying this gain. Comparison of a bird's mass at multiple captures is a traditional method used to measure migrant mass gain. In this setup, a bird is weighed and banded when it is first captured at a site. If the bird is caught again and weighed at a later date in the same season, its mass change may be calculated. While this method is able to detect mass gain in migrants, there are confounds that have caused its reliability to be questioned (Winker *et al.* 1992). For example, because not all birds are equally likely to be recaptured, mass gain data may be representative of only a segment of the migrant population (Winker *et al.* 1992). Additionally, sick or otherwise

injured birds may remain at a site longer than normal, thus increasing their probability of recapture and skewing recapture mass change calculations to be lower than reality for a given population (Winker *et al.* 1992).

Studies of migrant mass gain have adopted an alternative way of calculating rate of gain that does not rely on recaptures. Regressing a body condition variable—such as mass—against hour after sunrise allows data from every newly captured bird to be included in the analysis. This increases sample size by including all newly captured birds, instead of only recaptures, and assures a more representative sampling of the migrant community, rather than a subset that may have a skewed likelihood of recapture. For our study design, this also meant that we were not repeatedly sampling individuals, thereby eliminating confounds associated with a lack of independence between noise on and off blocks. By adding covariates such as time of season, wing length, or age and sex classes, the regression can be further refined, although addition of these variables requires sample sizes to be large (Dunn 2000). Previous research has used an index of body condition such as size adjusted mass for the regression (Winker *et al.* 1992), however other indices of migrant condition exist that might also be used to the same effect if they measure condition on a fine enough scale.

Introduction to the Laboratory Experiment

Research on foraging and vigilance in terrestrial organisms has shown that animals decrease foraging when there is increased perceived or real predation risk (for a review see Verdolin 2006). Since a decrease in a prey animal's ability to detect predator cues increases their perceived predation risk, it follows that foraging animals exposed to noise would increase vigilance while decreasing intake rates. Based on a wealth of

previous research on the impacts of altering the foraging-vigilance tradeoff, we determined that one likely avenue for reduced migrant stopover efficiency may be explained by a change in the foraging-vigilance tradeoff. During migration, bird time budgets are largely constrained to resting, foraging, and vigilance (Hedenstrom 2008), therefore a change in vigilance will result either in a reduction in foraging (and consequent changes in body condition), greatly increased energy expenditure, or missed opportunity costs (Verdolin 2006).

The foraging-vigilance tradeoff has been investigated in birds: specifically, foraging granivorous birds (Chaffinch, *Fringilla coelebs*) were found to decrease their foraging rates and increase vigilance when exposed to white noise (Quinn *et al.* 2006). It is thought that when a bird is foraging, it uses two types of vigilance: when its head is up, it uses visual vigilance; when its head is down and visual vigilance is decreased, a bird may use auditory vigilance instead (Quinn *et al.* 2006). However, when background noise is increased to a level at which a bird is no longer able to use auditory vigilance, it must adjust by increasing the amount of time spent being visually vigilant. Chaffinches exposed to white noise increased their visual vigilance to compensate for loss of auditory vigilance by raising their head more often (Quinn *et al.* 2006). As a result of their increased visual vigilance, Chaffinch seed intake rates decreased. Although white noise, which has a broad range of frequencies, does not occur in nature, this test demonstrated a useful principle that forms a foundation for further sensory ecology research. Here, I expand upon the principles demonstrated by Quinn *et al.* by exposing a granivorous species to road noise treatments at 55 and 61 dB(A). Playing road noise at two different levels allowed us to test whether sparrows showed a gradient response based on dB level,

versus a simple response to noise on/off. By testing another granivorous bird, the White-crowned Sparrow, in the presence of road noise, we can make useful conclusions about the effects of traffic noise on the foraging-vigilance tradeoff of birds exposed to roads.

Foraging during migration is critical to songbirds since they need to gain large amounts of fat stores during a short stopover period. Inability to gain mass quickly could result in a longer stopover duration and delayed migration. Studying the impacts of road noise on mass gain of an entire migrant community may also reveal varying impacts on different species, taxa, or foraging guilds, giving insight into community-wide impacts by road noise.

Traffic Noise Decreases Body Condition and Stopover Efficiency of Migrating Songbirds

To be submitted to *Science*

We have known for decades that human infrastructure shapes animal distributions, communities, and behaviors (Fahrig and Rytwinski 2009; Benítez-López *et al.* 2010). A meta-analysis of 49 datasets across four continents found that bird and mammal populations decline within 1 and 5 km of human infrastructure, respectively, including roads (Benítez-López *et al.* 2010). Observational studies of birds near actual roads implicate traffic noise as one of the main factors causing these declines (Francis and Barber 2013). However, without altering noise levels experimentally, previous research could not eliminate aspects such as visual disturbance, collisions, chemical pollution, and edge effects as possible causes (Francis and Barber 2013). Road ecology research has also shown strong negative correlations between traffic noise levels and songbird reproduction (e.g., Reijnen and Foppen 2006; Halfwerk *et al.* 2011a).

Furthermore, birds with song frequencies masked by traffic noise are the species most affected by roads (Goodwin and Shriver 2010). In addition to correlational road studies, ‘natural experiments’ in gas extraction fields have shown that noisy compressor stations alter nest success and reduce species richness compared to quieter well pad areas (Bayne *et al.* 2008; Francis *et al.* 2009); these studies offer the best support to date that anthropogenic noise alone can drive ecological changes. In these and other investigations that have implicated noise as a causal factor in population declines, many individuals remain, but at what cost? Here we parse the independent role of traffic noise experimentally, by playing traffic sounds back through an array of speakers in a roadless area during songbird autumn migration, creating a ‘phantom road.’ We focus on the subset of individuals that remained despite the noise, allowing us to investigate the physiological costs of noise exposure.

Proposed causes of decreased fitness for birds in traffic noise include song masking, interference with mate evaluation, non-random distribution of territorial individuals, disruption of parent-chick communication, reduced foraging opportunities, and/or alterations in the foraging/vigilance trade-off (Halfwerk *et al.* 2011a; Francis and Barber 2013). During the breeding season, all of these hypotheses are possible, but during migration time budgets are streamlined. Foraging, vigilance, and rest dominate activity (Hedenstrom 2008). Here we focus on migrating birds, allowing us to concentrate our work on foraging and anti-predator behavior while largely excluding other possible mechanisms of road impacts.

Balancing foraging and vigilance is important for all animals because this trade-off has direct consequences for survival (Lima and Dill 1990; Purser and Radford 2011).

Human-caused disturbance might disrupt the foraging-vigilance tradeoff by acting as a form of perceived predation risk (Frid and Dill 2002; Shannon *et al.* 2014) or by reducing sensory awareness via distraction or acoustic masking (Francis and Barber 2013). During migration, balancing foraging and vigilance is particularly crucial as energy demands are high and birds make landfall in areas with unknown predator densities (Schmidt *et al.* 2010). To meet the amplified physiological needs of sustained nocturnal migratory flights, birds must increase foraging during periods of stopover while maintaining appropriate vigilance levels (Berthold 1996; Hedenstrom 2008). Any interference with foraging will decrease stopover efficiency and reduce migration speed—a likely surrogate for fitness (Hedenstrom 2008)—thereby increasing exposure to migration-related mortality risks. Increasing risk exposure during this time period can be deadly, since migration can account for up to 85% of annual mortality in birds (Berthold 1996).

With an array of speakers, we recreated the soundscape of a 0.5 km section of highway along a ridge in southwest Idaho. This approach enabled us to turn the traffic noise *on* and *off* throughout fall migration at our phantom road site, and compare it with a nearby quiet control site, creating a modified before-after-control-impact design. By alternating noise on and off blocks every four days we sampled a different set of migrants during each noise playback block as birds arrived and departed from the stopover site (*see Supplementary Materials and Methods*). We measured sound levels (hourly level-equivalent, or LEQ) continuously throughout the season using acoustic recording units placed at mist net locations. This approach allowed us to quantify the acoustic environment over the entire duration of our study, a component absent from road ecology research to date. When the noise was on, sound levels at the phantom road increased by

11 dB(A) to an average of 48 (s.e.=0.26) dB(A), while the control site nets averaged 2 dB(A) louder when the noise was on (mean 41dB(A) +/- 0.17; Fig. 1). When the noise was off, background sound levels at the mist nets averaged 39 (s.e.= 0.18) dB(A) at the control site and 37 (s.e.=0.26) dB(A) on the phantom road. Using this study design, we previously found over a one-quarter decline in songbird abundance during noise-on periods at the experimental site (McClure *et al.* 2013). Here, we look beyond abundance results, investigating the costs for birds that remain in noisy areas.

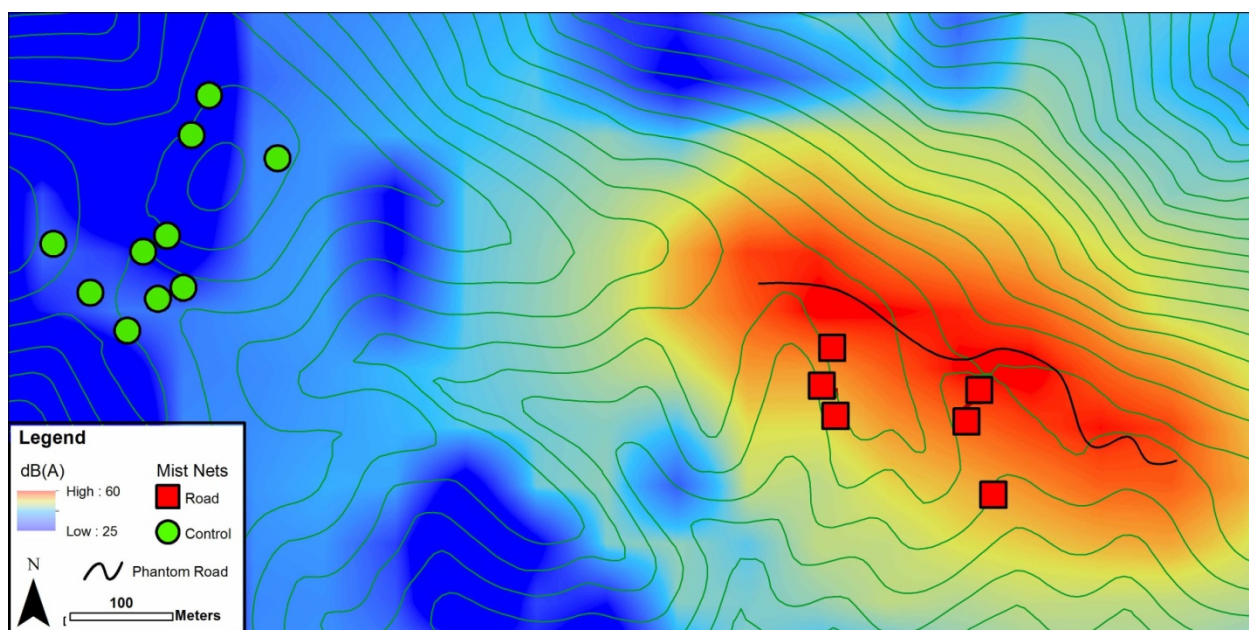


Figure 1 Background Sound Levels. Estimated background sound levels (dB(A) 1 h LEQ) during periods when speakers were turned on at our study site in the Boise Foothills in southwestern Idaho from early August through early October 2012 and 2013. Background sound level was modeled using NMSIM (Noise Model Simulation; Wyle Laboratories, Inc., Arlington, VA) where inputs were chosen to match observed values at Acoustic Recording Units (co-located with mist nets) while the phantom road noise was playing (McClure *et al.* 2013). Circles represent locations of control capture sites, and squares represent capture sites along the phantom road.

Using data collected from birds caught and banded at the control and phantom road sites, we examined differences in body condition index (BCI) of newly captured birds across a gradient of noise exposure. BCI is a size-adjusted metric of body mass

(calculated as mass/natural wing chord) measured in g/mm, so small changes in BCI represent large differences in condition (Winker *et al.* 1992). In preparation for migration, birds' body condition increases as they add the energy stores needed for long migratory flights (Berthold 1996). We also calculated stopover efficiency by regressing BCI of new captures against time of day. This method measures migrants' ability to increase body condition in preparation for migratory flight—i.e. their *stopover efficiency*. Comparing stopover efficiency between sites can give a good metric of the relative value of habitat to migrants (Winker *et al.* 1992; *see Supplementary Materials and Methods 1.3.2 on the exclusion of recaptures in analysis*). In addition to our previous point count work, we compared mist-net capture rate (birds caught/net/hr) across site (control vs phantom road) and noise treatment (on vs off) to further investigate whether birds were leaving or staying when exposed to phantom road noise (*see Supplementary Materials and Methods*).

We used the same set of models (*see Supplementary Materials and Methods and Appendix A*) to run three separate analyses for overall BCI, stopover efficiency, and capture rate. For overall BCI, the global model including a continuous covariate for dB(A) was the top model, showing that as the phantom road dB(A) increased, overall BCI of birds remaining at the site decreased (β for dB(A) = $-1.08e-04 \pm 4.76e-05$; Fig. 2). For stopover efficiency the top model was the global model, which included an interaction between dB(A) x minute after sunrise. These model estimates show that stopover efficiency of birds that stayed decreased when dB(A) levels increased—*birds gained condition nearly half as quickly when the phantom road was on* (interaction $\beta = -6.76e-07 \pm 4.48e-07$; Fig. 3). BCI and stopover efficiency at the phantom road site when

the noise was off did not differ from the control site, indicating that the phantom road was an otherwise suitable stopover location (Fig. 2 & 3; Tables A1 & A2). The top multi-species model for capture rate was a global model including an interaction between noise and site. Capture rate was significantly lower at the phantom road site when noise was playing, indicating some birds left the phantom road when the noise turned on but remained at the control site (interaction = $-6.09e-03 \pm 1.70e-03$; Table A3).

