



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

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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.

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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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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

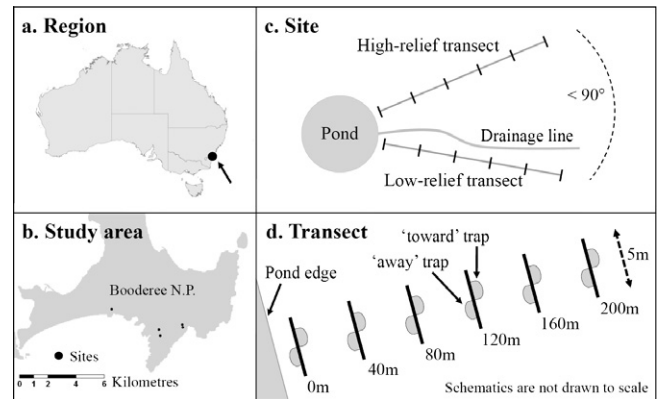


Fig. 1. Map of the study area, showing a schematic of the trapping design.

heath are also common, predominantly on shallow soils at higher elevations (Taws, 1997).

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),

with many authors instead using radio-tracking data to describe the behavior of a small number of individual animals (e.g. Bulger et al., 2003; Rittenhouse and Semlitsch, 2007; Sztatecsny and Schabetsberger, 2005). Our approach allowed direct comparison of use of different terrestrial locations in an experimental framework.

We established two transects at each pond, with each transect running for 200 m from a point within 5 m of the waters' edge (Fig. 1). We chose 205 m as our maximum study distance because it was the mean minimum core terrestrial habitat area identified by Semlitsch and Bodie (2003) in their meta-analysis of movement studies of 19 frog species. Trapping at distances shorter than 205 m would therefore be unjustified by the ecological literature, while larger distances were logistically unfeasible. The first transect (low-relief) at each pond followed a drainage line, with the second transect (high-relief) placed at the point on the waters' edge with the steepest slope that occurred within 90° of compass orientation of the first transect. Each transect consisted of six drift fences at 40 m intervals, with each fence oriented parallel to the waters' edge. Fences were 5 m long and had a 10 l pitfall bucket buried on each side, with the rim positioned at ground level. These two buckets were used to differentiate between individuals moving away from water (caught on the close-to-water side of the fence), from those moving toward water. We added a 'lip' (~5 cm wide) at the rim of each bucket to stop frogs from climbing out of the pitfall traps.

In our study design, we controlled for a number of factors that had the potential to introduce confounding in the key drivers of variation in frog movement behavior. First, we ensured that transects did not cross boundaries (either those between adjoining vegetation types, or roads or tracks), which could confound our analysis of the effect of distance from water on capture rates (Carruthers et al., 2009). Second, we released all captured individuals on the opposite side of the drift fence from where they had been captured, to minimize any effect of the study design on total distance travelled. Third, we ensured that vegetation structure varied as little as possible between low-relief and high-relief transects, to avoid confounding between vegetation type and topography.

Our study design included 120 buckets (5 sites × 2 transects × 6 distance classes × 2 directions), checked daily from 12th August to 17th September 2008 (37 days). This period includes the spring peak breeding season for a number of Australian frog species (Barker et al., 1995; Lemckert and Mahony, 2008). We took all captured animals to a nearby field station, where we weighed them and took four morphological measures; snout-vent length, tibia length, head width, and internarial distance. We photographed and clipped one toe from each animal to enable individual identification, before re-releasing each animal on the opposite side of the fence at which they had been captured. We re-opened our traps at the end of summer (between 17th January and 28th February 2009; 42 days) to collect data on dispersing juveniles. During this second period, we repeated our trapping method exactly, except that recapture rates from the first trapping period (eight recaptures from 475 captures, or <2%) were too low for the continuation of toe clipping to be necessary or justifiable. We differentiated adults and juveniles by plotting snout-vent length against tibia length and looking for discontinuities in size (see Fig. S1). The minimum SVL measurements for adults calculated using this method were 16.0 mm for *Crinia signifera*, 22.5 mm for *Paracrinia haswelli*, and 20.0 mm for *Uperoleia tyleri* (Fig. A.1).

