Animal occurrence and space use change in the landscape of anthropogenic noise

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ABSTRACT

Habitat fragmentation, destruction, and disturbance are major threats to biodiversity. Global road networks represent one of the most significant human impacts on ecosystems, and a spatially extensive source of anthropogenic disturbance and noise. We developed a novel approach by combining traffic monitoring with noise mapping on the basis of a standardized traffic-noise stimulus generated by controlled vehicle operation to investigate temporal and spatial heterogeneity of traffic noise. We used animal presence or absence, radio-telemetric monitoring of space use, and remotely sensed habitat characteristics with occupancy modeling and spatial analysis to assess influences of distance from roads, habitat characteristics, and traffic noise level on site occupancy and space use of Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*). Traffic noise had spatially extensive and negative effects on site occupancy. Animal occurrence decreased as traffic noise increased after accounting for distance from roads. Traffic noise levels in animal core home ranges were lower than noise levels within total home ranges. Our study disentangled effects of traffic noise from confounding environmental characteristics and demonstrated the chronic impacts of traffic noise on animal distribution. We highlight the importance of incorporating spatial and temporal heterogeneity of traffic noise at a local scale when investigating effects of anthropogenic noise on wildlife.

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1. Introduction

Habitat fragmentation, destruction, and disturbance are major threats to biodiversity (Millennium Ecosystem Assessment, 2005). Impact of anthropogenic noise is of concern due to an increasing human population, expanding infrastructure and energy development, and growth in air travel as well as motorized recreation in natural areas (Miller, 2008; United Nations, 2011). Noise that arises from infrastructure such as oil compressors can affect animal communication and behavior, reduce reproductive success and further influence habitat quality and animal distribution (Barber et al., 2010; Bayne et al., 2008; Francis and Barber, 2013).

Measuring nearly 65 million km in length, road networks across the world represent one of the most significant human impacts on nature and wildlife, and a spatially extensive source of anthropogenic disturbance and noise (Central Intelligence Agency, 2014; Forman and Alexander, 1998). Animal abundance and richness are reduced near roads and impacts of roads on population density and community structure can extend to several kilometers from the road (Benítez-López et al., 2010; Fuentes-Montemayor et al., 2009). Vehicles cause wildlife mortality and introduce disturbance including vehicular noise, movement, vibration, exhaust fumes, dust, headlight illumination and

human presence (Trombulak and Frissell, 2000). Traffic noise is often related to animal avoidance of areas adjacent to roads (Barber et al., 2010). However, few studies separate effects of traffic noise from other confounding environmental factors or forces related to distance from roads. Environmental changes associated with edges created by roads may affect habitat quality and further influence animal populations and distribution (Murcia, 1995). Coincidence between increase in richness or abundance with increasing distance from roads, and the negative relationship between traffic noise and distance from roads, have been taken as evidence that traffic noise affects diversity (Barber et al., 2010; Fahrig and Rytwinski, 2009; Summers et al., 2011). Recently, acute effects of traffic noise on species richness of migratory birds were demonstrated by introducing traffic noise to roadless areas through playback experiments (McClure et al., 2013). Nevertheless, studies and evidence of chronic impacts of traffic noise on habitat quality and animal occurrence are scarce. To better understand how habitat fragmentation and human disturbance affect animal populations and to inform management and mitigation for expanding anthropogenic disturbance, it is important to disentangle effects of traffic noise from distance to roads and environmental characteristics.

In this study, we used an endangered forest dependent species, the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), as our study organism to test hypotheses to explain negative effects of roads on animal occurrence. We developed a novel approach to investigate temporal and spatial heterogeneity of traffic noise by combining

traffic monitoring with noise mapping on the basis of a standardized traffic-noise stimulus generated by controlled vehicle operation. We used animal presence or absence, radio-telemetric monitoring of movement, and three-dimensional remote sensing (LiDAR, Light detection and ranging) to quantify environmental characteristics in combination with site occupancy models and spatial analysis to assess influences of distance to roads, environmental characteristics, and traffic noise level on animal occurrence and space use.

2. Material and methods

2.1. Study area and study species

The southwestern United States represents one of the most important regions for biodiversity in North America (Stein, 2002) and the isolated montane forests known as sky islands are refugia for many species. However, continued expansion of the human population and associated infrastructure development (Arizona Department of Transportation, 2006) along with long term projections of significant redistribution and fragmentation of forests due to climate change (Opdam and Wascher, 2004; Weiss and Overpeck, 2005) threaten survival of endemic species and exacerbate levels of isolation in the region. Our study was conducted in 149.5 ha of mixed-conifer forest >3000 m elevation atop Mt. Graham, an isolated, 3267-m peak located in the Pinaleño Mountains, Graham County, Arizona, USA (32° 42′ 06″ N, 109° 52′ 17″ W), and home to critically endangered Mt. Graham red squirrels. The North American red squirrel is a small (<300 g), diurnal tree squirrel with a wide-ranging distribution in Canada and the United States (Steele, 1998). The Mt. Graham red squirrel is a subspecies that is isolated and endemic to high elevation forests (>2000 m) of the Pinaleño Mountains, and represents the southernmost population of red squirrels (Brown, 1984; Steele, 1998). Red squirrels relies on cone scale piles known as middens to store food for winter survival (Hurly and Lourie, 1997; Steele, 1998). Middens are typically located in forests with dense canopy and understory cover and provide a cool and moist microclimate that prevents cones from opening and releasing seeds (Merrick et al., 2007; Smith and Mannan, 1994; Zugmeyer and Koprowski, 2009). Because of geographic isolation, low population numbers (~300 individuals, Sanderson and Koprowski, 2009), and habitat destruction, Mt. Graham red squirrels were listed as federally endangered in 1987 (U.S. Fish and Wildlife Service, 1987). In addition to habitat loss, severe fire, and insect damage, a potential threat to Mt. Graham red squirrels is human disturbance from recreation, road traffic, and habitat modification associated with road improvement (Buenau and Gerber, 2004; U.S. Fish and Wildlife Service, 2011; Zugmeyer and Koprowski, 2009).

We focused our work on 3.7 km of 3 graded dirt roads: Arizona State Highway 366 also known as Swift Trail (6- to 13-m wide, annual average daily traffic [AADT]: 50 vehicles, hereafter, high traffic), the Bible Camp Road (4- to 9-m wide, AADT: 25 vehicles, hereafter, medium traffic), and Soldier Trail (3- to 24-m wide, AADT: 7 vehicles, hereafter, low traffic). Speed limit was 40 km/h. Roads were closed to the public from 15 November to 15 April annually due to snow. The forest was dominated by Douglas-fir (Pseudotsuga menziesii), southwestern white pine (Pinus strobiformis), and corkbark fir (Abies lasiocarpa var. arizonica) interspersed with Engelmann spruce (Picea engelmanii), aspen (Populus tremuloides) and ponderosa pine (Pinus ponderosa, Sanderson and Koprowski, 2009).

