Landscape and Urban Planning 178 (2018) 228–237

Contents lists available at ScienceDirect

Landscape and Urban Planning

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

Research Paper

Accessible habitat and wetland structure drive occupancy dynamics of a threatened amphibian across a peri-urban landscape

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ARTICLE INFO

Keywords:
Accessible habitat
Endangered amphibian
Habitat fragmentation
Occupancy modeling
Road ecology
Urbanization

ABSTRACT

Populations of aquatic-breeding amphibians are declining from habitat loss, fragmentation and degradation. Identifying how populations are affected by landscape barriers such as roads is essential for conservation and requires understanding the processes underpinning species occupancy in fragmented landscapes. Here, I assessed relationships between the occupancy dynamics of the threatened green and golden bell frog (*Litoria aurea*) and accessible habitat; i.e., the area of breeding and non-breeding habitat around a wetland that can be reached by an amphibian without having to cross a highway. I hypothesised that relationships between occupancy and accessible habitat would be stronger than relationships with the area of extant native vegetation, road density or distance to the highway. I also examined relationships with local habitat variables over a three-year period. Relationships with accessible habitat were stronger and more certain in explaining *L. aurea* occupancy and colonisation than other landscape variables. Accessible habitat was positively associated with wetland occupancy, which suggests the highway is having a barrier effect on the population. There was a positive relationship between road density and the probability of local extinction. Occupancy rates at highway compensatory ponds increased from near-zero within six months of pond construction, to > 30% after 12 months. There was a negative relationship between local extinction and aquatic vegetation cover, highlighting the importance of habitat structure for *L. aurea*. Urban planners should consider accessible habitat when managing amphibian species in rapidly urbanising landscapes, so that all habitats required throughout a species' life cycle are protected.

1. Introduction

Human populations are rapidly increasing and it is predicted that there will be an almost three-fold increase in global urban land cover from 2000 to 2030 (Seto, Güneralp, & Hutyra, 2012). Massive population growth in cities and towns is driving rapid landscape transformation and loss of biodiversity (Grimm et al., 2008; Vitousek, Mooney, Lubchenco, & Melillo, 1997). Urbanisation often entails the loss of natural vegetation and wetlands, which are replaced by buildings and roads, fragmenting natural habitats into smaller patches (Lee et al., 2006; McKinney, 2002; Theobald, Miller, & Hobbs, 1997).

The number of roads is predicted to increase dramatically to service growing cities (Laurance et al., 2014), and the ecological effects of roads on aquatic and terrestrial habitats are numerous and diverse (Findlay & Bourdages, 2000; Trombulak & Frissell, 2000), ranging from direct mortality of wildlife by vehicles to alteration of the biophysical environment in a road-effect zone (Forman, 2000). Consequently, urbanisation and roads are endangering many animal species, including wetland-dependent species such as amphibians (Czech, Krausman, & Devers, 2000; Hamer & McDonnell, 2008).

Amphibians are considered more threatened with extinction than either birds or mammals, with many declines attributed to habitat loss and fragmentation, often resulting from urbanisation (Cushman, 2006; Stuart et al., 2004). Wetland loss removes breeding sites for aquatic-breeding amphibians, and can impede dispersal among breeding and non-breeding (terrestrial) habitats within larger metapopulations (Marsh & Trenham, 2001; Semlitsch, 2002). Amphibians are highly vulnerable to road mortality because they move between terrestrial and aquatic habitats, and have slower rates of movement and smaller body size relative to other vertebrate taxa (Beebee, 2013; Glista, DeVault, & DeWoody, 2008; Rytwinski & Fahrig, 2012). High mortality rates on roads can occur during dispersal (Hels & Buchwald, 2001; Sutherland, Dunning, & Baker, 2010), particularly on high-traffic roads (Mazerolle, 2004). Genetic studies suggest some amphibian populations are fragmented by roads (Lesbarrères, Primmer, Lodé, & Merilä, 2006). Consequently, roads can lead to regional declines in the distribution of many amphibian species (Cosentino et al., 2014; Marsh et al., 2017).

The composition of the landscape surrounding amphibian breeding sites determines its permeability for dispersal (Cline & Hunter, 2016; Gibbs, 1998). Significant barriers to dispersal such as roads often

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https://doi.org/10.1016/j.landurbplan.2018.06.008
Received 17 October 2017; Received in revised form 17 March 2018; Accepted 21 June 2018

decrease occupancy rates at ponds due to disrupted colonisation dynamics within metapopulations, leading to reduced species richness and abundance (Eigenbrod, Hecnar, & Fahrig, 2008a; Hartel, Schweiger, Öllerer, Cogălniceanu, & Arntzen, 2010). Amphibian species with high dispersal abilities are expected to encounter roads and traffic more frequently than sedentary species, and so are likely to be more vulnerable to road mortality and barrier effects (Carr & Fahrig, 2001).

The effects of roads on amphibian populations have been elucidated using variables measured within concentric circles (buffers) around a wetland (e.g., road density; Houlahan & Findlay, 2003; Pellet, Guisan, & Perrin, 2004). The use of circular buffers assumes that a species is affected by roads equally in all directions around a wetland; however, roads are barriers to dispersal and can therefore disrupt movement patterns (Hamer, Langton, & Lesbarrères, 2015). Hence, the use of circular buffers will not realistically depict the total area within the buffer available to the species, and may lead to the wrong conclusions being reached regarding the effects of roads on wetland occupancy. Zanini, Klingemann, Schlaepfer, and Schmidt (2008) demonstrated that barrier-based buffers, in which inaccessible areas around a wetland are removed from the calculation, better explained amphibian species distribution than traditional circular buffers. Furthermore, Eigenbrod, Hecnar, and Fahrig (2008b) used barrier-based buffers around amphibian breeding sites to assess the effects of roads on amphibian distribution, using the term accessible habitat to define the area of aquatic and terrestrial habitat around a focal wetland that can be reached through movement by an aquatic-breeding species, without individuals having to cross a major barrier such as a highway. This definition of accessible habitat implies that emigration is occurring from a focal wetland, with immigration of a dispersing amphibian into a habitat patch within the buffer. Eigenbrod et al. (2008b) showed that accessible habitat was more strongly related to species richness than total forest cover, road density or distance to the highway, and concluded that using only habitat amount or road density may underestimate the effects of roads on occupancy patterns. While these studies examined relationships between accessible habitat and species distributions, no studies to date have used barrier-based buffers to assess occupancy dynamics within amphibian populations.