2.3. Statistical analysis

We modeled occurrence of frogs in traps using Generalized Linear Mixed Models (GLMMs; Pinheiro and Bates, 2000). Using GLMMs enabled us to quantify the probability of capturing an animal at each trap in relation to both spatial and temporal covariates.

Since this was a trap-level analysis with low recapture rates, we excluded records of second captures of single individuals from our analysis. Site-level fixed effects were: distance from water (0–200 m), topographic relief (high or low) and direction (toward or away from water). Visit-level fixed effects were the amount of rainfall in the previous 24 h (log-transformed) and Julian date. To account for our nested study design, and to enable us to investigate both visit-level and site-level covariates, we included five levels of nested random effects: visit (38 visits per bucket for the spring trapping period); bucket ($n = 120$); fence ($n = 60$, 10 for each of six distance classes); transect ($n = 10$, five each for high- and low- topographic relief) and site ($n = 5$).

Our approach to modeling these data was to create a single model that we applied to all species, enabling us to compare relative effect sizes of each covariate across species. We included all variables as additive fixed effects, plus a small number of possible interactions that we used to test for particular responses to spatially and temporally varying conditions. First, we tested whether frogs could move more easily along low-relief transects (interaction between distance and transect). Second, we tested whether frogs moved further following rain (interaction between rainfall and distance). Third, we tested whether frogs were more restricted to low-relief locations in the absence of rainfall (interaction between transect and rainfall). Finally, we tested whether nature of the interaction between topographic relief and distance from water was affected by rainfall (i.e. a three-way interaction between these variables). Our approach was different from the more common method of choosing a 'best' model with fewer covariates; we felt that such an approach was inappropriate because of the constraints of our study design, and also because of non-trivial issues regarding the interpretation of information criteria for selection between models that include random effects (Grevén and Kneib, 2010; Vaida and Blanchard, 2005). We used the lme4 package (Bates et al., 2011) in the R statistical program (R Core Development Team, 2010) for all analyses.

To compare captures of adults versus juveniles, we used Fisher's exact test to compare proportions of captures in each of four classes. Fisher's exact test works by comparing the proportion of captures from a dataset in two sets of binary categories. In each case, the first binary variable was the number of adult versus juvenile captures. In three tests for each species, we chose corresponding variables that evenly divided the total number of traps in half. These variables were simplified versions of our spatial variables of interest, i.e. topography (high versus low relief), distance from water (0–80 m versus 120–200 m), and direction of travel (towards or away from water). Where Fisher's test gave a P value ≤ 0.05 , we took this as evidence of a significant difference in adult versus juvenile captures for the spatial comparison in question.

2.4. Quantifying the importance of high versus low relief locations

The final stage of our analysis was to estimate the total proportion of frogs using high or low relief landscape elements. This was important because the approach employed thus far – directly comparing frog occurrence on high-relief versus low-relief transects – implied that both transect types represent equal proportions of the pond edge, an assumption that was clearly invalid for the ponds in question.

To quantify the relative availability of high and low relief locations, we used satellite imagery to measure the circumference of each pond, and the proportion of the circumference in each topographic class. We then multiplied the number of captures on each transect type (high or low relief) by the proportion of the pond edge in each of the respective classes. This gave us an estimate of relative frog abundance in high versus low relief locations. We then converted our estimated abundance data to percentages, and

averaged the percentage of individuals using high versus low relief locations across all sites.