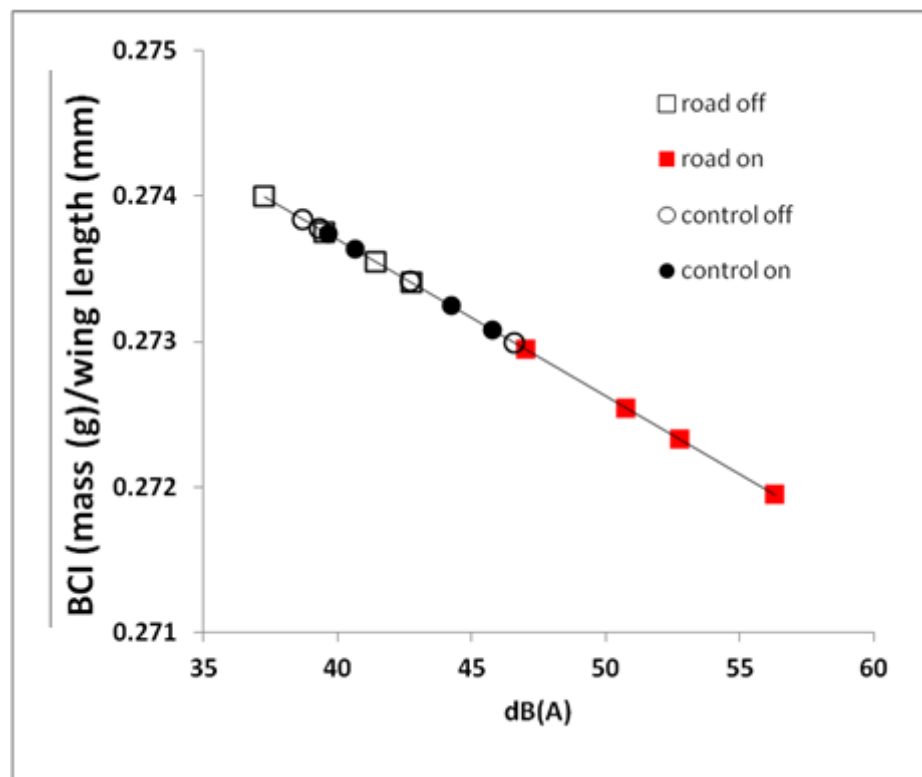


Figure 2 Body Condition Index. Global Model estimate values of BCI vs. dB(A). Estimates are for all captures combined, with species as a random intercept.

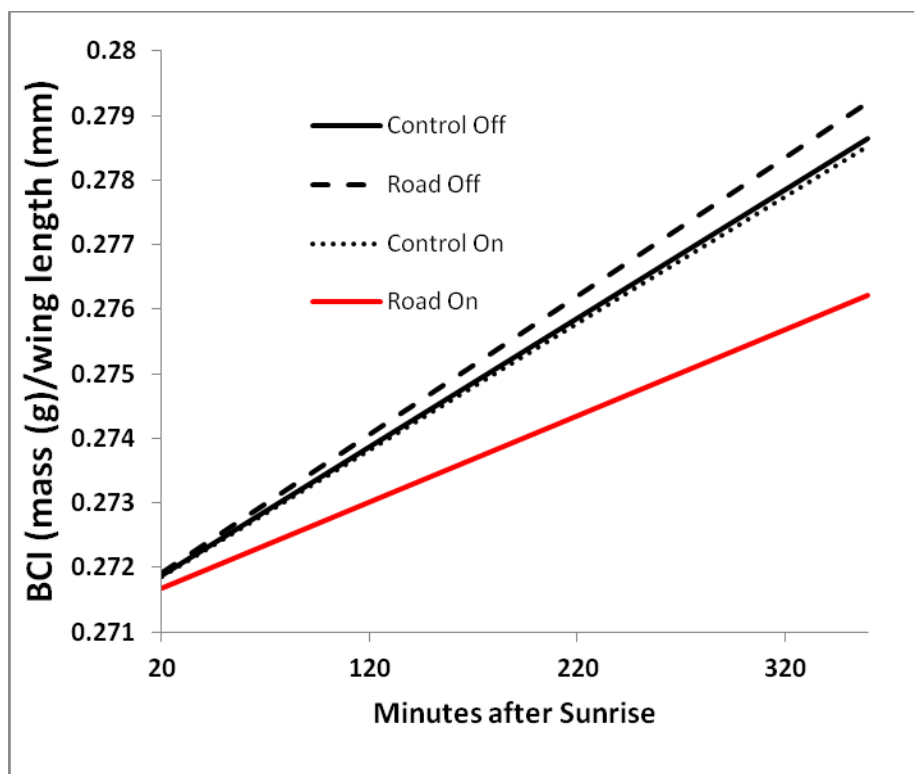


Figure 3 Stopover Efficiency. Global Model estimate values of stopover efficiency for the control site when the road was off (dB(A) 42), control site with road on (dB(A) 43), phantom road with noise turned off (dB(A) 40), and the phantom road with the noise on (dB(A) 51). Birds gained condition at 46% of the normal rate when the phantom road was turned on.

In support of our field results, we conducted a controlled laboratory study to investigate if traffic noise alters the foraging-vigilance tradeoff in songbirds and could thus mechanistically underpin our field data (*see Supplementary Materials and Methods*). We focused on the second most common species in our field study, white-crowned sparrows (*Zonotrichia leucophrys*), to investigate the reduction in foraging and increase in vigilance implied by our BCI data. We quantified head-down duration (i.e., foraging rate) and head-up rate (i.e., vigilance) as these are known measures of avian visual vigilance that change when auditory surveillance is limited, and correlate strongly with food intake and ability to detect predator attacks (Quinn *et al.* 2006). Using the same playback file that we used for the phantom road, we played 61 dB(A) and 55 dB(A)

traffic noise treatments, plus a silent control track (32B(A)) to foraging sparrows (n=20). Following Quinn *et al.* (2006), we used video of 30-second foraging bouts to measure foraging and vigilance behavior when birds were exposed to different levels of traffic noise. White-crowned sparrows decreased foraging by ~8% and increased vigilance levels by ~21% when exposed to traffic noise (61dB(A)): i.e., birds showed more head lifts ($\beta=0.005\pm0.002$) and decreased the amount of time spent with their heads down searching for seeds ($\beta= -0.003\pm0.001$; Fig 4) during noise playback compared to ambient conditions. (Mean head up rate (head lifts/sec) for 61 dB(A)= 0.79 ± 0.06 , 55 dB(A)= 0.77 ± 0.05 , 32 dB(A)= 0.65 ± 0.05 . Mean head down duration (sec): 61 dB(A)= 0.41 ± 0.03 , 55 dB(A)= 0.44 ± 0.04 , 32 dB(A)= 0.50 ± 0.04 .) Vigilance behavior of individuals did not change based on the number of trials experienced, suggesting the birds did not habituate to the noise ($\beta=0.012 \pm 0.031$) (*see Supplementary Materials and Methods* and Table A4). See *supplementary materials and methods* 2.4 for model selection details.

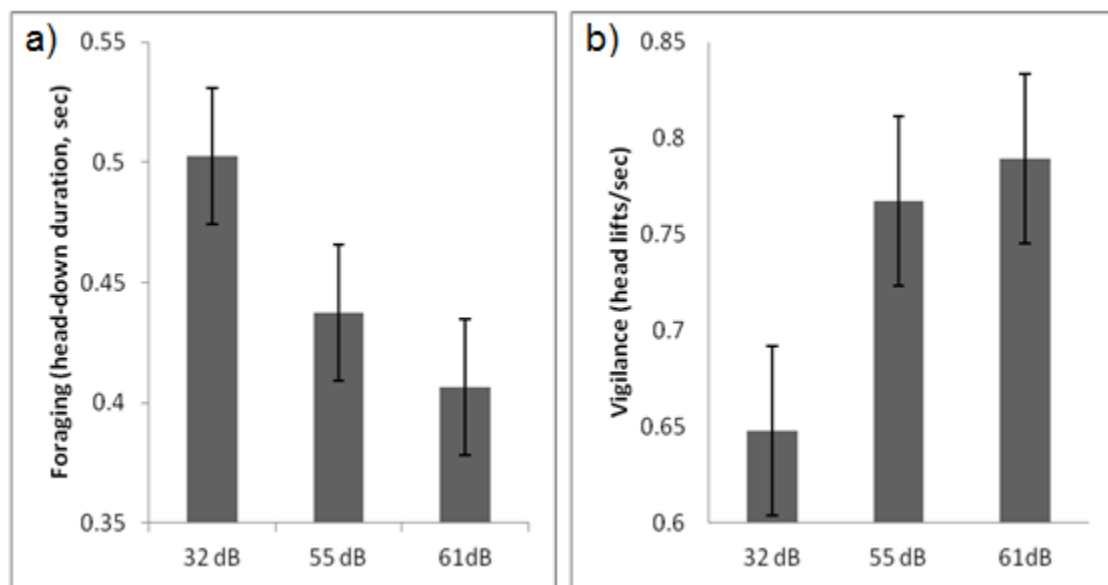


Figure 4 White-crowned Sparrow Foraging and Vigilance. White-crowned sparrows foraging in traffic noise at 61 and 55 dB(A) had reduced foraging rates (a) and

increased vigilance (b) compared to foraging bouts in ambient conditions (32 dB(A)). Data are means \pm standard error.

Previous work that has failed to find a change in animal distributions near roads or other infrastructure has often assumed a lack of negative impacts from loud human activities (see Francis and Barber 2013). Our results demonstrate that individuals may remain in an area with high levels of noise yet suffer costs. Because both foraging and vigilance behaviors are critical for survival, it is unlikely birds could compensate for a reduction in foraging or vigilance rates without a detrimental alteration to either condition or time budgets (Lima and Dill 1990). During energetically demanding periods in a bird's life, increasing vigilance has been shown to reduce survival because of increased starvation risk (Watson *et al.* 2007). Birds could likely forage longer during the day to compensate, however this could increase energy expenditure or reduce the amount of time spent resting (Lima and Dill 1990). In contrast to song masking, which can be at least partially overcome by frequency shifting (Mockford and Marshall 2009; Halfwerk *et al.* 2011b), release from masking is not possible for the types of auditory cues necessary for aural vigilance (Barber *et al.* 2011). With limited auditory information, animals must resort to other methods such as visual scans to compensate for the increase in perceived predation risk driven by masking of communication calls and predator-generated sounds (Quinn *et al.* 2006; Gavin and Komers 2006). Migrants face greater challenges compared to resident birds because they are exposed to an unknown risk landscape at stopover sites and must therefore rely heavily on increased vigilance to compensate (Thomson *et al.* 2006; Schmidt *et al.* 2010). For migrants, reduction in condition or delay in migration could have carry-over effects into the overwintering or breeding seasons (Harrison *et al.* 2010).

Our laboratory tests offer strong evidence that the body condition changes measured in the field were due, at least in part, to a change in foraging and vigilance behavior, but our field results could be due to a combination of factors. For example, noise might also increase physiological stress levels (Blickley *et al.* 2012, but see Crino *et al.* 2011) that could cause additional weight loss and add to the cost of remaining in noisy areas. We showed that traffic noise directly influences foraging-vigilance behavior in the lab. In addition to the interaction measured in the lab, in a natural setting noise may indirectly change foraging rates through alteration of other behaviors such as prey search time, sleep, or territoriality. For instance, the phantom road playback may have disrupted foraging behavior by reducing the acoustic detectability of insect prey (Montgomerie and Weatherhead 1995) or altering insect numbers. We did not test for changes in insect abundance or distribution but because we found noise impacts on a mixed community of both frugivorous and insectivorous birds (Table 1), altered insect numbers seem unlikely to be contributing significantly to the patterns we observed. Effects were consistent between the 4-day noise-on blocks throughout the season, so it is more likely that changes in an aspect of bird behavior, rather than variation in habitat or food, drove these immediate responses. Our experimental design was not able to rule out whether noise disrupts territoriality or dominance hierarchies during stopover. However, because some of the species that showed negative effects of noise (*see Supplementary Materials and Methods*) are known to be non-territorial during migration (e.g., White-crowned Sparrow, Ruby-crowned Kinglet; Poole 2005), it is unlikely that disruption of territoriality was the main driver of our results. It is also possible that our stopover efficiency results were driven by a change in species composition, rather than a change in body condition of

individuals, over the course of a day at our site. If birds with lower body condition were leaving over the course of a morning, it is possible we would see the same change in the relationship between community body condition and minute after sunrise as predicted by a change in stopover efficiency. With further testing we might expect to find that noise causes a combination of these direct and indirect effects on the time and energy budgets of individuals that each contribute to the BCI and foraging changes we measured. Because provisioning is a constant requirement throughout the year, other effects of noise that occur outside of migration (e.g., Reijnen and Foppen 2006; Halfwerk *et al.* 2011a) would be in addition to, rather than instead of, the impacts on foraging and BCI.

