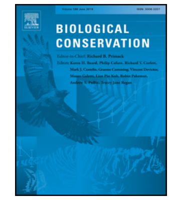
Biological Conservation 199 (2016) 33–40

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc



Barrier effects of roads on an endangered forest obligate: influences of traffic, road edges, and gaps

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ARTICLE INFO

Article history:
Received 28 August 2015
Received in revised form 11 March 2016
Accepted 18 March 2016
Available online xxxx

Keywords:
Habitat fragmentation
Gap avoidance
Forest roads
Forest structure
Small mammals
Road impacts

ABSTRACT

Habitat fragmentation and destruction caused by development of infrastructure such as roads threaten biodiversity. Roads act as barriers by impeding animal movements and restricting space use. Understanding factors that influence barrier effects is important to discern the impacts of habitat fragmentation and to develop appropriate mitigations. We combined telemetry and demographic data in 2008 to 2012 with remote sensing imagery to investigate barrier effects of forest roads and assess effects of traffic, road edges, and canopy gaps on space use of an endangered, endemic forest obligate, the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). We mapped low to high traffic roads, road edges, canopy gaps, and random lines in forests to serve as references. We determined if red squirrels included these linear features in their total and core home ranges, and used this metric as an indicator of crossing and preference for habitat adjacent to the linear features. Forest roads acted as barriers regardless of traffic volume and had long-term impacts on animal space use. Animals did not avoid entering roadside areas, and probability of crossing linear features in the forest was not affected by distance to roads. In contrast, greater canopy cover increased probability of crossing, and gaps in canopy impeded animal movements. Higher likelihood of road crossing was associated with more variable tree height and mating activity. We demonstrated that narrow forest roads with low traffic volume were barriers for forest dependent species, and suggest that gap avoidance inhibits road crossings.

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1. Introduction

Habitat fragmentation and destruction caused by development of infrastructure such as roads and bridges are recognized as major threats to biodiversity (Czech and Krausman, 1997; Forman and Alexander, 1998). To maintain habitat connectivity, genetic variability, and population persistence, the facilitation of movements of animals through landscapes is critical (Frankham, 1996; Hanski and Gilpin, 1991). Roads and traffic can serve as barriers that impede animal movements, decrease accessibility of resources such as food, shelter or mates, lead to reduction in reproductive success and gene flow, and ultimately threaten population persistence (Strasburg, 2006; Trombulak and Frissell, 2000). Barrier effects of roads have been documented in a diversity of terrestrial fauna, including insects (Bhattacharya et al., 2003), reptiles (Shepard et al., 2008), amphibians (Marsh et al., 2005), birds (Laurance et al., 2004) and mammals (Burnett, 1992), but the causes and mechanisms of road avoidance are not fully understood (Bissonette and Rosa, 2009; Chen and Koprowski, 2013; Roedenbeck et al., 2007).

The barrier effects of roads are driven by several distinct but not mutually exclusive mechanisms that include traffic, edge, and gap avoidance (Barber et al., 2010; Forman et al., 2003; Greenberg, 1989; Jaeger et al., 2005). Traffic avoidance includes avoidance of vehicles as well as traffic disturbance that arises from vehicular noise, movements, vibration, exhaust fumes, dust, headlight illumination and human presence, and has been related to reduction in animal abundance at roadside areas (Barber et al., 2010; Goosem, 2002). Edge avoidance results when animals avoid entering roadside areas due to physical and biotic changes caused by an abrupt transition of ground surface or vegetation (Ford and Lenore, 2008; Forman et al., 2003). Edge effects due to roads can affect the distribution, density and abundance of wildlife in adjacent habitat (Goosem, 2000). Yet, how road edges impact animal movements and space use has been assessed less frequently. Gap avoidance occurs when species avoid clearings with low canopy or understory closure such as roads and forest clearcuts, perhaps because of increased predation risk (Greenberg, 1989) and evolutionary constraints (Laurance et al., 2004).

One fundamental question in road ecology is "what is the relative importance of the different mechanisms by which roads affect population persistence?" (Roedenbeck et al., 2007). Effects of roads on animal populations depend on species life history traits as well as behavioral responses to roads (Benítez-López et al., 2010; Jaeger et al., 2005; Rytwinski and Fahrig, 2012). Previous research on barrier effects has focused on one or two of these potential mechanisms contributing to road avoidance. However, to comprehensively understand barrier

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http://dx.doi.org/10.1016/j.biocon.2016.03.017
0006-3207/© 2016 Published by Elsevier Ltd.

effects of roads and develop appropriate mitigation, studies that simultaneously address the relative importance of these different mechanisms are needed. For example, barrier effects of roads due to road avoidance should be distinguished clearly from the effects due to road mortality, as both causes lead to reduced individuals cross roads, but the mechanisms are fundamentally different and require different mitigation (Fahrig and Rytwinski, 2009). Both avoidance of vehicles and avoidance of traffic disturbance result in a decreased rate of road crossings, but avoidance of traffic disturbance can also lead to reduction in animal abundance at roadside areas (Forman and Alexander, 1998; Jaeger et al., 2005).