3. Results

We captured a total of 965 frogs from seven species: 538 in our spring trapping period, and 427 in our summer trapping period. However, during our spring trapping period, three species – *Pseudophryne bibronii*, *Litoria jervisiensis* and *Heleioporus australiacus* – were represented by only a single individual, and we captured only four adults from a fourth species (*Limnodynastes peronii*). This left three species that were sufficiently common to enable us to construct models of adult occurrence from our spring trapping dataset: *C. signifera* ($n = 171$), *P. haswelli* ($n = 174$) and *U. tyleri* ($n = 130$). These three species are all small (<50 mm), pond-dwelling members of the family Myobatrachidae (Cogger, 1996).

We found that capture probabilities decreased significantly with increasing distance from water, and increased significantly following rainfall, for all three species (Table 1). However, the effect of topography on capture rates varied between species, and was strongly mediated by both rainfall and distance from water. For *C. signifera*, increased captures following rainfall were concentrated on low-relief transects ($\beta_{(\text{distance:transect:rain})} = 0.23 \pm 0.13$, $P = 0.078$). There was a similar effect for *P. haswelli*, with the majority of additional captures following rainfall occurring at short distances from water ($\beta_{(\text{transect:rainfall})} = 0.15 \pm 0.08$, $P = 0.067$). Finally, captures of *U. tyleri* were higher on low-relief than high-relief transects after rainfall; but this pattern was reversed during drier periods (Fig. 2). Supplementary analysis of individual distance classes showed that captures were significantly higher on low-relief transects at distances of up to 80 m from water for both *C. signifera* ($P = 0.010$) and *P. haswelli* ($P = 0.032$) but only at the shortest distance class from water for *U. tyleri* ($P = 0.01$).

We found limited evidence of migratory movement in spring, with only *U. tyleri* showing evidence of higher levels of movement towards water ($\beta_{(\text{direction})} = 0.57 \pm 0.30$, $P = 0.061$). Capture rates also increased throughout the trapping period for both *U. tyleri* ($\beta_{(\text{date})} = 0.11 \pm 0.01$, $P < 0.001$) and *C. signifera* ($\beta_{(\text{date})} = 0.04 \pm 0.01$, $P < 0.001$). Increasing captures over time in these species was not due to confounding with rainfall, since rainfall and time were poorly correlated (Pearson's correlation = 0.16), with high rainfall events occurring almost weekly throughout the study period (rainfall >10 mm on days 12, 18 and 26).

Results from our second trapping period (in late Summer/early Autumn) were less conclusive than those from our spring trapping period. Although we captured a reasonable number of juvenile frogs in our second trapping period (*C. signifera* = 28, *P. haswelli* = 145, *U. tyleri* = 32), most were from a single site ($n = 171$, 83%), and we did not observe any mass dispersal events. These factors limited the degree of inference that could be drawn from

linear models of the kind constructed for adult captures. We therefore restricted our analysis to comparison of the proportion of adult and juvenile captures between different treatments (Table 2). Fisher's exact test showed no significant difference between adults and juveniles of any species, in terms of the proportion of individuals captured on low-relief versus high-relief transects (P values: *C. signifera* = 0.36; *P. haswelli* = 0.45; *U. tyleri* = 0.84), or with increasing distance from water (P values: *C. signifera* = 0.82; *P. haswelli* = 0.19; *U. tyleri* = 0.79). The only significant difference between adult and juvenile captures was that juvenile *P. haswelli* were significantly more likely to move away from water than were adults of the same species ($P = 0.006$).

Using satellite imagery, we found that the total circumference of ponds averaged 658 m, while low relief locations chosen for investigation in our study averaged 28 m of the pond boundary (<6%). This suggested that our raw data on relative numbers of captures (see Table 2) were not representative of the overall importance of high- versus low-relief locations in pond riparian margins. Although 67% of captures on average were on low-relief transects (*C. signifera* = 71%; *P. haswelli* = 74%; *U. tyleri* = 56%), once these numbers were weighted according to the area covered by steep and shallow slopes, we found that >90% of all animals would be likely to occur in relatively high-relief locations (*C. signifera* = 91%; *P. haswelli* = 89%; *U. tyleri* = 95%).