2.2. Quantification of traffic noise and background sound level

Acoustic landscape of noise, defined as the spatial extent of noise exposure, is complicated by spatial and temporal variation. Transmission of traffic noise is affected by road condition, vegetation, vehicle types, traffic load and traffic speed (Garg and Maji, 2014). Noise playback experiments have been used to control these factors, but the full frequency spectrum of traffic noise and temporal aspects of noise source cannot be generated by this approach (Pater et al., 2009). We controlled these factors while maintaining the sound profile of traffic noise and obtained information of spatial variation of noise transmission by using controlled vehicle operation as a standardized traffic-noise stimulus. We explored temporal variation of traffic noise by monitoring traffic intensity through a year.

2.2.1. Measurement and mapping of traffic noise level

To generate a standardized traffic-noise stimulus, we drove a sport utility vehicle (SUV, 2009 Escape Hybrid, Ford Motor Company, Dearborn, Michigan, USA) at 32 km/h on high and medium traffic roads and at 24 km/h on the low traffic road. The driving speed was determined on the basis of speed limit and road condition. We used an extension for ArcGIS (Environmental Systems Research Institute), XTool Pro (Data East LLC, Novosibirsk, Russia), to create a sampling grid with 50 m × 50 m grid size and randomly selected 50% of grid cells to measure sound pressure levels (dB) of the standardized traffic-noise stimulus in a random order. Most vehicle noise events last for 20 s (Brown et al., 2013). Therefore, we measured traffic noise for 20 s beginning when the SUV was 100 m from the sampling locations with a handheld CEL-244 integrating basic sound-level meter (Casella CEL, Buffalo, New York) equipped with a small foam windscreen, set to A weighting, 30–100 dB range, and impulse response. Sound level meters were calibrated with a CEL-120/2 calibrator (Casella CEL, Buffalo, New York) before use. We recorded equivalent continuous sound level (L_{eq}) and maximum power (L_{max}) with a 5 dB exchange rate and recorded ≥4 measurements at each location from 8:00 to 17:00, during which red squirrels are active and when most traffic occurs. We used polynomial regression models to assess how traffic noise attenuates with increased distance from roads. We used the Ordinary Kriging geostatistical interpolation method under GeoStatistical Analyst extension in ArcMap 10.1 (Environmental Systems Research Institute) to create the surfaces (25-m resolution) of L_{eq} and L_{max} of the standardized traffic-noise stimulus for the entire study area (Fig. 1). We evaluated performance of created surfaces by comparing measured values with the predicted values and assessing standard errors of observation and prediction. If our prediction is unbiased, the mean standardized prediction error should be near zero. We combined estimated traffic noise levels and recorded traffic volume to create traffic noise indices for occupancy modeling.

2.2.2. Traffic monitoring

We used bi-directional traffic counters (TRAFx Vehicle Counter Model G3, TRAFx Research Ltd., Canmore, Alberta, Canada) to record traffic on the 3 roads in 2013. Traffic counters were placed at the roadside for each road and set to a slow rate, 3 s delay, 014 threshold of sensitivity with time stamp mode that records time when vehicles are detected. Additionally, we placed 1 traffic counter (slow rate, 0.5 s delay, 008 threshold of sensitivity) at a paved section of Swift Trail, which was at lower elevation on Mt. Graham. Many sources of anthropogenic noise show daily, weekday versus weekend, and seasonal variation (Halfwerk et al., 2011). To understand the temporal pattern of traffic noise, we used one-way analysis of variance (ANOVA) to compare hourly traffic volume among 24 h, daily traffic volume among 12 months, and daily traffic volume between weekdays and weekends.

2.2.3. Influences of driving speed, vehicle type, and road surface

To better anticipate how noise level changes with different traffic and road conditions, we investigated effects of driving speed and type of vehicle on traffic noise level. We drove the SUV (mass = 1737 kg) and a truck (mass = 2418 kg, 2011 Silverado Pickup 4 × 4, Chevrolet, Detroit, USA) at 24 km/h, 32 km/h and 40 km/h on Swift Trail and measured L_{eq} and L_{max} at 6 locations (0–175 m from roads) with the same methods stated above. We tested effects of road pavement on traffic noise level by driving the SUV on paved sections of Swift Trail at 32 km/h and recorded L_{eq} and L_{max} at 18 locations (0–100 m from
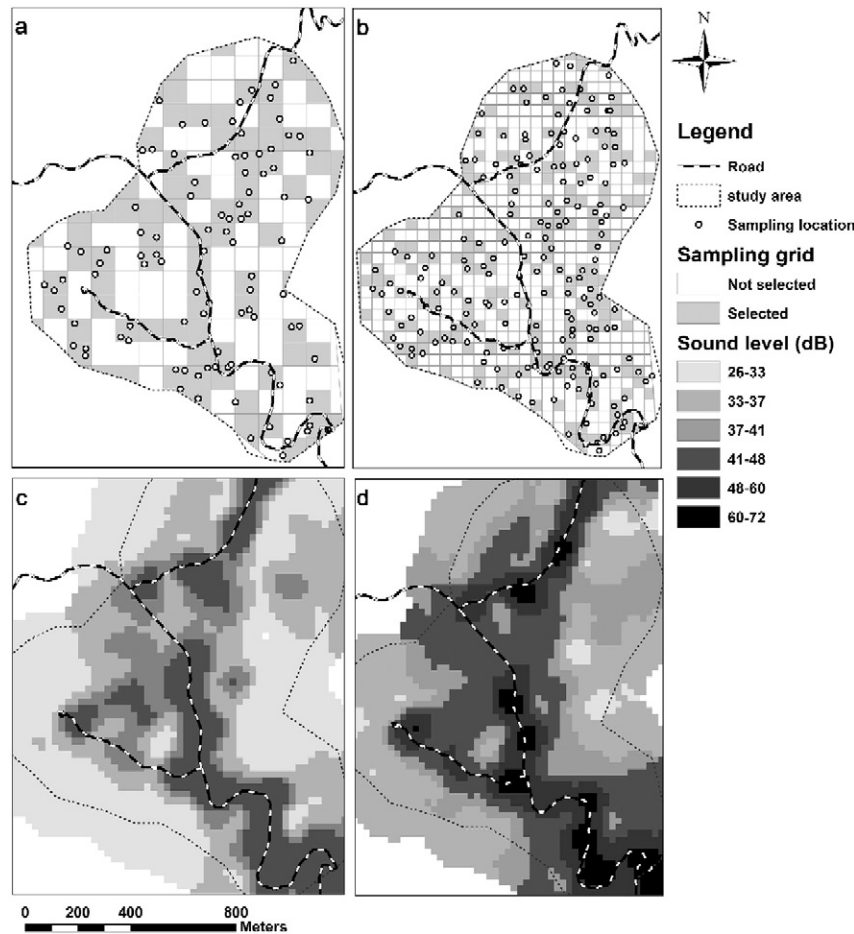
Fig. 1. Maps of study area, roads, sampling grids with noise measuring locations of background noise (a) and traffic noise (b), and estimated equivalent continuous sound level (L_{eq}, c) and maximum power (L_{max}, d) of a standardized traffic-noise stimulus, Mt. Graham, Arizona, USA.

roads). We used multiple regression models to assess effects of driving speed, vehicle type, and road pavement on traffic noise.