Because we turned the phantom road off overnight to match typical diel traffic patterns, it is likely that nocturnal migrants chose to land at our site when it was quiet, before the phantom road playbacks began in the morning. In effect, diurnally-varying traffic noise might function as an ecological trap (Robertson and Hutto 2006) for migrants. Though staying in traffic noise has a cost, the energetic outlay for individuals to leave a site might be even higher. Birds with low body condition are less likely to embark on migratory journeys than those in good condition, and may not have the ability to leave once landed (Smith and McWilliams 2014). Average BCI was lower when the phantom road was on; birds that stayed were in worse condition than the average migrant at our site. If we had found reduced BCI combined with *no* change in capture rates, we might infer that the reduced condition was due to slower weight gain in birds already present at the site. However, we saw both reduced BCI and reduced bird numbers, suggesting that birds with sufficient energetic stores chose to leave the site and escape the costs of remaining in noise (Smith and McWilliams 2014). This decision to stay or leave is

critical for migrants during stopover. Notably, during nesting, birds have limited mobility because nest desertion may have too high a cost (Székely *et al.* 1996), therefore birds may not choose to leave during the breeding season as they would during migration.

Migratory songbirds are in decline worldwide, and habitat loss and degradation have been identified as major contributing factors (Robbins *et al.* 1989; Sanderson *et al.* 2006). Recognizing traffic noise as another environmental attribute contributing to habitat degradation might help explain the significant decrease in songbird numbers globally. When our phantom road was turned on, the addition of traffic noise alone, without the other variables associated with roadways, was enough to decrease the value of a stopover site for migrants, effectively degrading habitat quality (Fig. 3). Songbird stopover site protection is limited worldwide, and as key areas are identified, protection from noise pollution and other forms of habitat degradation needs to be a priority (Robbins *et al.* 1989; Sanderson *et al.* 2006).

Transportation noise continues to increase around the world and many protected areas do not currently manage for anthropogenic noise pollution (Barber *et al.* 2011). Fortunately, unlike many aspects of roads, noise impacts can be minimized without removing the road itself. Altering the substrate or reducing speed limits on existing roads can significantly lower decibel levels (Wayson 1998). We played the phantom road back at levels similar to many suburban neighborhoods (55-60 dB(A); Wayson 1998). Many protected areas and high-value habitats are already exposed to these levels, and would likely benefit from noise relief measures (Lynch *et al.* 2011). While reducing noise is nontrivial, we can collaborate with acoustical engineers to do so. Alternatively, in rare habitats or areas where fragmentation is also a significant factor, road closures should be

considered, and efforts should be made on existing protected land to maintain roadless areas wherever possible.

Our results reveal the need for attention to noise impacts beyond distributional shifts (Francis and Barber 2013). For individuals that remain in areas disturbed by loud human activities, noise pollution represents an invisible source of habitat loss that has previously been ignored—traffic noise degrades habitat value but leaves no physical signs of change. We found that noise interferes with migrant stopover efficiency. Further understanding of this impact is key, since fuel stores are known to influence migrant stopover behavior, speed, and success (Smith and McWilliams 2014). Unlike other aspects of roads, the impact of noise reaches far beyond the physical footprint of human infrastructure. For conservation efforts to be maximally effective, we must recognize anthropogenic noise as another source of habitat degradation. When managing migratory birds and other taxa facing habitat loss, we should ensure that the areas we protect are of high quality, including the quality of the acoustic environment.

Table 1 Summary of songbird captures and model output results. Sample sizes of the 51 songbird species captured at the Phantom Road and control sites in southwestern Idaho during fall migration in 2012 and 2013. Twenty-one species had large enough sample sizes to allow for testing individually (those with $n > 100$) and showed varying responses to traffic noise at the phantom road study site. Responses to increased noise are indicated as positive (+), negative (-), or no response (blank).

Species	<i>Latin name</i>	<i>n</i>	BCI	Stopover Efficiency	Capture Rate
<i>All species</i>		9924	-	-	-
ruby-crowned kinglet	<i>Regulus calendula</i>	2677	+		-
white-crowned sparrow	<i>Zonotrichia leucophrys</i>	1220	-		
dark-eyed junco	<i>Junco hyemalis</i>	760	-		
yellow-rumped	<i>Setophaga coronata</i>	582			-

Species	<i>Latin name</i>	<i>n</i>	BCI	Stopover Efficiency	Capture Rate
warbler					
dusky flycatcher	<i>Empidonax oberholseri</i>	473			-
western tanager	<i>Piranga ludoviciana</i>	418	-		
yellow warbler	<i>Setophaga petechia</i>	409			
spotted towhee	<i>Pipilo maculatus</i>	370		-	-
orange-crowned warbler	<i>Oreothlypis celata</i>	310			
MacGillivray's warbler	<i>Geothlypis tolmiei</i>	305	-	-	
warbling vireo	<i>Vireo gilvus</i>	285			
Cassin's vireo	<i>Vireo cassinii</i>	198	+		
Hammond's flycatcher	<i>Empidonax hammondii</i>	174			
Wilson's warbler	<i>Cardellina pusilla</i>	166			-
nashville warbler	<i>Oreothlypis ruficapilla</i>	165			
Townsend's solitaire	<i>Myadestes townsendi</i>	144			
Townsend's warbler	<i>Setophaga townsendi</i>	132			
chipping sparrow	<i>Spizella passerina</i>	126			
American robin	<i>Turdus migratorius</i>	118	-		-
hermit thrush	<i>Catharus guttatus</i>	113			
Cassin's finch	<i>Haemorhous cassinii</i>	112	-	+	-
Swainson's thrush	<i>Catharus ustulatus</i>	95	Species-specific models not run on those with n < 100		
mountain chickadee	<i>Poecile gambeli</i>	89			
red-breasted nuthatch	<i>Sitta canadensis</i>	85			
black-headed grosbeak	<i>Pheucticus melanocephalus</i>	62			

Species	<i>Latin name</i>	<i>n</i>	BCI	Stopover Efficiency	Capture Rate
lazuli bunting	<i>Passerina amoena</i>	48			
golden-crowned kinglet	<i>Regulus satrapa</i>	44			
Brewer's sparrow	<i>Spizella breweri</i>	42			
pine siskin	<i>Spinus pinus</i>	37			
"western" flycatcher species complex	<i>Empidonax occidentalis/difficilis</i>	29			
fox sparrow	<i>Passerella iliaca</i>	25			
house wren	<i>Troglodytes aedon</i>	22			
western wood-pewee	<i>Contopus sordidulus</i>	19			
black-capped chickadee	<i>Poecile atricapillus</i>	18			
golden-crowned sparrow	<i>Zonotrichia atricapilla</i>	11			
brown creeper	<i>Certhia americana</i>	6			
gray flycatcher	<i>Empidonax wrightii</i>	6			
cedar waxwing	<i>Bombycilla cedrorum</i>	4			
willow flycatcher	<i>Empidonax traillii</i>	4			
Bullock's oriole	<i>Icterus bullockii</i>	3			
least flycatcher	<i>Empidonax minimus</i>	3			
Lincoln's sparrow	<i>Melospiza linconii</i>	3			
American redstart	<i>Setophaga ruticilla</i>	2			
song sparrow	<i>Melospiza melodia</i>	2			
vesper sparrow	<i>Pooecetes gramineus</i>	2			
Cape May warbler	<i>Setophaga tigrina</i>	1			
evening grosbeak	<i>Coccothraustes vespertinus</i>	1			
pacific wren	<i>Troglodytes pacificus</i>	1			

Species	<i>Latin name</i>	<i>n</i>	BCI	Stopover Efficiency	Capture Rate
rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	1			
savannah sparrow	<i>Passerculus sandwichensis</i>	1			
Steller's jay	<i>Cyanocitta stelleri</i>	1			

Supplementary Materials and Methods

1. Field Experiment

1.1 Study site and data collection

We conducted our study at two adjacent sites in southwestern Idaho, USA (43°36'N, 116°05'W) during the 2012 and 2013 fall bird migration seasons. Both study sites are located on the Idaho Fish and Game's Boise River Wildlife Management Area along the southernmost edge of the Boise Foothills (Figure 1). Our control site was located on Lucky Peak and is the banding site for the Intermountain Bird Observatory's long-term fall migration study; it has operated for the last 17 years. The second site was newly pioneered in 2012 for the purpose of this experimental study and is located 0.95 km east of Lucky Peak. Both the experimental and control sites are characterized by a habitat mosaic of (i) mountain shrubland: dominated by bittercherry (*P. emarginata*) with a mix of other shrubs including chokecherry (*Prunus virginiana*) and Scouler's willow (*Salix scouleriana*), (ii) conifer forest: dominated by Douglas-fir (*Pseudotsuga menziesii*) with a mountain ninebark (*Physocarpus malvaceus*) understory, and (iii) shrub steppe: consisting of mountain big sagebrush (*Artemisia tridentata vaseyana*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus* sp.) with a grassy understory (see

Carlisle *et al.* 2004 for more in-depth site information). Both sites are on the south-facing slope of the ridge (Fig. 1).

Birds were netted at both sites between 19 Aug-9 Oct in 2012, and 2 Aug-8 Oct in 2013. We captured birds using Ecotone brand mist nets (12 x 2.6 m, 32-mm mesh) placed in the mountain shrubland habitat on the southern slope in locations that would maximize capture rates (Ralph *et al.* 1993). The control site at Lucky Peak had 10 nets, while the phantom road site had 6. We placed nets so that habitat and shrub height were similar between sites and net locations remained the same between years. We began netting at sunrise and continued for 5 hours, except occasions with heavy precipitation or high winds. Sunrise ranged from 0620 at the start of the season to 0800. We cleared nets on 20-30 minute intervals, depending on weather. Because of data collection activities for a concurrent trial study at the phantom road site, we only operated nets on the first, second, and fourth days of every four-day interval, and netted every day at the control site.

Once captured, we returned birds to the banding station where they were fitted with standard, individually numbered aluminum USGS leg bands. We identified each bird to species, and aged and sexed individuals based on Pyle (1997). We recorded the date and time of capture to the nearest 10 minutes and collected additional data on each bird following the standard protocol of the Intermountain Bird Observatory's long-term study (Carlisle *et al.* 2005). We also recorded the mass in grams, and unflattened wing chord of each bird to the nearest millimeter.

1.2 Phantom Road

At the phantom road site, we placed 30 paired speakers in Douglas-fir trees at a height of 4 meters from the crest of the ridge, at the interface between forest and

mountain shrubland habitat. We amplified the speakers (Dayton Audio—Springboro, OH, USA—RPH16 Round 16' PA Horns paired with MCM Electronics—Centerville, OH, USA—40 W midrange compression drivers (+5 dB(A), 400–3000 Hz)) with Parts Express (Springboro, OH, USA) 2 W x 2channel, 4-ohm, Class D amplifiers and played back sound files (MP3, 128 kbps) using Olympus (Center Valley, PA, USA) LS-7 and Roland (Los Angeles, CA, USA) R-05 audio players. We powered amplifiers and audio players with arrays of LiFePO₄ (Batteryspace, CA, USA) batteries housed in waterproof plastic containers. One speaker of each pair pointed north into the conifer forest while the other faced south into the mountain shrubland. We spaced the speaker pairs at approximately 30m intervals along the ridge in order to create a “line source” of sound that replicated an actual highway. The geometry of a sound source can have profound impacts on the scale of noise exposure. Point sources (e.g., generators, gas-compressor stations, a single car) lose sound energy at approximately 6 dB per doubling of distances, whereas line sources (e.g., a busy roadway, train) fall off at approximately 3 dB per doubling of distance.

We played traffic noise recorded within Glacier National Park. To create the playback file, we combined files of 12 individual cars recorded at known distances, decibel levels and speeds. We chose car pass-by events based on clarity of recording, decibel level, and speed. We created a 1 min file of 12 car pass-by events and repeated this file without shuffling. Because any possible habituation would have only reduced our ability to detect changes, we see this as a minor concern. Our playback file therefore contained 720 pass-by events per hour of cars traveling at approximately 45 miles per hour—traffic levels and speeds found along roads in some of the most visited protected

areas globally. Our playback file further simulated the frequency profile of typical traffic noise with most of the energy of the noise between 0 and 3 kHz with a peak around 1 kHz (See Figure 1B in McClure *et al.* 2013).

We set the speaker levels so that the 1 minute LEQ reading was $\sim 55\text{dB(A)}$ ($\pm 3\text{dB}$) at 50m from the phantom road. LEQ values are the level of a constant sound over specified time period that has the same energy of the actual, fluctuating energy over that same time period (Barber *et al.* 2011). We played MP3 files of traffic noise in four-day blocks, alternating with four days without noise playback. During noise-on days, noise played from 0430 until 2100 local time, with a 30min fade-on and fade-off period to approximate typical traffic flow patterns and to avoid startling birds. During noise playback, noise levels were 11 dB(A) higher at the phantom road site and 1 dB(A) higher at the control site. The nearest drivable dirt road was 750m from the phantom road site, and the nearest paved road was 4km away. The drivable path near our site was a gated, dead end road used to provide access to the study site for the research team.

We chose 4-day long noise-on and noise-off blocks because almost all species that use our site during autumn stopover remain for fewer than 8 days on average (Carlisle *et al.* 2005). Thus, each noise-on/noise-off block was likely independent as individuals left during the course of a block—no individual bird was likely to be present for more than one noise-on or noise-off period.

To measure dB(A) at our site, we used 6744 hours of recordings from 8 acoustic recording units that ran simultaneously during the 2012 and 2013 fall migration seasons. This amount of continuous recording is, to date, the most thorough quantification of the acoustic environment to be undertaken in road ecology research. Using a custom program

(Damon Joyce, NPS, AUDIO2NV SPL), we converted the MP3 recordings into an hourly sound pressure level format. We then converted those values to hourly LEQ values in dB(A) using another custom program (Damon Joyce, NPS, Acoustic Monitoring Toolbox). We averaged the hourly background LEQ during noise-on hours (05.00 through to 21.00) across the noise-on and noise-off blocks, creating separate noise-on and noise-off LEQs.