4. Discussion

For this study, we aimed to quantify the extent of topographic bias in the movement behavior of three frog species. We found that low-relief drainage lines providing the majority of inflow into breeding ponds were preferentially used by these frogs. More specifically, we found statistically significant differences in frog occurrence between high- and low-relief transects for all three species, although this effect was mediated by rainfall and distance to water (Fig. 2). While this would appear to reinforce the importance of drainage lines as priority locations for frog movements, one third of all captures were on high-relief transects, which was a higher proportion than we had expected at the outset of the study. Because drainage lines are linear features of landscapes that cover only a small proportion of pond edge, we were able to show that the absolute proportion of individuals from these three species that preferentially used low-relief locations is likely to be small.

Our finding that only a small proportion of frogs use low-relief pond margins, a pattern that was consistent for all three species for which data were available, has important implications for landscape planning and frog conservation. Some authors (e.g. Baldwin et al., 2006; Roe and Georges, 2007) have suggested that reducing the radius of buffers around breeding ponds, and proportionally increasing the width of buffers centered on stream networks, would increase the representation of commonly used areas for

Table 1
Variable estimates from Binomial GLMMs.

Type	Variable	<i>C. signifera</i>	<i>P. haswelli</i>	<i>U. tyleri</i>
Spatial	Intercept	-3.11 ± 0.68 (P < 0.001)	-2.05 ± 0.57 (P = 0.001)	-6.64 ± 0.74 (P < 0.001)
	Distance from water	-0.64 ± 0.16 (P < 0.001)	-0.87 ± 0.20 (P < 0.001)	-0.43 ± 0.20 (P = 0.030)
	Steep topography	-0.91 ± 1.01 (P = 0.368)	-0.87 ± 0.85 (P = 0.304)	2.18 ± 0.82 (P = 0.008)
	Moving towards water	0.13 ± 0.21 (P = 0.533)	-0.10 ± 0.25 (P = 0.670)	0.57 ± 0.30 (P = 0.061)
Temporal	Rainfall	0.44 ± 0.20 (P = 0.031)	0.66 ± 0.21 (P = 0.002)	1.39 ± 0.30 (P < 0.001)
	Date	0.04 ± 0.01 (P < 0.001)	0.001 ± 0.01 (P = 0.986)	0.11 ± 0.01 (P < 0.001)
Interactions	Distance: topography	-0.32 ± 0.31 (P = 0.306)	0.05 ± 0.33 (P = 0.889)	-0.96 ± 0.38 (P = 0.011)
	Distance: rainfall	0.10 ± 0.07 (P = 0.128)	0.15 ± 0.08 (P = 0.067)	-0.10 ± 0.11 (P = 0.387)
	Topography: rainfall	-0.45 ± 0.36 (P = 0.213)	-0.39 ± 0.37 (P = 0.285)	-1.54 ± 0.43 (P < 0.001)
	D:T:R	0.23 ± 0.13 (P = 0.078)	0.08 ± 0.15 (P = 0.591)	0.56 ± 0.19 (P = 0.003)

Values with $P \leq 0.05$ are given in bold.