2.2.4. Background sound level

We created a sampling grid with 100 m × 100 m grid size and randomly selected 50% of grid cells to measure background sound level without presence of anthropogenic noise generated by vehicles, aircraft, construction, or human. We set the sound-level meters to A weighting, 30–100 dB range, and slow response and recorded L_{eq} and L_{max} for 20 s with a 5 dB exchange rate. At each sampling location, we recorded ≥6 measurements from 8:00 to 17:00 during May to August in 2013. We also measured mean wind speed (km/h) for 20 s with a Kestrel 3000 pocket weather meter (Loftopia, LLC, Birmingham, Michigan, USA). We used multiple regression models to assess effects of distance from roads and wind speed on background sound levels.

2.3. Effects of traffic noise on animal occurrence and space use

2.3.1. Midden residency and animal space use

Red squirrels are an ideal species to investigate effects of traffic noise on site occupancy. Because they are territorial and center their territories on conspicuous middens (Gurnell, 1987), which served as sites for the purpose of occupancy modeling ($n = 149$). The ability to detect presence of a species may be affected by loud traffic noise, especially for avian species (Francis and Barber, 2013). Feeding sign of red squirrels, which is the scale of conifer cones at middens, allowed us to detect squirrels without influence by traffic noise. To track red squirrels and determine midden residency, we used standard methods (Koprowski et al., 2008) to trap, fit unique ear tags and affix radio collars on

squirrels. We trapped and surveyed middens every 3 months annually to assess squirrel body condition, reproductive status and determine midden residency. Residency was denoted by presence of squirrels or visible signs of activity including cone caches and feeding remains. Sex, age class (juvenile, subadult, adult), reproductive status, and identity of resident squirrels were noted (Wood et al., 2007).

We located red squirrels during daylight hours and estimated the location of each animal via simultaneous biangulation (Koprowski et al., 2008). We used radio telemetry data to estimate 95% (total) and 50% (core) fixed kernel home ranges for individual squirrels each season (spring: March to May, summer: June to August, fall: September to November, winter: December to February, Koprowski et al., 2008). Field efforts were conducted under permits from the United States Department of Agriculture Forest Service, Arizona Game and Fish Department, United States Fish and Wildlife Service, and the University of Arizona's Institutional Animal Care and Use Committee (Protocol #08-024).

2.3.2. Environmental characteristics and traffic noise level

We quantified environmental characteristics near middens at 2 spatial scales: midden (hereafter, midden characteristics) and 100-m surrounding middens (hereafter, environmental characteristics). We chose 100 m on the basis of the mean size of 95% fixed kernel home ranges from 2009 to 2012 [mean (SE) = 2.65 (0.23) ha]. For each midden, we calculated distance to the nearest road (m), distance to the nearest midden (m), distance to the nearest midden with at least 1 record of squirrel residency among 4 surveys in 2013 (distance to occupied midden, m), and distance to recent fire boundaries (Clark Peak Fire in 1997 and Nuttall Complex Fire in 2004, m). We extracted slope, aspect (degree to north) and measures of forest structure including

mean tree height (m), standard deviation of tree height (m), live and total basal area (m²/ha), and canopy cover (%) from GIS layers (25-m resolution) derived from LiDAR data (Mitchell et al., 2012). To quantify environmental characteristics around middens, we used the Geospatial Modeling Environment (GME, Beyer, 2012) to calculate mean, minimum and maximum value of distance to roads, distance to fire boundaries, slope, aspect, and forest structure for each 100-m buffer. We used 5 indices to represent traffic noise level at middens: L_{eq} and L_{max} of the standardized traffic-noise stimulus extracted from the GIS surfaces that we created, mean daily traffic volume (low, medium, high) of the nearest road in 2013, and total daily noise exposure (L_{eq} or $L_{max} \times$ mean daily traffic volume of the nearest road).

2.3.3. Occupancy modeling

Occupancy links site-specific processes determining species occurrence with detection processes that govern observations of animal presence or absence is an appropriate method for estimation and inference about animal occurrence with imperfect detection (MacKenzie et al., 2002; Royle and Dorazio, 2006). By specifying models of site occupancy and detectability, we can estimate probability of occurrence for individual middens and infer effects of distance from roads, traffic noise level, and environmental characteristics on midden occupancy after accounting for variation in detectability. We used midden residency data in 2013 for site occupancy modeling (single season model with 4 surveys). As in other populations, Mt. Graham red squirrels typically only use a single midden (Vahle, 1978) and rarely change resident middens in a year. Thus, it is not very likely to violate the assumption of closure in a single-season occupancy model. Site covariates for occupancy included midden characteristics (distance to the nearest midden, distance to the nearest occupied midden, aspect, slope, distance to recent fire boundaries, forest structure), environmental characteristics (zonal statistics of aspect, slope, distance to recent fire boundaries, and forest structure within 100-m buffer), distance from middens to the nearest road, and traffic noise indices at middens. We standardized continuous variables for occupancy modeling, so estimated coefficients of variables would be interpreted as the amount of change in the logit of occurrence probability with 1 SD change in the variable from its mean.

Because freshness of cone scales and feeding sign may affect detection probability, we modeled the detection process as a function season (spring, summer, fall, winter), so detectability varied among surveys. We used a two-step approach (Gray and Steidl, 2015) to assess whether traffic noise is influential after accounting for distance from roads and important habitat characteristics. We first modeled occupancy that only included distance from roads, and influential midden and environmental characteristics ($p < 0.10$ based on a Z test). For variables that were highly correlated ($r > 0.7$), we added variables to the models individually and selected the one with lower p value. We then added traffic noise to a model that retained only influential site covariates from the first step and assessed the significance on the basis of Z test. We ran occupancy models with the unmarked (Fiske and Chandler, 2011) packages in R (version 3.1.0 – "Spring Dance", R Development Core Team, 2014). To conduct goodness-of-fit tests, we used a generic parametric bootstrapping function embedded in unmarked.

2.3.4. Effects of traffic noise on animal space use

We used data of home ranges of adult red squirrels collected in 2013 to understand effects of traffic noise on space use. We included 120 seasonal home ranges of 49 red squirrels in our analysis. We used GME to calculate mean traffic noise levels (L_{eq} and L_{max} of the standardized traffic-noise stimulus) within core (50%) and total (95%) home range and used paired t-tests to compare traffic noise between core and total home ranges of individual squirrels. If red squirrels select areas with lower traffic noise levels, we expected the traffic noise levels will be lower within core home ranges than within total home ranges.

