Biological Conservation 153 (2012) 169–176

Contents lists available at SciVerse ScienceDirect

Biological Conservation

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

Limited influence of stream networks on the terrestrial movements of three wetland-dependent frog species

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ARTICLE INFO

Article history:
Received 19 February 2012
Received in revised form 16 April 2012
Accepted 28 April 2012
Available online 29 June 2012

Keywords:
Amphibian
Anuran
Hydrological networks
Migration
Topography

ABSTRACT

Quantifying functional connectivity is essential for understanding factors that limit or promote animal dispersal in fragmented landscapes. Topography is a major factor influencing the movement behavior of many animal species, and therefore the extent of functional connectivity between habitat patches. For pond-breeding frogs, areas of low topographic relief (such as streams or drainage lines) offer damp microhabitats that can facilitate movement through otherwise dry landscapes. However, the extent of topographic bias of frog movements has rarely been quantified. We used a replicated study to compare captures in high- and low-relief transects, for three species from a pond-breeding frog community in southeastern Australia. We captured frogs significantly more often on low-relief transects. However, capture rates decreased with increasing distance from water at similar rates on both high-relief and low-relief transects, and we observed few differences between adult and juvenile movements. Our results suggest that although low-relief drainage lines are important for the pond-breeding frogs in question, ecologists and landscape managers should not discount the role of high-relief locations. Because low-relief drainage lines represent a low proportion of the pond margin, >90% of movements are likely to occur across high-relief locations. Therefore, for the species that we studied, buffer zones designed to conserve only hydrological networks would provide insufficient protection of frequently used pond margins, while drainage lines are unlikely to act as vital networks facilitating connectivity between breeding ponds. Our study suggests that movement across slopes may be most important for facilitating functional connectivity.

1. Introduction

Habitat fragmentation, caused by large-scale human modification of ecosystems, is a major driver of biodiversity loss (Fahrig, 2003; Kingsford et al., 2009; Lindenmayer and Fischer, 2006). Conceptual landscape models which emphasize patch-matrix habitat distributions (derived from Island Biogeography Theory; MacArthur and Wilson, 1967) can be useful for describing fragmented landscapes, and have therefore been influential throughout the development of landscape ecology (Haila, 2002). Applications of these models commonly assume that viable metapopulations are maintained by dispersal (Hanski, 1998; Leibold et al., 2004), while acknowledging that dispersal can be strongly influenced by properties of the intervening matrix (Vogt et al., 2009). Quantifying the extent to which parts of the landscape facilitate animal movement – a concept known as 'functional connectivity' (Baguette and Van Dyck, 2007; Lindenmayer and Fischer, 2007) – provides a basis for understanding the effects of matrix alteration on patch-dependent animal populations (see Storfer et al., 2010).

Functional connectivity is a particularly relevant concept for frog populations. Pond-breeding frogs are commonly described as a naturally occurring model of a fragmented system, because ponds appear like patches in a terrestrial matrix (Bradford et al., 2003; Marsh and Trenham, 2001). For this reason, metapopulation theory (Hanski, 1998) has commonly been used as a model for describing frog populations (Smith and Green, 2005). However, dispersal rates are highly variable between frog species (e.g. Driscoll, 1997; Smith and Green, 2006), and the role of landscape resistance in explaining this variation remains unclear (Stevens et al., 2006). In particular, topographic features represent barriers to movement in some species and locations (e.g. Funk et al., 2005; Richards-Zawacki, 2009; Richter-Boix et al., 2007) but not others (e.g. Davis and Roberts, 2005; Driscoll, 1998; Zhan et al., 2009). Functional connectivity therefore provides a framework for investigating the influence of landscape variation on frog dispersal and for deciding, in turn, which management interventions are likely to be effective for conservation (see Petranka and Holbrook, 2006).

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0006-3207/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2012.04.030

Although there has been much research into terrestrial habitat use by frogs (Baldwin and deMaynadier, 2009; Bulger et al., 2003; Parker and Anderson, 2003; Patrick et al., 2008; Semlitsch and Bodie, 2003), relatively little work has focused on the concept of functional connectivity at fine spatial scales (although see e.g. Popescu and Hunter, 2011; Stevens et al., 2006; Todd et al., 2009). This is unusual given that conditions in the pond margin can strongly influence both landscape resistance (Semlitsch et al., 2009) and emigration orientation (Mazerolle and Vos, 2006; Timm et al., 2007b), thereby inducing large differences in functional connectivity between patches at landscape scales. It is important, therefore, that investigations of landscape resistance for frogs include research into behavior at the pond margin.

In this paper, we describe a study designed to address the question: Do frogs preferentially use areas of low topographic relief within pond margins? High-relief movement paths require more energy to cross than low relief paths (Lowe et al., 2006), and contain proportionally fewer damp microhabitats that provide refugia from desiccation (Rittenhouse et al., 2009). Further, there is evidence both that some species rely on drainage-lines to facilitate terrestrial movements (Rittenhouse and Semlitsch, 2007), but also that overland dispersal can be an important process facilitating species persistence in some cases (Grant et al., 2010; Hazell et al., 2001). These examples suggest that the role of topographically defined barriers and movement corridors warrants further attention in relation to functional connectivity for frogs. However, the influence of topography on frog movements has received proportionally less attention than factors such as vegetation structure (e.g. see Semlitsch et al., 2009 and references therein).