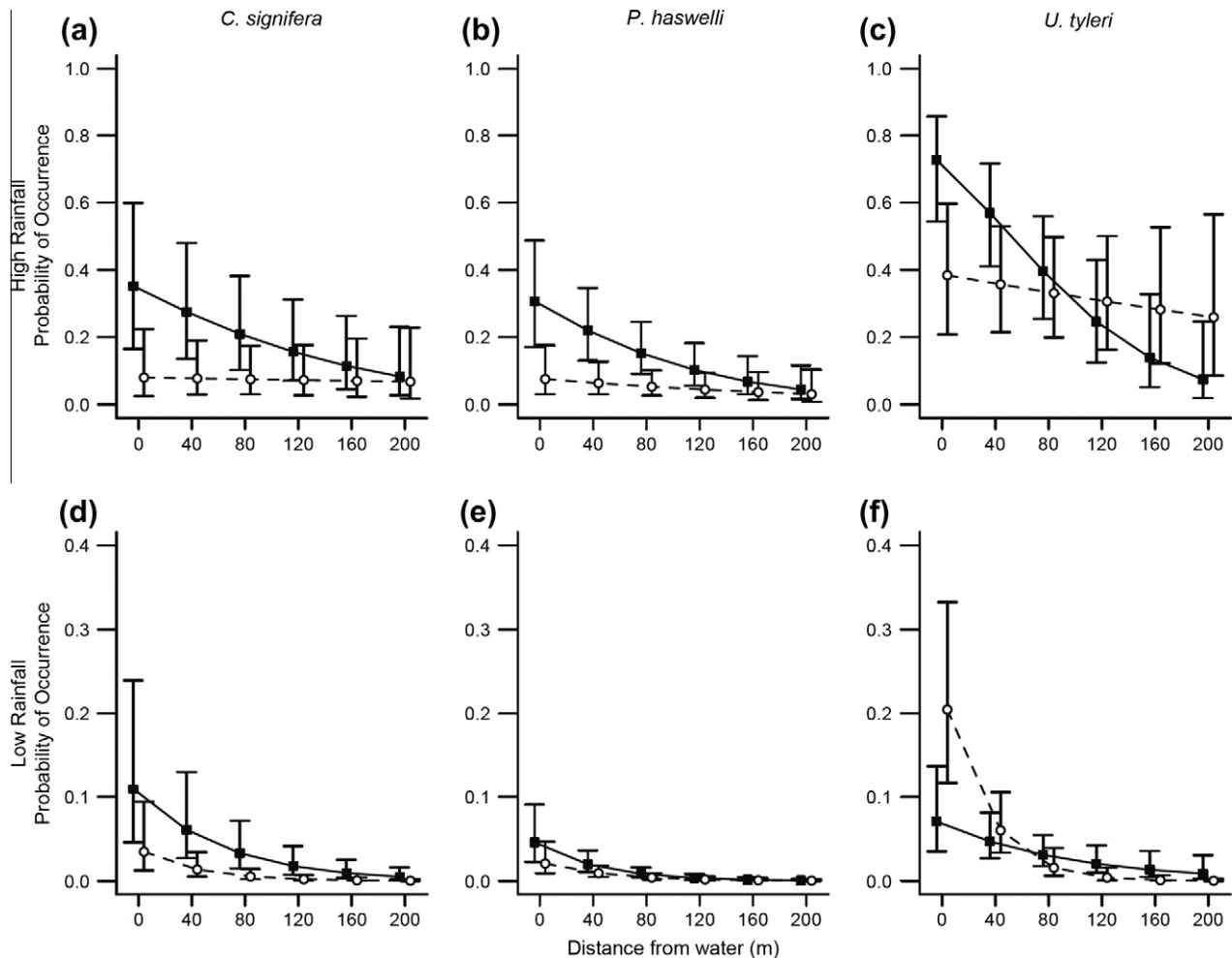


Fig. 2. Probability of occurrence with increasing distance from water, as given by GLMMs. Columns give results for each species, while rows give results for different amounts of rainfall. Solid lines (filled squares) give estimates for low-relief transects; dashed lines (open circles) give estimates for high-relief transects.

Table 2

Number and proportion (in parentheses) of captures of adult and juvenile frogs from three species. *P* values show significance of Fishers' exact tests on proportions of adult and juvenile captures in each category, with values ≤ 0.05 given in bold.