Tree squirrels (*Sciurus* and *Tamiasciurus*) are an ideal group for assessing the impacts of roads on forest dependent species. Arboreal squirrels are widespread, common, and are readily sampled and tracked by radio telemetry because of moderate home range size (Gurnell and Pepper, 1994; Koprowski et al., 2008). Previously, barrier effects of roads have been assessed primarily by capture-recapture methods and translocation (e.g. McDonald and St Clair, 2004). Although such techniques increase understanding of road crossing behavior by highly motivated individuals, the pattern of spontaneous movements or the relationship between home range boundaries and roads is difficult to discern (Ford and Lenore, 2008; Laurance et al., 2004). Techniques like radio telemetry that quantify individual movements can alleviate these issues (Clark et al., 2001). Herein, we combine long-term radio telemetry data and traffic monitoring with high-resolution remote sensing data to examine barrier effects of roads and traffic on animal space use and movements. We use an endangered, endemic forest obligate — the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) as a model to (1) investigate whether forest roads are barriers and assess the relative importance of traffic, edge, and gap avoidance, and (2) examine factors that influence animal movements and identify environmental features and road characteristics that may improve road permeability.

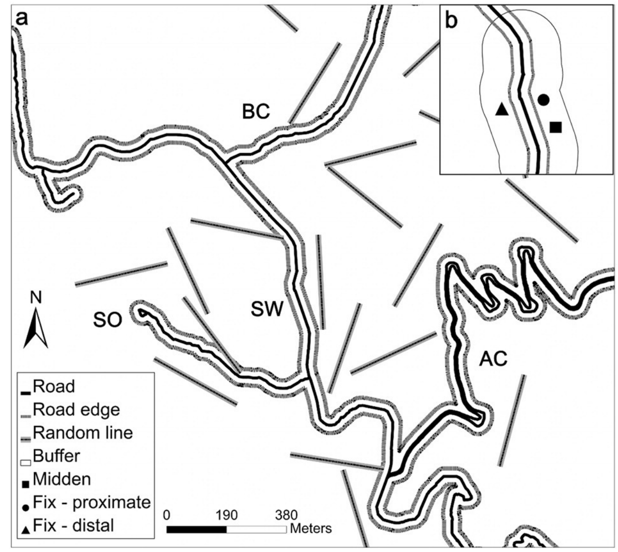

Fig. 1. Illustration of linear features on Mt. Graham, Arizona. (a) Location of roads, road edges and random lines. SW: Arizona State Highway 366, AC: access road, BC: Bible Camp Road, SO: Soldier Trail. (b) Illustration of midden of Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*), 100-m buffer surrounding a road section, and examples of red squirrels locations on the proximal (fix-proximal) and distal side of the road (fix-distal).

2. Material and methods

2.1. Study area and study species

Our study was conducted in 342 ha of mixed-conifer forest > 3,000 m elevation in the Pinaleño Mountains (Graham Mountains), Graham County, Arizona, USA (32° 42′ 06″ N, 109° 52′ 17″ W). We used bi-directional traffic counters (TRAFx Vehicle Counter Model G3, TRAFx Research Ltd, Canmore, Alberta, Canada) to monitor 6.6 km of 4 graded dirt roads (Fig. 1a): Arizona State Highway 366 also known as Swift Trail (6 to13-m wide, annual average daily traffic [AADT]: 50 vehicles, hereafter, high traffic), the access road to the Mount Graham International Observatory (4 to 10-m wide, AADT: 23 vehicles, hereafter, medium 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. No wildlife road crossing structures were installed in the study area. The forest is 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).

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). Red squirrels are territorial and center their territories on conspicuous cone-scale piles with cones in caches known as middens (Gurnell, 1987; 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). Mt. Graham red squirrel is a subspecies that is isolated and endemic to high elevation forests (>2,000 m) of the Pinaleño Mountains, which are surrounded by desert and grassland, and represents the southernmost population of red squirrels (Brown, 1984; Steele, 1998). Because of geographic isolation, declining and 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).

2.2. Animal space use

We used standard methods to trap, fit unique ear tags and affix radio collars on red squirrels, and located red squirrels during daylight hours and estimated the location of each animal via biangulation (Koprowski et al., 2008). We used radio telemetry data to estimate 95% (total) and 50% (core) fixed kernel home ranges for individual red squirrels each season (spring: March–May, summer: June–August, fall: September–November, winter: December to January, Koprowski et al., 2008). For this study, we used home ranges from December 2008 (when airborne LiDAR data were collected) to November 2012 during which no major forest disturbance occurred. During natal dispersal, movement patterns of juvenile red squirrels are different from adults (Larsen and Boutin, 1994), so we only included adult and subadult red squirrels that have completed natal dispersal in our analyses. Home ranges estimated with <15 fixes were excluded. Mean number of locations per home range was 40 fixes (SE 0.60, $n = 307$).

2.3. Linear features

We mapped low to high traffic roads with high-resolution aerial imagery obtained from the National Agriculture Imagery Program (NAIP) in 2007 (Fig. 1a). We defined road edges that were parallel to roads with a distance of 25 m from roads as boundaries of roadside areas (Fig. 1a). We chose 25 m because edge effects of roads usually decrease within the first 50 m of forests (Murcia, 1995). To resemble linear gaps

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