3. Results

3.1. Background sound and traffic noise level

3.1.1. Background sound level

Continuous background sound level (L_{eq}, mean [SE] = 32.29 [0.20] dB, 25% quantile = 30.4 dB, 75% quantile = 33.4 dB) decreased as distance from roads increased ($\beta = -0.007$, SE = 0.002, $t_{124} = -3.52$, $p < 0.001$) but was not affected by wind speed ($t_{124} = 1.53$, $p = 0.13$). Maximum power of background sound (L_{max}, mean [SE] = 36.71 [0.30] dB, 25% quantile = 33.53 dB, 75% quantile = 39.08 dB) decreased with increased distance from roads ($\beta = -0.02$, SE = 0.003, $t_{117} = -5.45$, $p < 0.001$), and was positively affected by wind speed ($\beta = 1.83$, SE = 0.88, $t_{117} = 2.07$, $p = 0.04$). Background sound levels were not correlated with forest structure measures (all $r < 0.1$, $p > 0.20$). Estimated traffic noise levels of the standardized traffic-noise stimulus at background noise sampling locations were not highly correlated with background sound levels (L_{eq}: $r = 0.42$, L_{max}: $r = 0.46$).

3.1.2. Spatial and temporal patterns in traffic noise level

Measured sound levels (L_{eq}, L_{max}) of the standardized traffic-noise stimulus decreased with increased natural-log transformed distance from roads (L_{eq}: $F_{1,189} = 473.93$, $p < 0.001$; L_{max}: $F_{1,189} = 616.63$, $p < 0.001$, Fig. 2), but were not highly correlated with distance from roads ($r = 0.6$). Traffic noise levels were estimated to attenuate to background sound levels (L_{eq}: 32.29 dB, L_{max}: 36.71 dB) at 165 to 232 m from roads (Fig. 2). Mean daily traffic volume in 2013 was 56 vehicles (SE 4.03, 0–
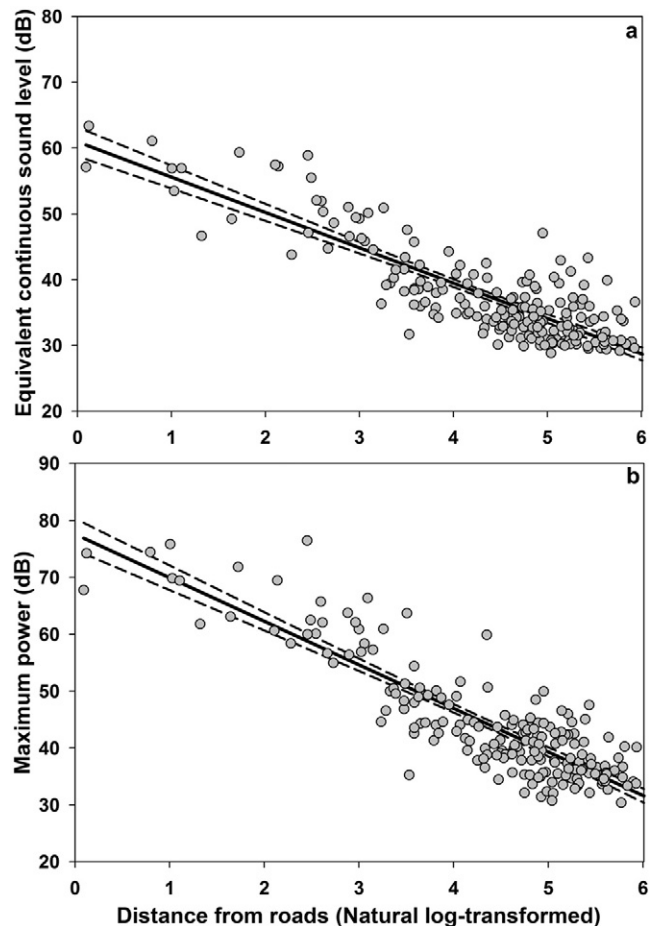

Fig. 2. Equivalent continuous sound level (L_{eq}) and maximum power (L_{max}) of a standardized traffic-noise stimulus as function of distance from roads (L_{eq} = 60.95–5.37 natural-log transformed distance from roads, a; L_{max} = 77.55–7.65 natural-log transformed distance from roads, b, dash line represents 95% confidence interval of the fit).

615 vehicle, $n = 365$) on 3 roads combined, 43 vehicles (SE 2.94, 0–372 vehicles, $n = 365$) on the high traffic road, 12 vehicles (SE 1.21, 0–243 vehicles, $n = 345$) on the medium traffic road, and 2 vehicles (SE 0.30, 0–33 vehicles, $n = 193$) on the low traffic road. Mean daily traffic volume on paved sections of Swift Trail was 196 vehicles (SE 9.41, 29–1402 vehicles, $n = 200$). Daily traffic volume changed through the year ($F_{11,353} = 33.35$, $p < 0.001$) with summer traffic more common (mean [SE] = 136 [6.23] vehicles) and lower in winter (mean [SE] = 3.68 [6.30] vehicles). Traffic volume on the weekend (mean [SE] = 86.61 [7.33] vehicles/day) was higher than on weekdays (mean [SE] = 43.66 [4.63] vehicles/day, $t_{363} = -4.96$, $p < 0.001$), and showed a daily peak between 11:00 and 14:00, whereas no peak was evident on weekdays.

3.1.3. Effects of driving speed, vehicle type, and road surface

Increased vehicle speed produced higher sound levels of traffic noise. Driving at 24 km/h had lower noise levels compared to 32 km/h and 40 km/h (L_{eq}: $F_{2,39} = 4.02$, $p = 0.03$; L_{max}: $F_{2,39} = 5.56$, $p = 0.008$) after accounting for effects of distance from roads. Driving the SUV at 40 km/h was 1 dB louder in L_{eq} and 1.5 dB louder in L_{max} than a speed of 24 km/h. The SUV and the truck did not differ in noise level (L_{eq}: $t_{44} = -1.41$, $p = 0.17$; L_{max}: $t_{44} = -1.39$, $p = 0.17$). Traffic noise levels of the SUV were not different on paved roads and on unpaved roads (L_{eq}: $t_{27} = -0.74$, $p = 0.47$; L_{max}: $t_{27} = -1.30$, $p = 0.21$).

3.2. Effects of traffic noise on animal occurrence and space use

Mean distance from middens to roads was 141.96 m (SE 8.15) with a range of 10.15–394.36 m. Mean L_{eq} and L_{max} of standardized traffic-noise stimulus at middens was 37.13 dB (SE 0.47) with a range of 26.82–54.75 dB and 43.27 dB (SE 0.63) with a range of 30.84–68.68 dB respectively.

3.2.1. Detection probability

Detection probability was lower in summer and spring (69% and 64% respectively) when red squirrels fed on stored conifer cones from previous years, compared to detectability in fall (84%) and winter (84%) when fresh cones were consumed (Table 1).