We chose to use the hours of 5.00 through 21.00 for two reasons: 1) because we only played traffic noise during those hours, and our goal was to measure the differences between sites during noise-on and noise-off blocks, and 2) the design of the wind screens used to protect the recorders provided shelter for nocturnal tree crickets. During night hours, tree crickets sang from perches on top of our MP3 recording units, creating LEQs of over 90 dB(A). Therefore, our nighttime recordings did not accurately represent the actual background sound levels of our site and could not be used for analysis.

All birds caught during this project were mist netted and banded under the Intermountain Bird Observatory's federal permit (# 22929) and Idaho Department of Fish and Game permit # 764-13-000039, and all experiments were approved by Boise State University IACUC (# 006-AC12-007).

1.3 Analysis

We used data from 51 bird species (9,924 individuals) to build three sets of models for 1) BCI, 2) stopover efficiency, and 3) capture rate, including combinations of variables for dB(A), minute after sunrise, noise, site, and linear and quadratic effects of day, plus random intercepts for year. We also built intercept-only models, and global models that included all factors. For all three model sets, we ran competing models using

noise as either a continuous variable (dB(A)) or a binary (on/off) variable (noise*site interaction models). We compared these noise models because they represent two separate hypotheses. Models including dB(A) test the hypothesis that birds show a functional response to noise and respond in a gradient to increasing noise intensity. Models using an interaction term of noise*site test the hypothesis that the presence of noise at the phantom road site, regardless of intensity, determines the response. In other words, these competing models were used to determine whether birds were responding to noise on a fine or coarse scale. We ranked and compared the models using Akaike's Information Criterion (Akaike 1974, Tables A1-A3). We considered covariates to be useful for inference if their 85% confidence intervals excluded zero. We used 85% confidence intervals instead of the traditional 95% because they are more appropriate when selecting models using AIC (Arnold 2010). We used species and the nearest acoustic recording unit as random variables. It was important to use the nearest recording unit as a random variable because some mist nets in our study were paired, and therefore shared one recording unit. For this study, we were interested in the avian community as a whole, and focus our analyses at that level, but see supplementary materials and methods 3.1-3.2 for details on individual species (those with $n > 100$; Tables 1, A1-A3).

1.3.1 Body Condition Index.

We used Body condition Index (hereafter "BCI": calculated as the birds' mass/wing chord) of newly captured birds as a proxy for the energetic condition of migrants at our site. BCI and fat scores were highly correlated in the migrating songbird community we studied, however fat scores were measured on a much coarser, categorical scale. Running the same models for fat (measured on a 5 point scale) showed identical

trends compared to our BCI models, however the parameter confidence intervals overlapped zero, likely based on the broad variation of fat stores characterized by each fat score value. Therefore, we used BCI for our model analysis as it offered a finer index of migrant condition. Additionally, while fat makes up the most substantial proportion of energy stores used by migrants during nocturnal flights, protein and hydration levels also play a role in determining a bird's migration flight potential (Klaassen *et al.* 2012). Therefore, body condition is a useful measure that incorporates condition indices such as fat and muscle that are easily quantified through external observations, as well as less-visible accumulations of protein. Increased mass during migration has potential to be detrimental at high levels, however evidence shows that carrying fuel loads is likely cheaper than previously predicted so that maximum flight range is not necessarily lowered by normal levels of fat storage (Kvist *et al.* 2001). In trans-saharan migrants crossing an ecological barrier, sedge warblers (*Acrocephalus schoenobaenus*) were found to have a reduced ability to evade predators at extreme fat loads (>60% lean body mass) (Kullberg *et al.* 2000). In species not facing an ecological barrier, such as the community we studied at Lucky Peak, a bird's risk of predation has not been found to increase within normal body mass ranges (van der Veen 1999). In fact, Dierschke (2003) found that lighter birds are more likely to be captured by predators than heavier individuals. For the purposes of our analyses and interpretation, we assume that birds in our study were not carrying above-optimal fat stores, since birds at our site do not accumulate fat scores of such magnitude, and migrant passerines are known to adaptively regulate their fat stores to balance the risks between starvation and predation (McNamara and Houston 1990; Witter and Cuthill 1993).

1.3.2 Stopover Efficiency.

We calculated the stopover efficiency of species at our site using multiple regression. By regressing the body condition index of each newly captured bird against capture time (calculated as minute after sunrise), we quantified migrants' ability to gain body condition throughout the day, i.e. their stopover efficiency (Winker *et al.* 1992; Dunn 2001; Carlisle *et al.* 2005; Bonter *et al.* 2007). In our study design, the noise-off days at the phantom road site acted as an internal control, while the data collected at the control site allowed further control for weather and migration variability. Using regression based on new captures to calculate condition gain is thought to be a less-biased method of calculating gain during stopover. The regression of new captures against time of day is thought to accurately measure condition gain of a population at a stopover site (Dunn 2001), however this could be biased if some migrants leave the site over the course of the sampling period (in this case during the 5 hours after sunrise). In addition to a problem of small sample sizes, the historic method of using the mass of a single individual at multiple captures may be biased since an individual's condition influences its length of stay at a stopover site, and therefore its probability of recapture (Winker *et al.* 1992).

1.3.3 Capture Rate.

We calculated the capture rate as the number of birds caught per net hour, where one net-hour equals one net open for one hour. We considered capture rate an accurate index of migrant relative abundance at each site, based on past research and previous comparisons of netting and count surveys during migration at this and other sites (Wang and Finch 2002; Carlisle *et al.* 2004). And, because we controlled for the habitat around

mist nets at the control and phantom road sites in this study, we feel confident that capture rate is a valid comparison between sites. Since we ran the same set of models for BCI, stopover efficiency, and capture rate, we determined that comparing capture rate of birds netted to the BCI information was more appropriate than comparing BCI data to the point count data collected at our site.

1.3.4 Species-Specific Models

We analyzed data using the function `lmer` (Bates, D., M. Maechler, and B. Bolker. 2012. `lme4`: Linear mixed-effects models using Eigen and S4 classes in the package `lme4` in Program R (R Development Core Team 2011). We built linear mixed effect models for all 51 species combined, then tested the same set of models on 21 species individually (those with $n > 100$; Tables 1, A1-A3). In addition to multi-species results we present in the main text, seven species analyzed individually showed decreased stopover efficiency or BCI in noise (Table A2).

2. Laboratory Methods

2.1 Captive Sparrows

We mist-netted 20 Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) from Deer Flat National Wildlife Refuge in southwestern Idaho, USA under the Idaho Department of Fish and Game permit # 764-13-000039, and approved by Boise State University IACUC (# 006-AC12-007). We brought birds into the lab in groups of five, captured between March 16 and April 16, 2013. We individually marked each bird with an aluminum USGS band, under federal banding permit #22929. While birds were in captivity, we used strips of plastic tape wrapped around their federal bands to temporarily color mark individuals. The plastic was removed prior to release. Adjacent individual

cages allowed birds to remain within sight and sound of their flock mates while held in the Sensory Ecology Lab animal housing room at Boise State University, Idaho, USA. Birds had access to water *ad libitum* at all times, including during experiments, and we provided a seed mix *ad libitum* in their individual cages when foraging trials or pre-trial acclimations were not underway. The temperature-controlled housing room was set to 19°C and a 12.2:11.8 light:dark cycle with 30 minute twilights to match average outdoor conditions at the time of experiments. We kept birds an average of 5 days, and none were held longer than 7 days; they were released at the location of their original capture.

2.2 Experimental Set-up

We conducted experiments inside the flight room in the Sensory Ecology Lab at Boise State University. The flight room is a 38m² room lined with anechoic foam, which reduces the noise levels in the room to 32 dB(A). In the center of the room, we constructed a 1.5 x 2.5 m foraging arena covered in 2 cm of medium-grain sand. White Millet (*Panicum miliaceum*) seeds scattered evenly over the sand provided homogenous foraging conditions during trials. We maintained a high density of millet seeds (~100g) in the foraging arena so that the supply available to birds during a given trial was not depletable, allowing them to forage at their maximal rate without influencing search time. We placed three natural branches as perches at the edge of the foraging arena at a height of ~0.75 m. After initial capture, we placed birds in the flight room and allowed them to acclimate for a full day with access to seed in the foraging arena. We ensured that birds had learned to feed on the arena, access water dishes, and sit on the perches before we began trials.

During experiments, we allowed birds to feed in their individual cages for 30 min each morning before trials, and then removed access to food 1.5 hrs before the start of an individual's first trial of the day. During this period without food, birds spent 50 min in their individual cages, after which we moved a bird from its cage into the flight room and allowed it 40 additional minutes to acclimate to the room. During this time, the foraging arena was covered to prevent access to seed. At the beginning of each trial, we entered the room to remove the cover over the area and to start video recording. We then returned to an adjacent room where we could observe the trial on a live video feed and control noise playback.

Speakers (Bird speakers; frequency response 70 Hz - 25 kHz; ± 3 dB) at opposite ends of the flight room broadcast sound evenly (± 2 dB(A)) over the foraging arena during noise treatment trials. To allow for comparison between these results and the Phantom Road field experiment, we used the same sound files and matched dB(A) settings for both experiments. We used the phantom road file to create 8-minute-long sound files, adjusting the files to match the required dB(A) levels.

2.3 Behavioral Observations

Foraging trials lasted for 8 minutes and all bird activity and foraging behavior was video recorded during the experimental period. We used an HD video camera (Sony HDV 1080i and Canon XA10 models) to record foraging behavior of individuals during trials. During each foraging trial, we played one of three randomly-selected noise treatments: 61dB(A) traffic noise, 55 dB(A) traffic noise or a silent control track, for 8 minutes. The sound files used a 5 second fade-in at the beginning and end of the traffic

noise so that birds were not startled by the onset of the noise treatment. At the end of the 8 minutes, we stopped the video recording and covered the foraging arena.

We randomly selected treatment order and ran a focal bird through the three, 8-min noise trials. We covered food for 40 minutes between foraging trials to ensure birds were hungry at the start of the next experiment. By covering the foraging arena while allowing birds to remain in the flight room, we eliminated the need to capture and handle birds after each trial and thereby reduced their qualitative stress levels.

During preliminary trials, we found that all birds began investigating the covered foraging arena in search of food between 25-35 minutes after they had last eaten. We therefore chose a 40 min wait time to make sure that all birds were ready to forage at the start of the next trial. We chose an 8 min trial duration because birds did not forage for the entire 8 minutes during preliminary tests or during any trial, so we assumed that they were satiated before the end of the trial and would therefore be equally hungry at the start of each subsequent trial (i.e., the birds did not accumulate hunger throughout the day). By observing the sparrows' naturally-preferred foraging schedule, we were able create an experimental schedule that allowed for the most trials to be conducted in one day without prolonged food deprivation.

2.4 Analysis

We recorded several foraging and vigilance variables based on analysis of the 30 fps HD videos for each trial. By playing back the videos frame by frame we were able to track the exact timing of each movement during a foraging bout. For each trial, we analyzed a 30s foraging bout. We defined the start of a foraging bout as 5 consecutive pecks separated by less than 10s (Quinn *et al.* 2006). Following Quinn *et al.* (2006), we

recorded duration of head-up and down periods, and head-up and down rate for each 30s foraging bout. We defined head-up as when the sparrow's head was above the level of its back and head-down when the head was below the level of the back. We used head-up rate and mean duration of head-down period during trials to quantify the sparrows' vigilance during foraging bouts.

We built two sets of models for 1) head-up rate (head lifts/sec) and 2) mean head-down duration (sec), including combinations of variables for dB(A), time of day, trial number, and day, where trial number indicated the number of trials an individual sparrow had experienced. We also built intercept-only models, and global models that included all factors. We ranked and compared the models using Akaike's Information Criterion (*Akaike 1974*, Table A4). We used individual as a random variable. We considered covariates to be useful for inference if their 85% confidence intervals excluded zero. We used 85% confidence intervals instead of the traditional 95% because they are more appropriate when selecting models using AIC (*Arnold 2010*)

3. Field Study: Species-Specific Results

3.1 Results

Species-specific models indicate varied strategies in the migrant community in response to noise. Of those with significant changes in either BCI or capture rate, four patterns emerged: (1) Three species had lower BCI in noise, but did not leave the site (i.e., did not exhibit a lower capture rate in noise); (2) Five species decreased in abundance when the phantom road was on but individuals that remained did not show reduced BCI or stopover efficiency; (3) Two species showed reduced BCI in noise, *and* reduced capture rate when noise was on; (4) One species, Cassin's vireo (*Vireo cassinii*),

had increased BCI in noise, and did not leave the site. Cassin's finches had lower overall BCI, but compensated by increasing their stopover efficiency. Meanwhile, though no species had higher capture rates during noise, nine of the 21 species examined showed no negative response to the noise.