Here, I investigated relationships between accessible habitat and occupancy, colonisation and local extinction rates within a population of the green and golden bell frog (*Litoria aurea*). I hypothesised that within a circular buffer around a focal wetland, positive relationships with accessible habitat would be stronger and clearer than those with the amount of extant habitat or distance to a major road (highway), whereas relationships with road density would also be weaker. Local habitat variables are also known to affect amphibian distributions in urban regions of Australia (Hamer & Parris, 2011; Parris, 2006), and so I assessed relationships between occupancy and a suite of parameters measured at the wetland-scale. Elucidating the mechanisms behind dynamic processes affecting amphibian populations in rapidly urbanising regions will provide empirical information that urban planners require to effectively determine the relative impacts of new road projects. Moreover, studies on endangered amphibians in areas currently experiencing urban development are urgently needed to guide conservation strategies that cater for all life stages and foster long-term population persistence.

2. Methods

2.1. Study area

The study was conducted south of the township of Nowra on the south coast of New South Wales, Australia (see Google Earth image, Appendix A). This peri-urban area is experiencing rapid growth with a population of 19 716 people (194 persons/km^2) in 2015 (Australian Bureau of Statistics., 2017). The eastern portion of the study area is located on the floodplain of the Crookhaven River, which has been extensively modified by agricultural practices (Daly, 2014). Areas of higher topography support patches of dry forest and farming land. Residential areas and sealed two-lane roads cover much of the northern portion of the study area towards Nowra. The Princes Highway (herein referred to as the highway) runs through undulating hills to the west. The highway was upgraded from a two-lane to a four-lane divided road between 2011 and 2014 along a 6.3-km section. Annual mean precipitation in the study area is 902 mm and rainfall peaks in February (Bureau of Meteorology., 2017; Fig. A1).

2.2. Litoria aurea

Litoria aurea is listed as Vulnerable in Australia under the *Environment Protection and Biodiversity Conservation Act 1999*. Factors responsible for population declines may include habitat loss and fragmentation, the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*; herein referred to as *Bd*) and exotic fish predators (e.g., mosquitofish, *Gambusia holbrooki*; Mahony et al., 2013). *Litoria aurea* frequently moves over large distances (up to 1 km; Hamer, Lane, & Mahony, 2008), therefore making it susceptible to roads, and a suitable candidate to assess the effects of roads on amphibian populations.

A population of *L. aurea* occurs on the Crookhaven River floodplain in the eastern portion of the study area (see Google Earth image, Appendix A), and is regarded as one of the largest remaining populations in New South Wales. The species inhabits a variety of waterbody types including ephemeral wetlands on the floodplain (e.g., Brundee Swamp), drains, creeks and farm dams (Daly, 2014). The population appears to expand and contract during high and low rainfall periods, respectively, often peaking when breeding events coincide with heavy rain inundating Brundee Swamp (Daly, 2014). Urbanisation is driving the loss of aquatic-breeding frogs in the region, including *L. aurea* (Villaseñor, Driscoll, Gibbons, Calhoun, & Lindenmayer, 2017).

2.3. Compensatory habitat for L. aurea

The upgrade of the Princes Highway was expected to negatively affect the population because of direct mortality, habitat loss, fragmentation and degradation. Consequently, eight compensatory ponds were constructed 21–182 m from the highway in August 2013 (see Google Earth image, Appendix A; Fig A2). Mean area of the eight compensatory ponds was 199 m^2 (range: 119–331 m^2; SE: 31 m^2). These ponds were constructed of concrete with near-vertical pond walls to exclude the striped marsh frog (*Limnodynastes peronii*), which is unable to climb vertical surfaces (unlike *L. aurea*) and is a known *Bd* host (Stockwell, Clulow, & Mahony, 2010). Ponds could also be drained to exclude the mosquitofish known to eat the eggs and larvae of *L. aurea* (Pyke & White, 2001).

2.4. Site selection and field surveys

The study area includes many freshwater wetlands that are potential habitat for *L. aurea*. Following reconnaissance surveys in the field at approximately 100 wetlands in 2013, I selected 52 wetland sites within 5 km of a 10-km section of the Princes Highway (see Google Earth image, Appendix A). I assumed that long-distance movement of *L. aurea* could potentially occur between wetlands adjacent to the highway and at distances of up to 5 km from the road, based on movement distances of *L. aurea* (Pyke & White, 2001). As such, impacts of the highway upgrade may be influencing occupancy by *L. aurea* at these more distant wetlands. I selected sites to maximise variation in wetland size and type, ranging from constructed wetlands (e.g., farm dams, golf course dams, compensatory ponds) to agricultural channels and creeks (see Google Earth image, Appendix A). Mean wetland area was 2763 m^2 (range: 119 – 26532 m^2; SE: 738 m^2). I selected a 2.7-ha section of Brundee Swamp owing to previous records of *L. aurea* at this site (Daly, 2014). Because distance to the nearest wetland is an important