3.2.2. Effects of traffic noise on site occupancy

Traffic noise was influential after accounting for distance from roads and other environmental characteristics (Table 1). When distance from roads was fixed, red squirrels were more likely to occupy middens with lower traffic noise level (L_{eq}) at middens, lower daily traffic volume on the nearest road, higher live basal area at middens, higher canopy

cover and lower slope within 100-m buffer surrounding middens, at north-facing slope, and greater distance from other red squirrels (Table 1). According to estimated coefficient, probability of occupancy changes 37.28% with 5.68 dB change in traffic noise level from its mean (37.14 dB, Table 1). In general, predicted midden occupancy rate at our study area decreased to <50% when continuous traffic noise level was >43 dB, slightly louder than a voice spoken with normal effort (Everest and Pohlmann, 2009, Fig. 3).

3.2.3. Effects of traffic noise on animal space use

Noise levels of the standardized traffic-noise stimulus in core (50%) home ranges (L_{eq}: 36.86 dB [SE 0.45]; L_{max}: 38.39 dB [SE 0.68]) were lower than that of total (95%) home ranges (L_{eq}: 37.40 dB [SE 0.42]; L_{max}: 43.36 dB [SE 0.63]; L_{eq}: $t_{114} = -2.61$, $p = 0.01$; L_{max}: $t_{103} = -2.55$, $p = 0.01$).

4. Discussion

4.1. Animal occurrence decreases at sites with higher traffic noise level

Chronic noise exposure is a significant threat to the natural environment and an emerging issue in protected lands (Barber et al., 2010; Lynch et al., 2011). Over 20% of the land in the United States is affected by roads and traffic (Forman, 2000). Forest roads are thought to have reduced impacts on wildlife because roads are often narrow, unpaved, and lightly traveled. However, ecological effects of forest roads can be substantial due to their cosmopolitan distribution and facilitation of human disturbance to remote areas (Coghlan and Sowa, 1998; Forman and Alexander, 1998; Forman et al., 2003; Reed et al., 1996). Our results support the hypothesis that traffic noise is the major driver of reduced animal abundance near roads (Reijnen et al., 1995). We showed that traffic noise is an influential factor after accounting for distance from roads and other environmental covariates, and may have chronic negative impacts on site occupancy by a forest obligate. Even though a large body of literature documents impacts of traffic noise on avian species (e.g. Bayne et al., 2008; Parris and Schneider, 2009; Reijnen et al., 1997), to our knowledge, the current study is the first to investigate impacts of traffic noise on animal occurrence and space use of arboreal mammals. The impact of traffic noise on occupancy rate of red squirrels can be substantial and spatially extensive. Noise generated from linear sources such as roads or railways transmits farther than that generated by point sources like natural gas compressors and wind turbines (Francis and Barber, 2013). Although traffic volume in our study area is relatively low compared to other natural areas suffering from anthropogenic noise such as national parks (e.g. Grand Canyon National Park: 3616 vehicles/day, National Park Service, 2004;

Table 1
Estimated coefficients of midden occupancy by Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), 2013, Mt. Graham, Arizona, USA.

Covariates	Coefficient[a]	SE	Z	*p* value
Occupancy				
Traffic noise level (dB)	−0.52	0.26	−2.00	0.04
Daily traffic volume — medium vs. low	−1.60	0.68	−2.37	0.02
Daily traffic volume — high vs. low	−1.14	0.54	−2.13	0.03
Live basal area (m²/ha) at midden	0.31	0.21	1.48	0.14
Aspect (degree to north) at midden	−0.32	0.21	−1.52	0.13
Maximum slope (100-m buffer)	−0.49	0.21	−2.36	0.02
Minimum canopy cover (100-m buffer, %)	0.48	0.22	2.18	0.03
Distance to occupied middens[b] (m)	0.60	0.23	2.60	0.009
Distance from roads (m)	0.06	0.26	0.23	0.81
Detection				
Spring	0.81	0.24	3.39	<0.001
Summer	0.59	0.23	2.57	0.01
Fall	1.65	0.30	5.46	<0.001
Winter	1.65	0.30	5.46	<0.001

[a] For continuous variables, the value represents the degree of change in logit of occupancy with 1-SD change of the variable from its mean.
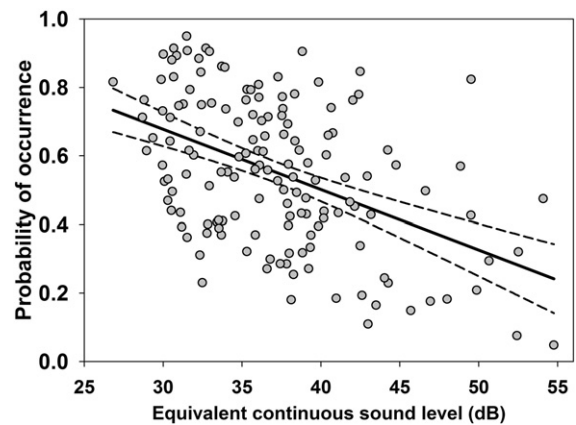[b] Nearest distance to middens with at least 1 detection of squirrels among surveys.

Fig. 3. Estimated probability of occurrence of Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) as a function of equivalent continuous sound level (occupancy rate = 1.21−0.0176 noise level), 2013, Mt. Graham, Arizona, USA.

Yosemite National Park: 2500–7000 vehicles/day, Lynch et al., 2011; National Park Service, 2011), over 50% of our study area is estimated to be affected by traffic noise, as traffic noise levels did not diminish to baseline ambient noise levels until 165 m from roads.

4.2. Why does animal occurrence decrease as traffic noise increase?

Slight levels of intrusion introduced by human presence for short periods of time do not decrease abundance of red squirrels (Gutzwiller and Riffell, 2008). However, we demonstrated that red squirrel occurrence decreased as traffic noise increased, although we could not completely exclude other traffic disturbance that may not have a linear relationship with distance to roads such as visual disturbance and chemical pollution. Consistent with previous study (Merrick et al., 2007; Smith and Mannan, 1994), red squirrels select middens with higher basal area and higher canopy cover, likely due to higher protection from avian predators and greater food production (Koprowski et al., 2008; Schauffert et al., 2002). Why is occurrence and space use of red squirrels reduced as traffic noise increase? Many species such as yellow-billed cuckoo (*Coccyzus americanus*; Goodwin and Shriver, 2011) and elk (*Cervus elaphus*; Rowland et al., 2000) select habitat with less noise from human activity. Anthropogenic noise can affect animal communication by masking animal acoustic signals (Barber et al., 2010). Consequently, species that vocalize in the frequency range generated by noise may be hindered in their ability to communicate, detect predators, defend territory, attract mates, and successfully reproduce, and ultimately lead to abandonment of the habitat or reduced population (Goodwin and Shriver, 2011; Parris and Schneider, 2009).