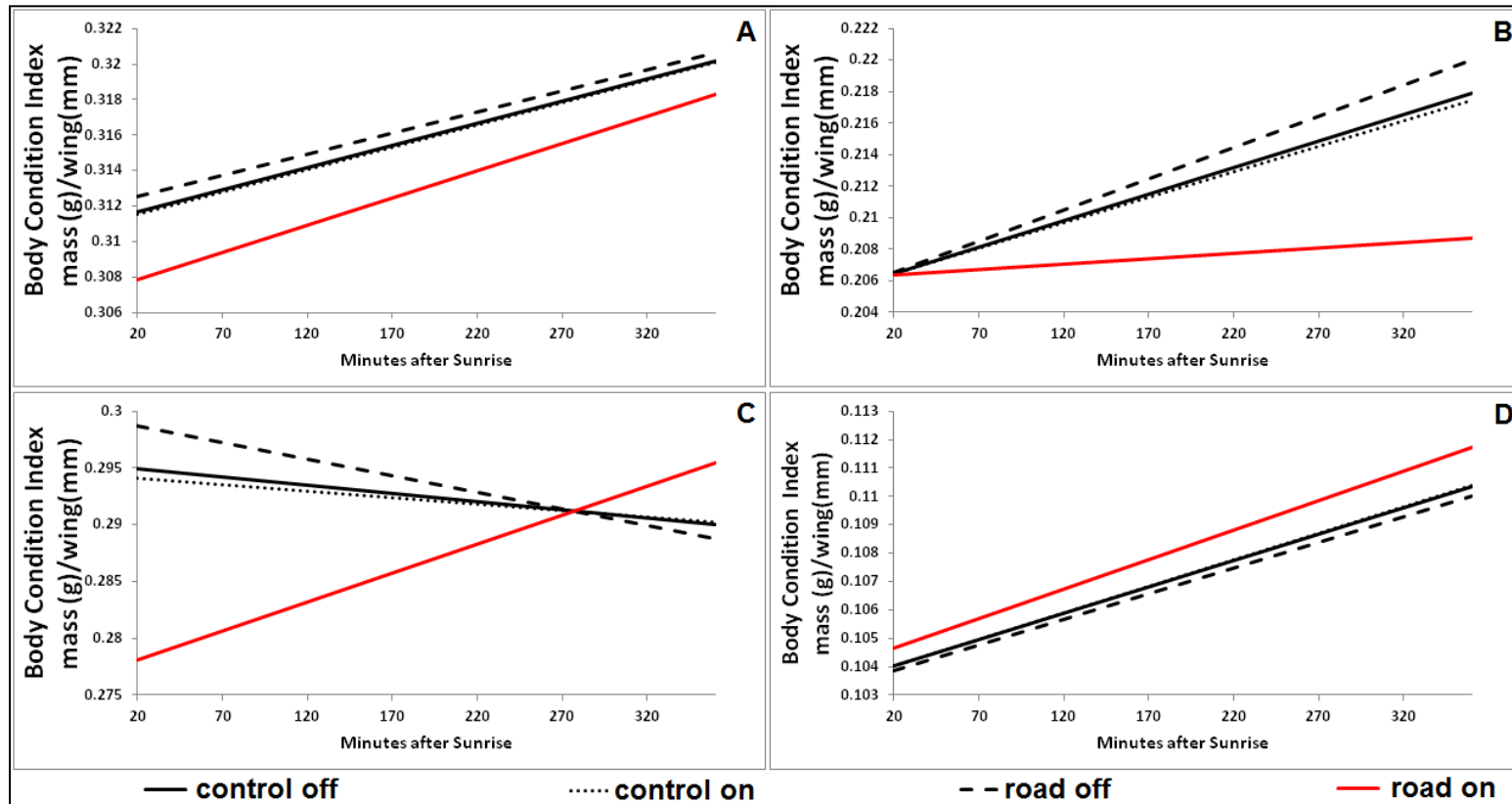


Figure 5 Species-specific Stopover Efficiency Results. Output values from the global model estimates of stopover efficiency for the control site when the road was off (dB(A) 42), control site with road on (dB(A) 43), phantom road with noise turned off (dB(A) 40), and the phantom road with the noise on (dB(A) 51) for three species: white-crowned sparrow (A), MacGillivray's warbler (B), Cassin's finch (C), and Ruby-crowned Kinglet (D). Each showed varying BCI and stopover efficiency responses in the presence of traffic noise.

3.2 Interpretation

Though at first glance it seems difficult to explain these varied responses, a few dynamics might be at play. First, variation in species' behavior likely affects the "choice" to stay in the noise or leave; i.e., the cost of searching for another stopover area might be perceived as higher than remaining in a suboptimal site. Second, if some sensitive individuals depart the noisy area and food availability remains the same, this could make foraging more efficient for the remaining birds. Thus, individuals of some species that remain in the noise might be able to make up for their increased vigilance by easier prey acquisition whereas foraging behavior of other species might not allow for increased efficiencies to offset costs to vigilance. For example, two species showed a positive response in body condition (Cassin's vireo and ruby-crowned kinglet). This result may be a manifestation of birds with high fat stores deciding to remain in noise while low-condition birds decide to leave. This may be the consequence of a difference in foraging requirements between lean and fat birds. Fat birds with enough energy stores to migrate the next night may not need to forage during the day, thus negating costs to their foraging-vigilance tradeoff caused by noise. Lean birds conversely rely heavily on foraging through the day to replenish energy stores (Berthold 1996). The cost of remaining in noise and reducing foraging may therefore be too great, causing lean birds to vacate the phantom road site. One species showed increased stopover efficiency (Cassin's finch), which suggests that at least some individuals of a species were able to take advantage of the reduced abundance of other migratory birds in noise. On the other hand, American robins showed reduced capture rates in noise but individuals that remained did not benefit from reduced competition. MacGillivray's warblers did not

show reduced capture rates in noise, and were the species that showed the strongest negative responses for both BCI and stopover efficiency, indicating that individuals stayed but did poorly in noise. For the entire community, it is likely that sensitive individuals were the first to leave in response to noise disturbance, while more tolerant individuals remained (Bejder *et al.* 2009, reviewed in Francis & Barber 2013). Only exploration of food availability and predator-prey dynamics with and without noise would allow us to further elucidate the different responses of migratory birds to experimental noise.

3.3 The Benefit of Community-Wide Analyses

While these species-specific results are interesting, our study design was optimized to address the entire songbird community as a whole. By testing an entire community, we were likely sampling not only the direct effect of noise on individual species, but also the indirect effects through changes in one species impacting others in the community. Using this community-wide approach likely allowed us to find a greater effect of noise than a single-species study design. Without additional studies specifically designed to address these individual patterns and their causes, it remains difficult to say why some species chose different strategies than others when exposed to traffic noise. Depending on the focal species chosen for a study of this kind, a single-species study could have failed to find an effect simply because of the species chosen, while many other species in the community may have shown an effect of noise.

Conclusion

Both our field and lab experiments offer evidence that traffic noise alone has a negative impact on birds. Our field experiment showed that migrants' stopover efficiency declines when they are exposed to road noise. Birds' ability to gain body condition in noise was cut by almost half (46%) when the phantom road broadcast traffic noise. Our lab experiment showed that white-crowned sparrows exposed to road noise decrease foraging rates and increase vigilance. These results are a significant addition to the road ecology literature, since previous work has never experimentally tested the impact of traffic noise alone on birds, or used community-wide sampling to examine the effects of noise on individuals that stay in noisy conditions. Based on our two experiments, it follows that if the decrease in foraging seen in the lab also occurs in the field, this could be a likely cause for the body condition declines seen in our field study. However, our work does not explicitly verify the connection between these results, and further testing is required if we are to strengthen the existing theoretical connection with supporting data.

To fully connect the foraging-vigilance changes seen in the lab to our field experiment, we would need to conduct in-the-field tests of foraging and vigilance rates. During the 2012 season, we attempted to examine foraging and vigilance behavior in migrants by placing feeding stations with video monitors at the control and phantom road sites. Initially, we used millet seeds, without success. As the season progressed, we attempted various methods for eliciting foraging in front of our cameras but were not able to accomplish this goal. We used a variety of seeds and fruits to attract birds to our foraging trays, and also attempted to capture natural foraging behavior by pointing our cameras at shrubs where birds were known to forage (those with many bitter cherries

[*Prunus sp.*]). The widely available food resources and large variety of foraging strategies used by the migrant community at Lucky Peak made these passive monitoring efforts even more difficult, since the likelihood of a bird foraging in the area in view of the camera was very small.

To successfully measure foraging behavior in our field experiment setup, the method most likely to be successful would probably be active monitoring of foraging birds using video equipment. Experimenters would be required to actively search out foraging birds, feeding at natural food concentrations, and capture video of their behavior. This method may have worked to capture foraging behavior of individuals, however, standardization of monitoring and quantification of foraging behavior would present challenges. It is relatively simple to monitor foraging of ground-feeding, granivorous birds when they are not in dense cover. However, the community at Lucky Peak is comprised of a large variety of species, many of which forage in shrubs and trees, or on the ground under dense cover and leaf litter.

A clear difference between foraging and vigilance behavior is not present in birds that use other foraging strategies. Birds searching for insects often turn their head in a variety of directions, probing in bark crevices, hanging from branches to inspect conifer needles, reaching under leaves with head and bill, or overturning leaves on the ground. Their bodies do not remain on a horizontal axis, making determination of ‘head lifts’ challenging, and with frequent head turning and probing it is difficult to determine whether a bird is scanning for food or predators. Because of songbirds’ laterally placed eyes, head movements along an axis other than the vertical plane are difficult to interpret, and the direction of a birds’ gaze is not often apparent. In order to measure vigilance on

the community of songbirds we tested in our field experiment, an entirely new paradigm for quantifying foraging and vigilance would need to be developed.

Additional lab experiments following a similar experimental set up to our previous tests would also help solidify the connection between reduced foraging and reduced body condition. During our laboratory experiments, each individual experienced each of the noise treatments in a repeated measures design. Therefore, in one day, each bird foraged in all three noise treatments. While this design worked well to reduce variability in our data by testing a bird in all conditions on the same day, it did not allow us to measure mass gain or loss in the lab. To test this, one would need to take birds into captivity for a longer period of time, and expose each individual to only one noise treatment. And unlike our experimental design where birds were provided food *ad libitum* when not involved in trials, birds could be allowed to forage only while exposed to their assigned noise treatment. Thus, birds could be weighed over a period of time to measure whether they lost body condition steadily when exposed to road noise. Though not as informative as a field experiment on an entire songbird community, this test would be relatively simple to conduct, cost effective, and would help describe the underlying mechanisms involved. Because of the difficulty in quantifying vigilance of birds with different foraging strategies, a lab experiment of this type should be conducted on ground feeding species.

When discussing foraging and vigilance in the context of our experiments, it is important to differentiate between the routine vigilance we measured, versus “induced” vigilance (Blanchard and Fritz 2007). Routine vigilance is used by animals while monitoring their environment when there are no obvious threats, while induced vigilance

is a behavior, often perceived as a “startle response,” in animals caused by a threat stimulus (Blanchard and Fritz 2007). Research shows that the routine vigilance we measured in the lab is a good indication of a bird’s ability to avoid predators (Quinn *et al.* 2006), and therefore should be the focus of any future studies on foraging-vigilance behavior in noise.

We measured a reduction in foraging and vigilance levels in birds exposed to traffic noise. Though we only examined this tradeoff in one species with a particular foraging strategy, many other species share similar foraging-vigilance tradeoff behaviors (Lima and Dill 1990). Though more testing is needed, theoretically any animal that uses as similar combination of both visual and auditory vigilance would experience comparable shifts in foraging vigilance behavior.

In addition to solidifying the connection between our measured declines in body-condition gain and reduced foraging, there are a variety of other research avenues opened by our study. We found that in many species some individuals left, while others remained. While we can hypothesize a few reasons for this, direct tests of this effect would be informative. Though not well explored, some research indicates that variations in individual “personalities” or “behavioral syndromes” result in a gradient of behavioral responses to a given stimulus (Sih *et al.* 2004). Testing of birds in a controlled setting could reveal whether some individuals are simply more sensitive to road noise than others, causing them to leave the site while others remain. This can be seen in animals’ responses to other startling stimuli, when some bold individuals respond weakly to a stimulus and more timid individuals respond more strongly (Bejder *et al.* 2009). It seems

plausible that variation in individual sensitivity to a stimulus or a birds “personality” could influence whether it stays or goes when exposed to noise.

Aside from variation in individual sensitivity to noise, birds may have made the decision of whether to depart from the site based on their own body condition. Previous research has shown that birds in poor condition with few fat stores are less likely to leave a site, since the cost of leaving is too high (Smith and McWilliams 2014, Schmaljohann and Naef-Daenzer 2011, Klaassen *et al.* 2012). Whereas birds with high condition can afford the cost of leaving a less-optimal site as well as the added costs of searching for and acclimating to a new site (Smith and McWilliams 2014). Additionally, the influence of noise on the foraging-vigilance tradeoff may affect birds differently based on body condition and foraging needs.

Another direction of research that we left unexplored was the role of predators in our system. We measured an obvious change in both numbers and condition of songbirds at our site. Therefore, it seems highly likely that the predator community also changed in response to the same stimulus, especially the migrant raptor community since they are also highly mobile. Fortunately for the interpretation of our results, most organisms, including birds, are more likely to change their behavior based on *perceived* predation risk, rather than actual predation risk (Lima and Dill 1990; Verdolin 2006). Therefore, if our field results were indeed caused by changes in foraging-vigilance behavior, it is unlikely that varying predator numbers would have significantly altered our conclusions from this study. Our lab results also support this conclusion since sparrows changed vigilance levels in response to noise in the complete absence of predators—their *perceived* predation risk increased, despite their actual predation risk remaining at zero.

One study found that passerines change their behavior and movement patterns in response to hawk numbers during stopover, but did not investigate foraging or vigilance behavior (Cimprich *et al.* 2005). An investigation into the interplay between perceived predation risk and actual risk, and their relative importance in determining bird foraging and vigilance in noise would be fruitful.