We used a replicated, trap-based approach to quantify fine-scale variation in frog movement behavior, taking into account several sources of variation including the effects of rainfall, migration, demography, and distance from water on capture rates, as well as topography. Our guiding assumption was that the need to avoid desiccation is an important mechanism driving spatial and temporal variability in frog terrestrial movements. Consequently, we anticipated that captures in relation to topographic relief would be influenced by both distance from water and rainfall.

Insights into the influence of topography on frog movements are important because they have practical implications for conservation efforts. In particular, frog species with a high proportion of hydrological network-biased movement will be effectively conserved using buffer zones surrounding streams and breeding ponds (see Semlitsch and Bodie, 2003), while species which predominantly display overland movements will not. More generally, our study provides a direct, replicable test of landscape resistance. Such studies are rare, but are fundamental to understanding and managing connectivity in fragmented landscapes (Fahrig, 2007).

2. Methods

2.1. Study area

Our study area was Booderee National Park, in the Jervis Bay Territory, south-eastern Australia (approximate coordinates 35°10′S 150°40′E; see Fig. 1). The park covers the majority of the southern peninsula of Jervis Bay. It is owned by the Wreck Bay Aboriginal Community, and co-managed in association with the Australian Department of Sustainability, Environment, Water, Population and Communities (SEWPaC). The study region has a temperate climate, with average annual rainfall of approximately 1200 mm that is largely consistent year-round. The majority of the park consists of *Eucalyptus botryoides* and *Eucalyptus pilularis* forest on deep sandy soils, but patches of woodland and coastal heath are also common, predominantly on shallow soils at higher elevations (Taws, 1997).

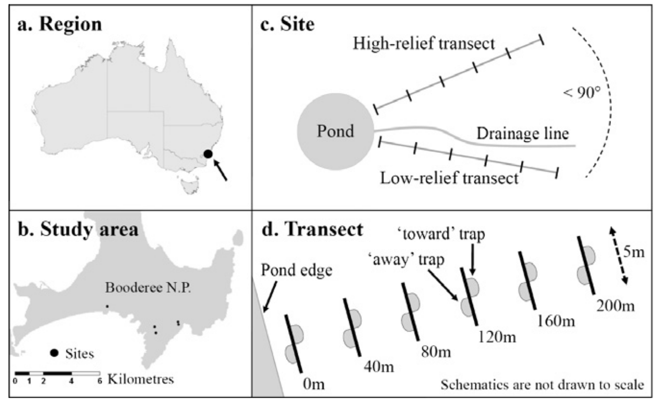

Fig. 1. Map of the study area, showing a schematic of the trapping design.

Booderee National Park contains a number of lakes and ponds formed by the blockage of existing drainage lines by sand dunes (Jones et al., 1995). These pools provide breeding habitat for the majority of frog species in the park (Westgate et al., 2012), although some species adapted to breed in ephemeral pools in coastal heaths also occur in our study area (Penman and Brassil, 2010). We chose five such ponds for this study, all of greater than 5 m diameter and surrounded by eucalypt forest. All five ponds remained flooded for the duration of the investigation. At each site, we identified a single drainage line at provided the majority of inflow from runoff, although none of these contained continuously flowing water for the duration of the study period.

The frog community in Booderee National Park consists of thirteen species split between the families Myobatrachidae (southern frogs, seven species) and Hylidae (tree frogs, six species). Both families include species that require open water for breeding (Cogger, 1996). Because hylids cannot be reliably sampled using pitfall traps (Todd et al., 2007), we focused this study on Myobatrachids.

2.2. Study design

Our study was primarily designed to investigate variation in frog movements between high and low relief locations in pond margins. However, topography has the potential to influence movement patterns of frogs through a number of mechanisms. First, low-relief locations collect and retain moisture more effectively than high-relief locations, thereby providing more favorable microclimates for frogs. Second, vegetation structure and composition can vary across topographic gradients in riparian locations (Merrill et al., 2006). Finally, the identity and abundance of both predator and prey species vary in relation to the above processes (e.g. Camper, 2009; Seagle and Sturtevant, 2005). Although we attempted to control for differences in vegetation and flowing water between high and low relief transects, our study therefore tested the combined effect of a suite of co-varying topographically-dependent attributes on frog movements.

We used a replicated trapping design to investigate the occurrence of frogs in relation to three spatial variables (distance from water, topography, and direction of movement), and two temporal variables (rainfall and Julian date). Our approach provides a different interpretation from pitfall trapping studies that investigate habitat use: rather than testing whether traps in more suitable locations detect more frogs, we tested whether some traps detected a larger number of frog movements as a result of their location. Comparatively few studies have used a trapping approach to investigate frog movements (although see Timm et al., 2007b),