Anthropogenic noise can also reduce animal awareness of predators by distraction and may mask of sounds produced by predators and territory intruders (Barber et al., 2010; Chan et al., 2010; Schmidt and Ostfeld, 2008). Many species use heterospecific signals to assess predation risk (Ridley et al., 2014). For example, red-breasted nuthatches (*Sitta canadensis*) respond alarm calls of black-capped chickadees (*Poecile atricapillus*) and alert to the presence of potential predators (Templeton and Greene, 2007). Eastern gray squirrels (*Sciurus carolinensis*) listen to vocalizations of potential cache robbers to assess risk of cache pilfering (Schmidt and Ostfeld, 2008). Traffic noise in general has high sound pressure at relatively low frequencies (1–1.5 kHz, (Brown et al., 2013; Warren et al., 2006). Frequency of vocalization by red squirrels ranges from 0.5 kHz to 6.5 kHz, and alarm calls, which are given when upon detection of potential predators and conspecific intruders, typically have frequencies ranging from 1–2 kHz (Smith, 1978). Because traffic noise might mask alarm calls and sounds of predator and intruder movement, red squirrels may select quiet middens and areas that minimize the influence of traffic noise on detection of predator and intruder or territorial announcement. Yet, effects of anthropogenic noise on predation risk and territorial defenses have not been demonstrated (Francis and Barber, 2013). Animals often perceive anthropogenic disturbance as a threat, and therefore decrease foraging time and increase stress response (Frid and Dill, 2002). California ground squirrels (*Otospermophilus beecheyi*) elevated vigilance near power-generating wind turbines compared to quiet control sites (Rabin et al., 2006). To further understand and anticipate impacts and ecological consequences of anthropogenic noise on animals, research that links acute and chronic behavioral and physiological responses of animals to short and long term noise exposure at the individual and population level is needed (Francis and Barber, 2013; Francis et al., 2012; Halfwerk et al., 2011).

4.3. Temporal and spatial variation of traffic noise

When traffic events are infrequent with high temporal variation, effectively sampling traffic noise is difficult. Several days of 24-h recording of traffic noise alone would not be representative and can be biased depending on sampling season. We confronted this difficulty by combined

traffic monitoring with controlled vehicle operations that allows us to record how traffic sound penetrates the study area. Understanding how noise changes with vehicle types, driving speed, and road surface can be useful for traffic noise management (Makarewicz and Kokowski, 2007; Steele, 2001). For instance, vehicles on roads with asphalt pavement produce lower noise level than on roads with gravel pavement (Leipus et al., 2010). Although noise levels at paved roads in our study area were not different from gravel roads, the daily traffic intensity on paved roads was 4 times greater than on gravel roads. Thus, overall daily traffic noise exposure will likely increase after road pavement.

Increase of sound level by a few decibels can cause reduction in alerting distance (Barber et al., 2010) and lead to substantial change in animal response, including reduced use (Landon et al., 2003), depressed density (Reijnen et al., 1997), decreased reproductive success (Halfwerk et al., 2011), and altered communication (Barber et al., 2010; Parris and Schneider, 2009). Although the traffic sound pressure that we measured and estimated represent relative degrees of traffic noise level rather than real time noise exposure, we showed a difference of 30 dB, the equivalent of 8 times the loudness and 1000-fold increase in sound level (Crocker, 1998), in traffic noise may influence habitat quality and affect animal occurrence. Animal activity can be affected by traffic intensity (Barber et al., 2010; Francis and Barber, 2013). For example, elk use habitat near a highway primarily when traffic volume is low (100 vehicles/h, Gagnon et al., 2007). Reproductive success of great tits (*Parus major*) is reduced in noisier areas, and traffic noise in April explains more variation in reproductive success than traffic noise in March, indicating degree of noise impacts varies with time and animal activities (Halfwerk et al., 2011). Traffic intensity in summer increased markedly in our study area, especially during weekends. Middens near the medium and high traffic roads had lower occupancy rates than middens near the low traffic road, suggesting that negative impacts of traffic noise are more severe in seasons with greatest traffic. Our results highlight the importance of considering the temporal and spatial heterogeneity of traffic noise at a local scale when investigating the impact of noise on wildlife. Yet, we were not able to incorporate temporal variation of traffic noise in occupancy modeling because site covariates were assumed to be constant through all surveys in single season models. Apply multi-season occupancy models to assess effects of seasonal traffic noise level on extinction and colonization of sites across seasons will provide insight on how temporal patterns of traffic noise affects animal occurrence.

5. Conservation implications

With increasing global human population, expanding urbanization and the proliferation of transportation corridors, as well as growing demands for outdoor recreational activities, anthropogenic noise is now recognized as a pollutant of international concern even in remote areas (Bowker et al., 2012; Food and Agriculture Organization of the United Nations, 2010). To better estimate noise exposure, scientists and managers need to integrate information of vehicle type, road surface, vegetation structure, landscape topography, spectrum and noise level of common vehicles, and temporal and spatial variation of traffic intensity (Garg and Maji, 2014; Warren et al., 2006). Possible mitigation measures include natural or artificial sound barriers with wildlife road crossing structures, dense vegetation belts along a road, and traffic control such as reducing speed limit and restriction of the number of vehicles (U.S. Department of Transportation, 2011; Van Renterghem et al., 2012). Anthropogenic disturbance like traffic noise is just one in a myriad of road impacts on the environment. Roads and traffic influence wildlife populations directly through mortality due to wildlife-vehicle collisions, and indirectly by changing animal behavior not only via visual and auditory disturbances but also through altering environment (Barber et al., 2010; Fahrig and Rytwinski, 2009; Forman and Alexander, 1998). Species that exhibit high noise and road surface avoidance are

most vulnerable to road impacts on population (Jaeger et al., 2005). Forest specialists like tree squirrels often avoid entering gaps with low canopy or understory cover, and hence are especially vulnerable to habitat fragmentation and barrier effects of roads (Koprowski, 2005; Laurance et al., 2009). Although avoidance of roads due to traffic noise may reduce risk of mortality, severity of fragmentation and barrier effects caused by roads may be exacerbated. The acoustical environment that animals perceive is a complicated world (Barber et al., 2010). Understanding the landscape of noise, spatial and temporal pattern of disturbance level, as well as immediate and chronic animal response to disturbance is critical to future conservation and management efforts.