In our study, we found that the average body condition of birds at our site decreased when the phantom road was on. Other research has found that compared to body condition of all migrants at a site, migrants with lower body condition are predated in greater proportions than birds with high body condition (Dierschke 2003). Therefore, birds exposed to traffic noise may be at greater risk of predation because of their reduced body condition.

Finally, testing the impact of traffic noise on prey detectability and predator attack rates would be worthwhile. Predators that use auditory cues to detect songbird prey may be at a disadvantage in noise. An investigation of skylarks (*Alauda arvensis*) and merlins (*Falco columbarius*) found that falcons were less likely to attack their songbird prey when the skylarks were singing (Cresswell 1994). Cresswell (1994) found that merlins determined the vigilance levels of potential quarry based upon whether they were singing or not. Larks that sang more were more vigilant, and were therefore attacked less by advertising this vigilance (Cresswell 1994). It is uncertain whether species in the community we studied also use vocalizations as a pursuit deterrent; however, if that is the case, it is highly likely that traffic noise would mask these calls and therefore change predator attack behavior. Investigation into this interaction would be intriguing, since traffic noise could cause predators (that suffer little cost from noise exposure themselves;

e.g., visual hunters) to attack prey more often than normal or inadequately evaluate prey vigilance, perhaps resulting in more unsuccessful pursuits. More predator attacks on otherwise vigilant birds could result in more energy expenditure for both predator and prey. Tests of this type would also need to focus on prey vigilance, determining whether prey are able to remain adequately vigilant in traffic noise, or whether the likelihood that they are captured increases.

Not only could traffic noise cause changes in predator-prey interactions, but the changes we measured in bird behavior and distribution could have cascading effects throughout the ecosystem. Like predator effects, the impacts of traffic noise could be broad. Some potential routes for future study include: investigation of changes in insect communities because of alteration in bird predation rates, consequent changes in rates of insect herbivory, and therefore changes in plant chemistry and overall physiology. A long-term absence of birds in an area could cause increased insect numbers and detrimental effects on plants. Anthropogenic noise is known to impact Pinyon Pine (*Pinus edulis*) communities by altering animal distributions, including avian seed dispersers (Francis *et al.* 2012). At Lucky Peak, where cherries and other fruiting plants rely on birds as a dispersal mechanism, a similar effect is perhaps likely.

Traffic noise may cause cascading effects that physically alter habitats, but it also causes changes in how habitat is perceived by birds. In our study, when we turned the phantom road on, birds were not able to increase body condition at the site. However, we found that the phantom road site was valuable as a stopover location when the noise was off. Birds were able to increase body condition 2.5 times faster when the noise was off at the same site. Thus, while the habitat remained unchanged, the value of that habitat for

stopover decreased because of traffic noise alone. This leads to some interesting questions about habitat degradation. If traffic noise causes habitat degradation, principles such as habitat loss and fragmentation may come into play. Traffic noise, by degrading habitat, may cause physically continuous chunks of habitat to become 'patchy.' More research is needed to test the outcome of such "fragmentation," especially since noise may degrade the value of habitat for one species differently than for another.

When considering the effects of traffic noise on animal populations, we must also pay attention to the role natural sound plays in shaping ecosystems. We don't fully understand all the roles sound plays, especially since natural sounds, like anthropogenic sounds, have the potential to mask signals of organisms. Understanding how natural soundscapes structure communities is an interesting future research direction. The role of natural sounds during migration has been tested and found to play a role in stopover site selection. Mukhin *et al.* (2008) found that nocturnal migrants will use acoustic cues alone to determine whether a location is suitable for stopover. By playing the sounds of bird species associated with wetland environments, they were able to trick wetland specialist birds to land at a desert site. This highlights the importance of natural sounds (e.g., running water, rustling leaves, and chirping insects or amphibians) as habitat cues for birds, especially nocturnal migrants such as songbirds that must choose where to land in dim pre-dawn light. Traffic noise that occurs during times when birds are making habitat selection decisions may mask important natural sounds. This could either cause birds to pass-over the proper habitat type, or—if on a large enough scale—may eliminate acoustic cues as a useful indicator of where birds should stopover, forcing them to choose habitat based on other cues, or "blindly" choose a stopover location if other cues do not exist. A

replication of Mukhin *et al.*'s research, in combination with both natural and anthropogenic noise playback, would be informative.

Though many questions remain, our research has brought to light some important and previously unexplored aspects of road ecology. While previous research determined that roads were having an effect on animal populations, we were able to determine that the traffic noise alone is enough to impact wildlife. Since anthropogenic noise pollution continues to increase, and many protected areas do not currently manage for noise pollution, this has important implications for how we manage roads and traffic in the future (Barber *et al.* 2011). Unlike other aspects of roads, noise is more easily controlled through a few relatively simple methods, when compared to the alternative of removing an entire road to control impacts. Altering the road substrate and tire type or changing speed limits are cost-effective strategies known to reduce noise levels (Wayson 1998). As the number of electric and hybrid cars increases, the impact from roads has the potential to decrease. However, there is already legislation in place requiring the next generation of energy-efficient cars to make *additional* noise (NHTSA 2013). Ecologists stand to face an entirely new set of impacts on a different set of species than previous if sounds become louder or incorporate a new range of frequencies. Since it is not likely that the number of roads in the US will decrease, evidence that noise is responsible for a substantial portion of roads' impact could help with mitigation efforts while not drastically changing or limiting future road projects.

As the world's population continues to grow, increases in traffic noise—and the global footprint of roads on the landscape—are inevitable. With the human population projected to reach 11 billion by the year 2100 (Gerland *et al.* 2014), wildlife across the

globe will face even more threats from anthropogenic impacts. By quantifying the impacts of various anthropogenic changes to habitat and managing for these effects, we may be able to reduce the amount of habitat lost to wildlife. Recognizing that noise reduces habitat quality is the first step in taking action to mitigate the impacts our roads have on organisms.

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APPENDIX

AIC Model Output Results

Table A.1 AIC model output results for body condition analysis.

All Species					
Model	k	AIC	Δ AIC	w_i	
dB(A) + day + day ² + year	5	-51180.75	0.00	0.75	
day + day ² + year	4	-51177.63	3.12	0.16	
day + year	3	-51175.29	5.46	0.05	
noise X site + day + day ² + year	7	-51174.93	5.82	0.04	
dB(A) + year	3	-51089.28	91.47	0.00	
null	2	-51085.86	94.89	0.00	
noise + year	3	-51061.98	118.77	0.00	
Ruby-crowned Kinglet					
Model	k	AIC	Δ AIC	w_i	
dB(A) + day + day ² + year	5	-18815.17	0.00	0.54	
noise X site + day + day ² + year	7	-18814.26	0.91	0.34	
day + year	3	-18811.63	3.54	0.09	
day + day ² + year	4	-18809.64	5.53	0.03	
dB(A) + year	3	-18796.00	19.17	0.00	
null	2	-18791.29	23.88	0.00	
noise + year	3	-18790.75	24.42	0.00	
White-crowned Sparrow					
Model	k	AIC	Δ AIC	w_i	
dB(A) + day + day ² + year	5	-5867.00	0.00	0.55	
noise X site + day + day ² + year	7	-5865.11	1.90	0.21	
day + year	3	-5863.93	3.07	0.12	
day + day ² + year	4	-5862.66	4.35	0.06	
dB(A) + year	3	-5862.25	4.75	0.05	
null	2	-5855.75	11.26	0.00	
noise + year	3	-5854.89	12.11	0.00	
Dark-eyed Junco					
Model	k	AIC	Δ AIC	w_i	
noise X site + day + day ² + year	7	-4199.38	0.00	0.41	
dB(A) + day + day ² + year	5	-4199.15	0.23	0.36	
day + year	3	-4197.27	2.11	0.14	
day + day ² + year	4	-4196.06	3.32	0.08	
dB(A) + year	3	-4191.12	8.27	0.01	
noise + year	3	-4189.59	9.79	0.00	
null	2	-4186.87	12.51	0.00	

Yellow-rumped Warbler

Model	k	AIC	Δ AIC	wi
day + year	3	-3867.85	0.00	0.62
day + day ² + year	4	-3866.02	1.83	0.25
dB(A) + day + day ² + year	5	-3864.03	3.82	0.09
noise X site + day + day ² + year	7	-3862.41	5.44	0.04
null	2	-3846.68	21.17	0.00
noise + year	3	-3845.00	22.85	0.00
dB(A) + year	3	-3844.68	23.17	0.00

Dusky Flycatcher

Model	k	AIC	Δ AIC	wi
day + year	3	-3054.97	0.00	0.45
noise X site + day + day ² + year	7	-3053.66	1.31	0.23
day + day ² + year	4	-3053.21	1.76	0.19
dB(A) + day + day ² + year	5	-3051.68	3.29	0.09
null	2	-3049.12	5.85	0.02
noise + year	3	-3048.29	6.68	0.02
dB(A) + year	3	-3047.51	7.46	0.01

Western Tanager

Model	k	AIC	Δ AIC	wi
dB(A) + day + day ² + year	5	-1670.06	0.00	0.50
day + day ² + year	4	-1669.10	0.96	0.31
dB(A) + year	3	-1665.79	4.27	0.06
noise X site + day + day ² + year	7	-1665.27	4.79	0.05
day + year	3	-1665.08	4.98	0.04
null	2	-1664.88	5.18	0.04
noise + year	3	-1662.93	7.13	0.01

Yellow Warbler

Model	k	AIC	Δ AIC	wi
day + year	3	-2463.95	0.00	0.44
day + day ² + year	4	-2463.59	0.36	0.37
dB(A) + day + day ² + year	5	-2461.82	2.13	0.15
noise X site + day + day ² + year	7	-2458.92	5.03	0.04
null	2	-2428.62	35.33	0.00
noise + year	3	-2427.63	36.33	0.00
dB(A) + year	3	-2426.65	37.30	0.00

Spotted Towhee

Model	k	AIC	Δ AIC	wi
day + day ² + year	4	-1492.68	0.00	0.32
noise X site + day + day ² + year	7	-1492.65	0.03	0.31
dB(A) + day + day ² + year	5	-1492.50	0.18	0.29
day + year	3	-1489.78	2.89	0.07
null	2	-1465.60	27.07	0.00
noise + year	3	-1464.32	28.36	0.00
dB(A) + year	3	-1463.96	28.72	0.00

Orange-crowned Warbler

Model	k	AIC	Δ AIC	wi
day + year	3	-1906.38	0.00	0.56
day + day ² + year	4	-1904.45	1.94	0.21
dB(A) + day + day ² + year	5	-1902.49	3.89	0.08
null	2	-1902.11	4.27	0.07
noise + year	3	-1901.06	5.32	0.04
dB(A) + year	3	-1900.22	6.16	0.03
noise X site + day + day ² + year	7	-1899.51	6.87	0.02

MacGillivray's Warbler

Model	k	AIC	Δ AIC	wi
dB(A) + day + day ² + year	5	-1711.34	0.00	0.60
day + year	3	-1708.63	2.71	0.15
day + day ² + year	4	-1708.58	2.76	0.15
noise X site + day + day ² + year	7	-1707.74	3.60	0.10
null	2	-1682.72	28.62	0.00
dB(A) + year	3	-1682.70	28.64	0.00
noise + year	3	-1682.02	29.32	0.00

Warbling Vireo

Model	k	AIC	Δ AIC	wi
null	2	-1623.38	0.00	0.40
dB(A) + year	3	-1621.91	1.46	0.19
day + year	3	-1621.54	1.84	0.16
noise + year	3	-1621.43	1.95	0.15
day + day ² + year	4	-1619.57	3.81	0.06
dB(A) + day + day ² + year	5	-1618.06	5.31	0.03
noise X site + day + day ² + year	7	-1616.59	6.79	0.01

Cassin's Vireo

Model	k	AIC	Δ AIC	wi
noise X site + day + day ² + year	7	-1094.87	0.00	0.87
day + year	3	-1089.20	5.67	0.05
day + day ² + year	4	-1087.63	7.24	0.02
noise + year	3	-1087.33	7.55	0.02
null	2	-1087.05	7.83	0.02
dB(A) + day + day ² + year	5	-1085.64	9.23	0.01
dB(A) + year	3	-1085.05	9.82	0.01

Hammond's Flycatcher

Model	k	AIC	Δ AIC	wi
day + day ² + year	4	-1140.84	0.00	0.46
day + year	3	-1139.07	1.77	0.19
dB(A) + day + day ² + year	5	-1138.87	1.96	0.17
null	2	-1137.44	3.40	0.08
noise X site + day + day ² + year	7	-1135.90	4.94	0.04
dB(A) + year	3	-1135.45	5.39	0.03
noise + year	3	-1135.44	5.39	0.03

Wilson's Warbler

Model	k	AIC	Δ AIC	wi
day + day ² + year	4	-1015.74	0.00	0.28
noise X site + day + day ² + year	7	-1015.30	0.44	0.23
dB(A) + day + day ² + year	5	-1014.98	0.77	0.19
day + year	3	-1013.96	1.79	0.12
null	2	-1013.16	2.59	0.08
noise + year	3	-1012.94	2.80	0.07
dB(A) + year	3	-1011.74	4.01	0.04