Criteria	<i>C. signifera</i>			<i>P. haswelli</i>			<i>U. tyleri</i>		
	Juvenile	Adult	<i>P</i>	Juvenile	Adult	<i>P</i>	Juvenile	Adult	<i>P</i>
Within 80 m of water	20 (0.71)	128 (0.75)	0.816	115 (0.79)	148 (0.85)	0.187	28 (0.88)	108 (0.83)	0.788
On low-relief transects	23 (0.82)	121 (0.71)	0.259	102 (0.70)	129 (0.74)	0.454	19 (0.59)	73 (0.56)	0.430
Moving towards water	18 (0.64)	84 (0.49)	0.157	101 (0.70)	94 (0.54)	0.006	21 (0.66)	83 (0.64)	1.00
Total	28	171		145	174		32	130	

semi-aquatic herpetofauna without increasing overall land allocation to conservation. Our results contrast with that view; a drainage-line buffer in this location would conserve areas used during <10% of frog movements for the species that we studied (see also Bulger et al., 2003). Our results suggest that circular buffers around breeding ponds would be a more appropriate use of resources for the conservation of valuable terrestrial locations (see Calhoun et al., 2005; Semlitsch and Bodie, 2003). Rather than conflicting with earlier research, however, these results reinforce the deeper message that empirical testing of frog movement behavior is important to ensure that buffers meet their goals of conserving viable frog populations (Gamble et al., 2007; Goates et al., 2007).

Use of high-relief transects by frogs was unexpectedly high in our study. This is particularly surprising considering that most studies of amphibian movements in riparian areas either use fences as enclosures to capture all migrating individuals (e.g.

Gibbons et al., 2006; Regosin et al., 2005), or else increase trap effort with increasing distance from water, such that a constant proportion of pond edge is represented at each distance class (e.g. Patrick et al., 2008). Such an approach was impossible in our study because drainage lines are linear features. Our methodology would therefore lead us to expect decreasing captures with distance on high-relief transects, simply as a result of lower proportional survey effort with increasing distance from water. However, if drainage lines act as movement corridors for frogs (Rittenhouse and Semlitsch, 2007), we would not expect a corresponding decrease in captures on low-relief transects. We were surprised, therefore, to find that capture rates decreased at similar rates with increasing distance from water on both high-relief and low-relief transects (Fig. 2). Although this result might have eventuated by chance if frogs commonly moved parallel to the pond edge, such movement is inconsistent with perpendicular movement observed for *U. tyleri*.

Therefore, the available evidence suggests that drainage lines are not acting as movement corridors. Instead, low-relief locations are functionally similar to high-relief transects, but with higher densities near the pond edge.

Despite our finding of decreasing occupancy of frogs with increasing distance from water (consistent with Semlitsch and Bodie, 2003), some frogs used terrestrial areas at large distances from water during the breeding season. Locations up to 80 m from water – a distance which exceeds mandated buffer zone widths in some jurisdictions (Goates et al., 2007) – had a >20% probability of capturing *C. signifera* or *U. tyleri* following rainfall (Fig. 2). This finding has two important implications. First, buffer zones up to 80 m from the waters' edge may be used throughout the breeding season, most likely for foraging. Interestingly, this is lower than some estimates; for example, *C. signifera* can be ubiquitous at distances of up to 500 m from water in some locations (Lauck, 2005). This reinforces the importance of comparatively large buffer zone widths (Harper et al., 2008). Second, locations >80 m from water supported a smaller increase in captures following rain, suggesting that rainfall did not increase the likelihood of long-distance adult movements (i.e. migration or dispersal). Although weather can strongly influence the probability of dispersive movements in frogs (Gibbons et al., 2006; Timm et al., 2007a) as well as in other animal taxa (e.g. Walls et al., 2005), our results support the view that favorable weather conditions may not initiate migratory or dispersive movements (see also Semlitsch, 2008).