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References

Arizona Department of Transportation, 2006. Arizona's Wildlife Linkages Assessment (Phoenix,AZ,USA).
Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189. http://dx.doi.org/10.1016/j.tree.2009.08.002.
Bayne, E.M., Habib, L., Boutin, S., 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conserv. Biol. 22, 1186–1193. http://dx.doi.org/10.1111/j.1523-1739.2008.00973.x.
Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biol. Conserv. 143, 1307–1316. http://dx.doi.org/10.1016/j.biocon.2010.02.009.
Beyer, H.L., 2012. Geospatial Modelling Environment.
Bowker, J.M., Askew, A.E., Cordell, H.K., Betz, C.J., Zarnoch, S.J., Lynne, S., 2012. Outdoor recreation participation in the United States—projections to 2060: a technical document supporting the Forest Service 2010 RPA Assessment. General Technical Report SRS-160. U.S. Fish and Wildlife Service, Asheville, North Carolina.
Brown, D.E., 1984. Arizona's Tree Squirrels. Arizona Game and Fish Department, Phoenix, Arizona, USA.
Brown, C.L., Reed, S.E., Dietz, M.S., Fristrup, K.M., 2013. Detection and classification of motor vehicle noise in a forested landscape. Environ. Manag. 52, 1262–1270. http://dx.doi.org/10.1007/s00267-013-0123-8.
Buenau, K.E., Gerber, L.R., 2004. Developing recovery and monitoring strategies for the endemic Mount Graham red squirrels (Tamiasciurus hudsonicus grahamensis) in Arizona. Anim. Conserv. 7, 17–22. http://dx.doi.org/10.1017/S1367943003001124.
Central Intelligence Agency, 2014. The World Factbook [WWW Document]. Cent. Intell. Agency (URL https://www.cia.gov/library/publications/the-world-factbook/, accessed 12.20.14).
Chan, A.A.Y.-H., Giraldo-Perez, P., Smith, S., Blumstein, D.T., 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biol. Lett. 6, 458–461. http://dx.doi.org/10.1098/rsbl.2009.1081.
Coghlan, G., Sowa, R., 1998. National Forest Road System and Use. USDA Forest Service Engineering Staff, Washington D.C. (Draft 1/30/98).
Crocker, M.J., 1998. Handbook of Acoustics. John Wiley and Sons, New York, New York, USA.
Everest, F.A., Pohlmann, K.C., 2009. Master Handbook of Acoustics. 5th ed. McGraw-Hill, New York.
Fahrig, L., Rytwinski, T., 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecol. Soc. 14, 21.
Fiske, I.J., Chandler, R.B., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.
Food and Agriculture Organization of the United Nations, 2010. Global forest resources assessment 2010 — main report. Forestry Paper 163, FAO, Forestry, Rome.
Forman, R.T.T., 2000. Estimate of the area affected ecologically by the road system in the United States. Conserv. Biol. 14, 31–35.
Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231.
Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R.L., Goldman, C.R., Heanue, K., Jones, J., Swanson, F., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. 2nd ed. Island Press, Washington, D.C., USA.
Francis, C.D., Barber, J.R., 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Front. Ecol. Environ. 11, 305–313. http://dx.doi.org/10.1890/120183.
Francis, C.D., Kleist, N.J., Ortega, C.P., Cruz, A., 2012. Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. Proc. R. Soc. B Biol. Sci. 279, 2727–2735. http://dx.doi.org/10.1098/rspb.2012.0230.
Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 11.
Fuentes-Montemayor, E., Cuarón, A.D., Vázquez-Domínguez, E., Benítez-Malvido, J., Valenzuela-Galván, D., Andresen, E., 2009. Living on the edge: roads and edge effects on small mammal populations. J. Anim. Ecol. 78, 857–865. http://dx.doi.org/10.1111/j.1365-2656.2009.01551.x.
Gagnon, J.W., Theimer, T.C., Dodd, N.L., Boe, S., Schweinsburg, R.E., 2007. Traffic volume alters elk distribution and highway crossings in Arizona. J. Wildl. Manag. 71, 2318–2323. http://dx.doi.org/10.2193/2006-224.
Garg, N., Maji, S., 2014. A critical review of principal traffic noise models: strategies and implications. Environ. Impact Assess. Rev. 46, 68–81. http://dx.doi.org/10.1016/j.eiar.2014.02.001.
Goodwin, S.E., Shriver, W.G., 2011. Effects of traffic noise on occupancy patterns of forest birds. Conserv. Biol. 25, 406–411. http://dx.doi.org/10.1111/j.1523-1739.2010.01602.x.
Gray, K.M., Steidl, R.J., 2015. A plant invasion affects condition but not density or population structure of a vulnerable reptile. Biol. Invasions 17, 1979–1988. http://dx.doi.org/10.1007/s10530-015-0851-1.
Gurnell, J., 1987. The Natural History of Squirrels. Christopher Helm, London, Great Britain.
Gutzwiller, K.J., Riffell, S.K., 2008. Does repeated human intrusion alter use of wildland sites by red squirrels? Multiyear experimental evidence. J. Mammal. 89, 374–380. http://dx.doi.org/10.1644/07-MAMM-A-122R1.1.
Halfwerk, W., Holleman, L.J.M., Lessells, C.M., Slabbekoorn, H., 2011. Negative impact of traffic noise on avian reproductive success. J. Appl. Ecol. 48, 210–219. http://dx.doi.org/10.1111/j.1365-2664.2010.01914.x.
Hurly, T.A., Lourie, S.A., 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. J. Mammal. 78, 529–537.
Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., von Toschanowitz, K.T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol. Model. 185, 329–348. http://dx.doi.org/10.1016/j.ecolmodel.2004.12.015.
Koprowski, J.L., 2005. The response of tree squirrels to fragmentation: a review and synthesis. Anim. Conserv. 8, 369–376. http://dx.doi.org/10.1017/S1367943005002416.
Koprowski, J.L., King, S.R.B., Merrick, M.J., 2008. Expanded home ranges in a peripheral population: space use by endangered Mt. Graham red squirrels. Endanger. Species Res. 4, 227–232. http://dx.doi.org/10.3354/esr00026.
Landon, D., Krausman, P., Koenen, K., Harris, L., 2003. Pronghorn use of areas with varying sound pressure levels. Southwest. Nat. 48, 725–728. http://dx.doi.org/10.1894/0038-4909(2003)0482.0.CO;2.
Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. Trends Ecol. Evol. 24, 659–669. http://dx.doi.org/10.1016/j.tree.2009.06.009.
Leipus, L., Butkus, D., Januševičius, T., 2010. Research on motor transport produced noise on gravel and asphalt roads. Balt. J. Road Bridg. Eng. 5, 125–131. http://dx.doi.org/10.3846/bjrbe.2010.18.
Lynch, E., Joyce, D., Fristrup, K., 2011. An assessment of noise audibility and sound levels in U.S. National Parks. Landsc. Ecol. 26, 1297–1309. http://dx.doi.org/10.1007/s10980-011-9643-x.
MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248. http://dx.doi.org/10.2307/3072056.
Makarewicz, R., Kokowski, P., 2007. Prediction of noise changes due to traffic speed control. J. Acoust. Soc. Am. 122, 2074–2081. http://dx.doi.org/10.1121/1.2769972.
McClure, C.J.W., Ware, H.E., Carlisle, J., Kaltenecker, G., Barber, J.R., 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proc. R. Soc. B Biol. Sci. 280, 20132290. http://dx.doi.org/10.1098/rspb.2013.2290.
Merrick, M.J., Bertelsen, S.R., Koprowski, J.L., 2007. Characteristics of Mount Graham red squirrel nest sites in a mixed conifer forest. J. Wildl. Manag. 71, 1958–1963. http://dx.doi.org/10.2193/2006-260.
Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis. World Resources Institute, Washington, D.C., USA.
Miller, N.P., 2008. US National Parks and management of park soundscapes: a review. Appl. Acoust. 69, 77–92. http://dx.doi.org/10.1016/j.apacoust.2007.04.008.
Mitchell, B., Walterman, M., Mellin, T., Wilcox, C., Lynch, A.M., Anhold, J., Falk, D.A., Koprowski, J., Laes, D., Evans, D., Fisk, H., 2012. Mapping vegetation structure in the Pinaleño Mountains using LiDAR–phase 3: forest inventory modeling. RSAC-10007-RPT1. Remote Sensing Applications Center, U.S. Forest Service, Salt Lake City, Utah, USA.
Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62. http://dx.doi.org/10.1016/s0169-5347(00)88977-6.
National Park Service, 2004. Grand Canyon National Park Traffic Package [WWW Document].
National Park Service, 2011. Yosemite National Park Transportation Improvement Strategies Report (YOSE-PMIS 139285).
Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol. Conserv. 117, 285–297. http://dx.doi.org/10.1016/j.biocon.2003.12.008.
Parris, K.M., Schneider, A., 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecol. Soc. 14.
Pater, L., Grubb, T., Delaney, D., 2009. Recommendations for improved assessment of noise impacts on wildlife. J. Wildl. Manag. 73, 788–795. http://dx.doi.org/10.2193/2006-235.
Rabin, L.A., Coss, R.G., Owings, D.H., 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (Spermophilus beecheyi). Biol. Conserv. 131, 410–420. http://dx.doi.org/10.1016/j.biocon.2006.02.016.