Nashville Warbler

Model	k	AIC	Δ AIC	wi
day + year	3	-1003.66	0.00	0.60
day + day ² + year	4	-1001.68	1.98	0.22
dB(A) + day + day ² + year	5	-1000.03	3.63	0.10
null	2	-998.13	5.53	0.04
dB(A) + year	3	-996.57	7.09	0.02
noise X site + day + day ² + year	7	-996.28	7.38	0.01
noise + year	3	-996.23	7.43	0.01

Townsend's Solitaire

Model	k	AIC	Δ AIC	wi
null	2	-775.04	0.00	0.25
dB(A) + year	3	-774.97	0.08	0.24
day + year	3	-774.49	0.56	0.19
day + day ² + year	4	-773.41	1.64	0.11
noise + year	3	-773.22	1.82	0.10
dB(A) + day + day ² + year	5	-773.03	2.01	0.09
noise X site + day + day ² + year	7	-768.25	6.79	0.01

Townsend's Warbler

Model	k	AIC	Δ AIC	wi
day + year	3	-800.83	0.00	0.45
day + day ² + year	4	-798.92	1.91	0.17
null	2	-798.23	2.60	0.12
dB(A) + day + day ² + year	5	-797.80	3.03	0.10
dB(A) + year	3	-797.79	3.03	0.10
noise + year	3	-796.15	4.68	0.04
noise X site + day + day ² + year	7	-793.07	7.75	0.01

Chipping Sparrow

Model	k	AIC	Δ AIC	wi
day + year	3	-718.31	0.00	0.36
dB(A) + day + day ² + year	5	-717.30	1.01	0.22
noise X site + day + day ² + year	7	-717.06	1.26	0.19
day + day ² + year	4	-716.75	1.56	0.17
null	2	-713.40	4.91	0.03
noise + year	3	-711.96	6.35	0.02
dB(A) + year	3	-711.92	6.40	0.01

American Robin

Model	k	AIC	Δ AIC	wi
noise + year	3	-315.18	0.00	0.33
null	2	-315.04	0.14	0.31
dB(A) + year	3	-313.67	1.51	0.15
day + year	3	-313.06	2.11	0.11
day + day ² + year	4	-311.68	3.50	0.06
dB(A) + day + day ² + year	5	-310.12	5.05	0.03
noise X site + day + day ² + year	7	-308.51	6.66	0.01

Hermit Thrush					
Model	k	AIC	Δ AIC	wi	
day + year	3	-523.034	0	0.34822	
day + day ² + year	4	-521.769	1.2643	0.185061	
null	2	-521.44	1.5937	0.156959	
dB(A) + day + day ² + year	5	-520.482	2.5521	0.097201	
noise X site + day + day ² + year	7	-520.013	3.0209	0.076891	
noise + year	3	-519.863	3.1707	0.071342	
dB(A) + year	3	-519.656	3.3777	0.064327	
Cassin's Finch					
Model	k	AIC	Δ AIC	wi	
dB(A) + day + day ² + year	5	-589.958	0	0.27326	
noise X site + day + day ² + year	7	-589.589	0.3684	0.22729	
dB(A) + year	3	-589.062	0.8953	0.174648	
day + day ² + year	4	-588.161	1.7963	0.111305	
null	2	-587.781	2.1762	0.092049	
day + year	3	-587.677	2.2805	0.087372	
noise + year	3	-585.794	4.1637	0.034075	

Table A.2 AIC model output results for stopover efficiency analysis.

All Species					
Model	k	AIC	Δ AIC	wi	
dB(A) X minute + day + day ² + year	7	-51270.02	0.00	0.57	
day X minute + year	5	-51268.08	1.94	0.22	
minute(day + day ²) + year	7	-51267.95	2.07	0.20	
noise X site X minute + day + day ² + year	11	-51261.53	8.49	0.01	
dB(A) X minute + year	5	-51183.05	86.97	0.00	
noise X minute + year	5	-51176.51	93.51	0.00	
null	2	-51085.86	184.16	0.00	
Ruby-crowned Kinglet					
Model	k	AIC	Δ AIC	wi	
dB(A) X minute + day + day ² + year	7	-18935.33	0.00	0.84	
day X minute + year	5	-18931.44	3.89	0.12	
noise X site X minute + day + day ² + year	11	-18928.16	7.17	0.02	
minute(day + day ²) + year	7	-18928.03	7.30	0.02	
dB(A) X minute + year	5	-18914.48	20.85	0.00	
noise X minute + year	5	-18908.90	26.43	0.00	
null	2	-18791.29	144.04	0.00	

White-crowned Sparrow

Model	k	AIC	Δ AIC	wi
dB(A) X minute + day + day ² + year	7	-5874.79	0	0.5946
minute(day + day ²)+ year	7	-5872.06	2.729	0.151925
day X minute + year	5	-5871.99	2.799	0.1467
noiseX site X minute + day + day ² + year	11	-5870.16	4.631	0.058697
dB(A) X minute + year	5	-5869.69	5.092	0.046613
noise X minute + year	5	-5862.71	12.073	0.001421
null	2	-5855.75	19.04	4.36E-05

Dark-eyed Junco

Model	k	AIC	Δ AIC	wi
dB(A) X minute + day + day ² + year	7	-4225.93	0	0.4082
day X minute + year	5	-4225.62	0.308	0.349938
minute(day + day ²)+ year	7	-4222.93	3.001	0.091036
noiseX site X minute + day + day ² + year	11	-4222.57	3.357	0.076192
dB(A) X minute + year	5	-4221.44	4.488	0.043283
noise X minute + year	5	-4220.8	5.133	0.031351
null	2	-4186.87	39.059	1.35E-09

Yellow-rumped Warbler

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-3883.5	0	0.713255
minute(day + day ²)+ year	7	-3879.72	3.783	0.107591
dB(A) X minute + day + day ² + year	7	-3879.52	3.984	0.097304
noiseX site X minute + day + day ² + year	11	-3879.17	4.332	0.081764
noise X minute + year	5	-3864.68	18.819	5.84E-05
dB(A) X minute + year	5	-3863.12	20.375	2.68E-05
null	2	-3846.68	36.815	7.23E-09

Dusky Flycatcher

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-3052.52	0	0.393163
dB(A) X minute + day + day ² + year	7	-3051.6	0.919	0.248322
minute(day + day ²)+ year	7	-3050.35	2.171	0.132784
noiseX site X minute + day + day ² + year	11	-3049.85	2.674	0.103257
null	2	-3049.12	3.406	0.071609
dB(A) X minute + year	5	-3047.23	5.29	0.027917
noise X minute + year	5	-3046.84	5.682	0.022948

Western Tanager

Model	k	AIC	Δ AIC	wi
dB(A) X minute + day + day ² + year	7	-1669.27	0	0.643712
minute(day + day ²) + year	7	-1666.41	2.853	0.154586
null	2	-1664.88	4.389	0.071719
dB(A) X minute + year	5	-1663.99	5.279	0.045959
day X minute + year	5	-1663.33	5.935	0.033107
noise X minute + year	5	-1662.9	6.371	0.026622
noiseX site X minute + day + day ² + year	11	-1662.71	6.554	0.024295

Yellow Warbler

Model	k	AIC	Δ AIC	wi
minute(day + day ²) + year	7	-2480.03	0	0.993151
day X minute + year	5	-2469.37	10.658	0.004816
dB(A) X minute + day + day ² + year	7	-2467.47	12.56	0.001861
noiseX site X minute + day + day ² + year	11	-2462.72	17.311	0.000173
noise X minute + year	5	-2429.59	50.439	1.11E-11
dB(A) X minute + year	5	-2429.58	50.447	1.1E-11
null	2	-2428.62	51.411	6.81E-12

Spotted Towhee

Model	k	AIC	Δ AIC	wi
noiseX site X minute + day + day ² + year	11	-1492.57	0	0.794264
dB(A) X minute + day + day ² + year	7	-1488.92	3.65	0.128049
minute(day + day ²) + year	7	-1486.92	5.656	0.046966
day X minute + year	5	-1486.07	6.505	0.03072
null	2	-1465.6	26.969	1.11E-06
noise X minute + year	5	-1463.31	29.265	3.51E-07
dB(A) X minute + year	5	-1460.28	32.293	7.72E-08

Orange-crowned Warbler

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-1906.36	0	0.727415
minute(day + day ²) + year	7	-1902.46	3.901	0.103441
null	2	-1902.11	4.255	0.08666
dB(A) X minute + day + day ² + year	7	-1900	6.361	0.030235
noise X minute + year	5	-1899.46	6.902	0.023069
noiseX site X minute + day + day ² + year	11	-1898.89	7.475	0.017322
dB(A) X minute + year	5	-1898.13	8.233	0.011858

MacGillivray's Warbler

Model	k	AIC	Δ AIC	wi
dB(A) X minute + day + day ² + year	7	-1720.25	0	0.872978
day X minute + year	5	-1714.83	5.423	0.057998
noise X site X minute + day + day ² + year	11	-1714.29	5.962	0.044297
minute(day + day ²) + year	7	-1713.12	7.128	0.024727
dB(A) X minute + year	5	-1689.71	30.545	2.03E-07
noise X minute + year	5	-1689.08	31.171	1.49E-07
null	2	-1682.72	37.529	6.19E-09

Warbling Vireo

Model	k	AIC	Δ AIC	wi
dB(A) X minute + year	5	-1624.28	0	0.340729
null	2	-1623.38	0.906	0.216608
day X minute + year	5	-1622.93	1.349	0.173571
noise X minute + year	5	-1622.93	1.352	0.173311
dB(A) X minute + day + day ² + year	7	-1621.03	3.249	0.067127
minute(day + day ²) + year	7	-1619.11	5.176	0.025613
noise X site X minute + day + day ² + year	11	-1614.85	9.438	0.003041

Cassin's Vireo

Model	k	AIC	Δ AIC	wi
noise X site X minute + day + day ² + year	11	-1100.18	0	0.454453
day X minute + year	5	-1099.28	0.903	0.289338
minute(day + day ²) + year	7	-1096.83	3.353	0.084995
noise X minute + year	5	-1096.7	3.489	0.079408
dB(A) X minute + day + day ² + year	7	-1095.95	4.23	0.054822
dB(A) X minute + year	5	-1095.13	5.052	0.036346
null	2	-1087.05	13.139	0.000637

Hammond's Flycatcher

Model	k	AIC	Δ AIC	wi
null	2	-1137.44	0	0.31947
minute(day + day ²) + year	7	-1136.94	0.495	0.249426
day X minute + year	5	-1136.89	0.546	0.243146
dB(A) X minute + day + day ² + year	7	-1135.64	1.795	0.130212
dB(A) X minute + year	5	-1132.59	4.85	0.028266
noise X minute + year	5	-1132.29	5.152	0.024305
noise X site X minute + day + day ² + year	11	-1129.19	8.246	0.005174

Wilson's Warbler

Model	k	AIC	Δ AIC	wi
minute(day + day ²) + year	7	-1015.4	0	0.329316
dB(A) X minute + day + day ² + year	7	-1014.68	0.72	0.229756
day X minute + year	5	-1014.13	1.266	0.174865
null	2	-1013.16	2.24	0.107449
noise X site X minute + day + day ² + year	11	-1012.88	2.513	0.093739
dB(A) X minute + year	5	-1011.07	4.33	0.037789
noise X minute + year	5	-1010.4	4.996	0.027086

Nashville Warbler

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-1006.02	0	0.617357
minute(day + day ²) + year	7	-1003.47	2.5434	0.173079
dB(A) X minute + day + day ² + year	7	-1001.82	4.1993	0.075626
noise X minute + year	5	-1001.45	4.5719	0.062771
dB(A) X minute + year	5	-1001.27	4.7505	0.057409
null	2	-998.131	7.8869	0.011965
noise X site X minute + day + day ² + year	11	-994.334	11.683	0.001793

Townsend's Solitaire

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-776.613	0	0.349795
dB(A) X minute + year	5	-775.762	0.8506	0.228617
null	2	-775.043	1.5693	0.159604
dB(A) X minute + day + day ² + year	7	-774.311	2.3013	0.110686
noise X minute + year	5	-773.48	3.133	0.073028
minute(day + day ²) + year	7	-773.461	3.1521	0.072334
noise X site X minute + day + day ² + year	11	-768.46	8.1529	0.005935

Townsend's Warbler

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-799.693	0	0.337532
dB(A) X minute + year	5	-798.55	1.143	0.190597
null	2	-798.227	1.4664	0.16214
noise X minute + year	5	-797.481	2.2119	0.111688
minute(day + day ²) + year	7	-797.31	2.3834	0.10251
dB(A) X minute + day + day ² + year	7	-797.081	2.612	0.091438
noise X site X minute + day + day ² + year	11	-790.869	8.8237	0.004095

Chipping Sparrow

Model	k	AIC	Δ AIC	wi
day X minute + year	5	-722.328	0	0.468486
dB(A) X minute + day + day ² + year	7	-721.133	1.1953	0.257716
minute(day + day ²) + year	7	-720.594	1.7344	0.196823
noise X site X minute + day + day ² + year	11	-717.811	4.5171	0.048958
dB(A) X minute + year	5	-715.114	7.2145	0.012708
noise X minute + year	5	-714.618	7.7107	0.009916
null	2	-713.399	8.9289	0.005393

American Robin

Model	k	AIC	Δ AIC	wi
null	2	-315.036	0	0.34235
day X minute + year	5	-314.433	0.6033	0.253201
minute(day + day ²) + year	7	-313.521	1.5149	0.160514
noise X minute + year	5	-313.149	1.8866	0.133291
dB(A) X minute + year	5	-312.44	2.5956	0.093507
dB(A) X minute + day + day ² + year	7	-308.979	6.0573	0.016563
noise X site X minute + day + day ² + year	11	-302.257	12.7792	0.000575

Hermit Thrush

Model	k	AIC	Δ AIC	wi
null	2	-521.44	0	0.476845
day X minute + year	5	-519.753	1.687	0.20514
minute(day + day ²) + year	7	-519.732	1.7081	0.202987
dB(A) X minute + day + day ² + year	7	-516.74	4.7	0.045476
noise X minute + year	5	-515.871	5.569	0.02945
dB(A) X minute + year	5	-515.7	5.7395	0.027043
noise X site X minute + day + day ² + year	11	-514.245	7.1954	0.013059

Cassin's Finch

Model	k	AIC	Δ AIC	wi
dB(A) X minute + day + day ² + year	7	-590.127	0	0.532096
dB(A) X minute + year	5	-588.234	1.8938	0.206422
null	2	-587.781	2.346	0.16465
minute(day + day ²) + year	7	-584.84	5.2879	0.037821
day X minute + year	5	-584.679	5.4483	0.034907
noise X minute + year	5	-582.626	7.5018	0.012502
noise X site X minute + day + day ² + year	11	-582.476	7.6515	0.011601

Table A.3 AIC model output results for capture rate analysis.

All Species				
Model	k	AIC	Δ AIC	wi
noise X site + day + day ² + year		-121739.60	0.00	0.97
dB(A) + day + day ² + year		-121732.40	7.20	0.03
day + day ² + year		-121728.00	11.60	0.00
day + year		-121718.50	21.10	0.00
noise X site + year		-121660.80	78.80	0.00
dB(A) + year		-121653.60	86.00	0.00
noise + year		-121649.00	90.60	0.00
null		-121647.6	92	1.02E-20
Ruby-crowned Kinglet				
Model	k	AIC	Δ AIC	wi
noise X site + day + day ² + year	9	4241.82	0.00	0.79
day + day ² + year	6	4245.46	3.64	0.13
dB(A) + day + day ² + year	7	4246.45	4.63	0.08
day + year	5	4317.38	75.57	0.00
noise X site + year	7	4523.72	281.90	0.00
dB(A) + year	5	4527.71	285.89	0.00
null	4	4528.53	286.71	0.00
noise + year	5	4528.893	287.078	3.64E-63
White-crowned Sparrow				
Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-1386.557	0	0.529979
dB(A) + day + day ² + year	7	-1386.099	0.458	0.421508
noise X site + day + day ² + year	9	-1381.775	4.782	0.048513
day + year	5	-1344.032	42.525	3.09E-10
null	4	-1317.029	69.528	4.23E-16
dB(A) + year	5	-1315.696	70.861	2.17E-16
noise + year	5	-1315.124	71.433	1.63E-16
noise X site + year	7	-1312.17	74.387	3.73E-17
Dark-eyed Junco				
Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-3748.552	0	0.521856
noise X site + day + day ² + year	9	-3747.349	1.203	0.285971
dB(A) + day + day ² + year	7	-3746.554	1.998	0.192172
day + year	5	-3680.84	67.712	1.03E-15
null	4	-3496.428	252.124	9.32E-56
dB(A) + year	5	-3494.85	253.702	4.24E-56

noise + year	5	-3494.508	254.044	3.57E-56
noise X site + year	7	-3492.91	255.642	1.61E-56

Yellow-rumped Warbler

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-5738.339	0	0.316208
dB(A) + day + day ² + year	7	-5738.321	0.018	0.313375
noise X site + day + day ² + year	9	-5737.667	0.672	0.225969
day + year	5	-5736.153	2.186	0.105996
null	4	-5732.305	6.034	0.015478
dB(A) + year	5	-5731.954	6.385	0.012986
noise X site + year	7	-5731.429	6.91	0.009988
noise + year	5	-5730.43	7.909	0.006061

Dusky Flycatcher

Model	k	AIC	Δ AIC	wi
noise X site + day + day ² + year	9	-10363.08	0	0.941261
dB(A) + day + day ² + year	7	-10356.41	6.67	0.033523
day + day ² + year	6	-10355.84	7.24	0.025209
day + year	5	-10339.4	23.68	6.79E-06
noise X site + year	7	-10104.94	258.14	8.3E-57
noise + year	5	-10104.21	258.87	5.77E-57
dB(A) + year	5	-10097.68	265.4	2.2E-58
null	4	-10096.75	266.33	1.38E-58

Western Tanager

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-5496.723	0	0.513612
noise X site + day + day ² + year	9	-5495.388	1.335	0.263478
dB(A) + day + day ² + year	7	-5495.039	1.684	0.221289
day + year	5	-5485.206	11.517	0.001621
null	4	-5459.489	37.234	4.22E-09
noise + year	5	-5458.925	37.798	3.18E-09
dB(A) + year	5	-5458.221	38.502	2.24E-09
noise X site + year	7	-5456.57	40.153	9.81E-10

Yellow Warbler

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-9632.233	0	0.673848
dB(A) + day + day ² + year	7	-9630.365	1.868	0.264808
noise X site + day + day ² + year	9	-9627.44	4.793	0.061344
day + year	5	-9579.675	52.558	2.6E-12

null	4	-9349.902	282.331	3.32E-62
dB(A) + year	5	-9348.424	283.809	1.59E-62
noise + year	5	-9348.151	284.082	1.38E-62
noise X site + year	7	-9345.328	286.905	3.37E-63

Spotted Towhee

Model	k	AIC	Δ AIC	wi
dB(A) + day + day ² + year	7	-11871.91	0	0.641802
day + day ² + year	6	-11870.48	1.43	0.313965
noise X site + day + day ² + year	9	-11866.56	5.35	0.044225
day + year	5	-11849.49	22.42	8.69E-06
dB(A) + year	5	-11812.95	58.96	1.01E-13
null	4	-11812.86	59.05	9.66E-14
noise + year	5	-11811.05	60.86	3.91E-14
noise X site + year	7	-11809.05	62.86	1.44E-14

Orange-crowned Warbler

Model	k	AIC	Δ AIC	wi
noise X site + day + day ² + year	9	-12375	0	0.61388
dB(A) + day + day ² + year	7	-12372.76	2.24	0.200297
day + day ² + year	6	-12372.61	2.39	0.185824
null	4	-12329.39	45.61	7.66E-11
noise + year	5	-12329.16	45.84	6.82E-11
noise X site + year	7	-12328.86	46.14	5.87E-11
dB(A) + year	5	-12328.38	46.62	4.62E-11
day + year	5	-12328.2	46.8	4.22E-11

MacGillivray's Warbler

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-13059.41	0	0.627627
dB(A) + day + day ² + year	7	-13058.02	1.39	0.313233
noise X site + day + day ² + year	9	-13054.65	4.76	0.058087
day + year	5	-13046.63	12.78	0.001053
null	4	-12863.21	196.2	1.56E-43
dB(A) + year	5	-12862.04	197.37	8.7E-44
noise + year	5	-12861.39	198.02	6.28E-44
noise X site + year	7	-12858.56	200.85	1.53E-44

Warbling Vireo

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-11895.10	0.00	0.54
noise X site + day + day ² + year	9	-11893.60	1.50	0.25

dB(A) + day + day ² + year	7	-11893.10	2.00	0.20
day + year	5	-11887.05	8.05	0.01
noise + year	5	-11826.04	69.06	0.00
null	4	-11824.79	70.31	0.00
noise X site + year	7	-11824.75	70.35	0.00
dB(A) + year	5	-11822.86	72.24	0.00

Cassin's Vireo

Model	k	AIC	ΔAIC	wi
day + day ² + year	6	-14579.84	0	0.55744
dB(A) + day + day ² + year	7	-14578.81	1.03	0.333071
noise X site + day + day ² + year	9	-14575.93	3.91	0.078914
null	4	-14572.37	7.47	0.013308
dB(A) + year	5	-14570.95	8.89	0.006543
day + year	5	-14570.64	9.2	0.005603
noise + year	5	-14570.46	9.38	0.005121
noise X site + year	7	-14568.54	11.3	0.001961

Hammond's Flycatcher

Model	k	AIC	ΔAIC	wi
noise X site + day + day ² + year	9	-16111.58	0	0.718425
day + day ² + year	6	-16109.03	2.55	0.20075
dB(A) + day + day ² + year	7	-16107.21	4.37	0.080807
noise X site + year	7	-16089.14	22.44	9.63E-06
null	4	-16087.67	23.91	4.62E-06
noise + year	5	-16085.99	25.59	1.99E-06
day + year	5	-16085.69	25.89	1.72E-06
dB(A) + year	5	-16085.68	25.9	1.71E-06

Wilson's Warbler

Model	k	AIC	ΔAIC	wi
noise X site + day + day ² + year	9	-16362.14	0	0.678254
dB(A) + day + day ² + year	7	-16360.16	1.98	0.252023
day + day ² + year	6	-16357.59	4.55	0.069722
day + year	5	-16325.39	36.75	7.1E-09
noise + year	5	-16313	49.14	1.45E-11
dB(A) + year	5	-16310.2	51.94	3.57E-12
noise X site + year	7	-16309.36	52.78	2.35E-12
null	4	-16309.32	52.82	2.3E-12

Nashville Warbler

Model	k	AIC	Δ AIC	wi
day + year	5	-14961.77	0	0.471212
day + day ² + year	6	-14960.8	0.97	0.290124
dB(A) + day + day ² + year	7	-14960.05	1.72	0.199399
noise X site + day + day ² + year	9	-14956.8	4.97	0.039264
null	4	-14919.73	42.04	3.5E-10
dB(A) + year	5	-14918.7	43.07	2.09E-10
noise + year	5	-14917.99	43.78	1.47E-10
noise X site + year	7	-14915.44	46.33	4.1E-11

Townsend's Solitaire

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-13636.33	0	0.459105
day + year	5	-13635.5	0.83	0.303165
dB(A) + day + day ² + year	7	-13634.65	1.68	0.1982
noise X site + day + day ² + year	9	-13631.42	4.91	0.03942
null	4	-13618.35	17.98	5.72E-05
noise + year	5	-13616.83	19.5	2.68E-05
dB(A) + year	5	-13616.75	19.58	2.57E-05
noise X site + year	7	-13613.6	22.73	5.32E-06

Townsend's Warbler

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-13463.09	0	0.420621
day + year	5	-13461.55	1.54	0.194753
dB(A) + day + day ² + year	7	-13461.11	1.98	0.156293
noise X site + day + day ² + year	9	-13459.78	3.31	0.080377
null	4	-13459.67	3.42	0.076076
noise + year	5	-13458.57	4.52	0.043892
dB(A) + year	5	-13457.67	5.42	0.027987
noise X site + year	7	-13455.78	7.31	0.010878

Chipping Sparrow

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-15817.23	0	0.476263
dB(A) + day + day ² + year	7	-15815.79	1.44	0.231822
day + year	5	-15815.61	1.62	0.21187
noise X site + day + day ² + year	9	-15812.2	5.03	0.038512
null	4	-15811	6.23	0.021136
dB(A) + year	5	-15809.79	7.44	0.011542
noise + year	5	-15809.26	7.97	0.008855

noise X site + year	7	-15805.62	11.61	0.001435
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American Robin

Model	k	AIC	Δ AIC	wi
dB(A) + day + day ² + year	7	-15527.37	0	0.986455
dB(A) + year	5	-15517.25	10.12	0.00626
day + day ² + year	6	-15516.47	10.9	0.004238
day + year	5	-15514.85	12.52	0.001885
noise X site + day + day ² + year	9	-15513.77	13.6	0.001099
null	4	-15507.19	20.18	4.09E-05
noise + year	5	-15506.01	21.36	2.27E-05
noise X site + year	7	-15504.1	23.27	8.73E-06

Hermit Thrush

Model	k	AIC	Δ AIC	wi
day + day ² + year	6	-17289.49	0	0.600972
dB(A) + day + day ² + year	7	-17288.25	1.24	0.32329
noise X site + day + day ² + year	9	-17285.07	4.42	0.065927
day + year	5	-17281.26	8.23	0.009811
null	4	-17240.58	48.91	1.44E-11
dB(A) + year	5	-17238.91	50.58	6.25E-12
noise + year	5	-17238.84	50.65	6.03E-12
noise X site + year	7	-17235.4	54.09	1.08E-12

Cassin's Finch

Model	k	AIC	Δ AIC	wi
dB(A) + day + day ² + year	7	-15038.74	0	0.876229
day + day ² + year	6	-15034.39	4.35	0.099547
noise X site + day + day ² + year	9	-15031.53	7.21	0.023822
day + year	5	-15022.06	16.68	0.000209
dB(A) + year	5	-15021.38	17.36	0.000149
null	4	-15018.24	20.5	3.1E-05
noise + year	5	-15016.38	22.36	1.22E-05
noise X site + year	7	-15015.49	23.25	7.83E-06

Table A.4 AIC model output results for foraging and vigilance analysis

Foraging: head down duration (sec)

Model	k	AIC	Δ AIC	wi
db	2	-54.134	0.00	0.51
db+trial+time	4	-52.2161	1.92	0.20
db+day	3	-52.1663	1.97	0.19
db+day+trial+time	5	-50.4667	3.67	0.08
null	2	-47.5941	6.54	0.02

Vigilance: head up rate (head lifts/sec)

Model	k	AIC	Δ AIC	wi
db+day	3	-23.543	0.00	0.70
null	2	-20.4975	3.05	0.15
db+day+trial+time	5	-19.7983	3.74	0.11
db	2	-17.2415	6.30	0.03
db+trial+time	4	-13.7057	9.84	0.01