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Reed, R., Johnson-Barnard, J., Baker, W., 1996. Contribution of roads to forest fragmentation in the Rocky Mountains. Conserv. Biol. 10, 1098–1106. http://dx.doi.org/10.1046/j.1523-1739.1996.10041098.x.

Reijnen, R., Foppen, R., Braak, C.T., Thissen, J., 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. J. Appl. Ecol. 32, 187–202. http://dx.doi.org/10.2307/2404428.

Reijnen, R., Foppen, R., Veenbaas, G., 1997. Disturbance by traffic of breeding birds: evaluation of the effect and considerations in planning and managing road corridors. Biodivers. Conserv. 6, 567–581.

Ridley, A.R., Wiley, E.M., Thompson, A.M., 2014. The ecological benefits of interceptive eavesdropping. Funct. Ecol. 28, 197–205. http://dx.doi.org/10.1111/1365-2435.12153.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. J. Wildl. Manag. 64, 672–684. http://dx.doi.org/10.2307/3802737.

Royle, J.A., Dorazio, R.M., 2006. Hierarchical models of animal abundance and occurrence. J. Agric. Biol. Environ. Stat. 11, 249–263. http://dx.doi.org/10.1198/108571106×129153.

Sanderson, H.R., Koprowski, J.L., 2009. The Last Refuge of the Mt. Graham Red Squirrel. University of Arizona Press, Tucson, Arizona, USA.

Schauffert, C.A., Koprowski, J.L., Greer, V.L., Alanen, M.I., Hutton, K.A., Young, P.J., 2002. Interactions between predators and Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*). Southwest. Nat. 47, 498–501. http://dx.doi.org/10.2307/3672515.

Schmidt, K.A., Ostfeld, R.S., 2008. Eavesdropping squirrels reduce their future value of food under the perceived presence of cache robbers. Am. Nat. 171, 386–393. http://dx.doi.org/10.1086/527497.

Smith, C.C., 1978. Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). J. Mammal. 59, 793. http://dx.doi.org/10.2307/1380144.

Smith, A.A., Mannan, R.W., 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. J. Wildl. Manag. 58, 437–445.

Steele, M.A., 1998. *Tamiasciurus hudsonicus*. Mamm. Species 586, 1–9.

Steele, C., 2001. A critical review of some traffic noise prediction models. Appl. Acoust. 62, 271–287. http://dx.doi.org/10.1016/S0003-682X(00)00030-X.

Stein, B.A., 2002. States of the Union: Ranking America's Biodiversity. NatureServe, Arlington, Virginia, USA.

Summers, P.D., Cunnington, G.M., Fahrig, L., 2011. Are the negative effects of roads on breeding birds caused by traffic noise? J. Appl. Ecol. 48, 1527–1534. http://dx.doi.org/10.1111/j.1365-2664.2011.02041.x.

Templeton, C.N., Greene, E., 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. Proc. Natl. Acad. Sci. U. S. A. 104, 5479–5482. http://dx.doi.org/10.1073/pnas.0605183104.

Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30.

U.S. Department of Transportation, 2011. Highway traffic noise: analysis and abatement guidance. FHWA-HEP-10-025. Federal Highway Administration, Washington, D.C., USA.

U.S. Fish and Wildlife Service, 1987. Endangered and threatened wildlife and plants; determination of endangered status for the Mount Graham red squirrel. Fed. Regist. 52, 20994–20999.

U.S. Fish and Wildlife Service, 2011. Draft Recovery Plan for the Mount Graham Red Squirrel (*Tamiasciurus hudsonicus grahamensis*), First Revision. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, New Mexico, USA.

United Nations, 2011. World Urbanization Prospects: The 2011 Revision. United Nations, New York, New York, USA.

Vahle, R.J., 1978. Red Squirrel use of Southwestern Mixed Coniferous Habitat. Arizona State University.

Van Renterghem, T., Botteldooren, D., Verheyen, K., 2012. Road traffic noise shielding by vegetation belts of limited depth. J. Sound Vib. 331, 2404–2425. http://dx.doi.org/10.1016/j.jsv.2012.01.006.

Warren, P.S., Katti, M., Ermann, M., Brazel, A., 2006. Urban bioacoustics: it's not just noise. Anim. Behav. 71, 491–502. http://dx.doi.org/10.1016/j.anbehav.2005.07.014.

Weiss, J.L., Overpeck, J.T., 2005. Is the Sonoran Desert losing its cool? Glob. Chang. Biol. 11, 2065–2077. http://dx.doi.org/10.1111/j.1365-2486.2005.01020.x.

Wood, D.J.A., Drake, S., Rushton, S.P., Rautenkranz, D., Lurz, P.W.W., Koprowski, J.L., 2007. Fine-scale analysis of Mount Graham red squirrel habitat following disturbance. J. Wildl. Manag. 71, 2357–2364. http://dx.doi.org/10.2193/2006-511.

Zugmeyer, C.A., Koprowski, J.L., 2009. Severely insect-damaged forest: a temporary trap for red squirrels? For. Ecol. Manag. 257, 464–470. http://dx.doi.org/10.1016/j.foreco.2008.09.020.