Our finding that terrestrial locations were commonly used by the frog species that we studied was exemplified by one species in particular. High captures of *U. tyleri* in high-relief and long distance-from-water locations might have been influenced by high levels of territoriality among male *U. tyleri* (Robertson, 1986). This is because territoriality could mitigate against concentration of individuals in locations with favorable microhabitat characteristics. More importantly, however, *U. tyleri* was the only species for which there was evidence of migratory behavior during our spring trapping period. This evidence included an initial absence of captures for this species (first capture on day 10), and some directional movement ($\beta_{\text{direction}} = 0.57 \pm 0.30$, $P = 0.061$). The fact that we found no corresponding evidence of topographically-biased movement for this species suggests that *U. tyleri* uses high-relief locations during migration and/or dispersal. These findings support our assertion that high-relief locations are likely to be important for ongoing persistence of local breeding populations for this species (see Harper et al., 2008).

We found no evidence for a difference in terrestrial movements between adults and juveniles of any species. The only exception was that directional movement of juveniles was greater than for adults in *P. haswelli* (Table 1). This difference was expected given that metamorphic juveniles must begin their movements from water (and can therefore only move away from their natal ponds), whereas adults may occur at a range of distances from water at the beginning of their migratory period. While these results may appear surprising given that juveniles are commonly thought to be the dispersive phase in the frog life cycle (Semlitsch, 2008), contrary evidence does exist for some species. Smith and Green (2006), for example, report that movements of Fowler's Toads (*Bufo fowleri*) are not demographically biased. Given the importance of juvenile dispersal for predicting demographic variation and the persistence of frog populations (Swanack et al., 2009), juvenile-biased dispersal should be carefully tested for, rather than assumed, in frog species.

To what extent are our results relevant for describing functional connectivity across landscapes? The answer to this question depends upon the extent to which our results are representative of dispersive movements for the species in question. Although there are prominent examples where frogs have made long-distance di-

rected movements toward breeding sites (Sjogren-Gulve, 1998), there is also evidence of frog species following undirected movement paths (Rothermel, 2004; Schwarzkopf and Alford, 2002). In the latter case, dispersal would result from a series of small foraging movements, rather than being a deliberate behavior (Hawkes, 2009; Van Dyck and Baguette, 2005). Even if foraging and dispersal are different behaviors, we are unaware of any evidence suggesting that topographic bias in frog movements varies between foraging and dispersal. In this case, our finding of limited differences between adult and juvenile behavior (Table 2) supports the argument that our results are representative of general movement behavior for the species in question. The available evidence therefore suggests that strong topographically-biased dispersal is unlikely at landscape scales for the species that we studied. This also implies that isolation of breeding ponds will predominantly be influenced by distance rather than topography, decreasing pond isolation, and thereby reducing the probability of local extinction (Griffen and Drake, 2009; Johst et al., 2011). However, studies at larger spatial scales would be necessary to confirm these expectations (Hovesadt et al., 2011; Jacobson and Peres-Neto, 2010).

5. Conclusions

Our study has shown that – for the pond-breeding frogs that we examined – the majority of individuals used terrestrial areas that were not located on drainage lines. This leads to two important conclusions for frog conservation in this location. First, buffer zones designed to conserve only hydrological networks would provide insufficient protection of locations that were commonly used by frogs in this study. Second, drainage lines are unlikely to be vital networks facilitating connectivity between breeding ponds for the species that we studied. Underlying these unexpected responses to topography were a series of unexpected movement behaviors in the frog species in question. These included: (1) near-continuous use of terrestrial areas at large distances (up to 80 m) from water during the breeding season. (2) Low incidence of directional or migratory movement. (3) Limited differences between adult and juvenile movements. Focusing on the nexus between fine-scale movement behavior and landscape scale connectivity has therefore provided novel insights into behaviors which underlie variation in terrestrial movement behavior by frogs in this location. However, further work is required to determine the extent to which the patterns we have identified apply more generally. In particular, larger frogs are generally capable of dispersing with low risk of dehydration (Tracy et al., 2010), while frogs that are closely related, but ecologically dissimilar, may use terrestrial locations in different ways (Rowley and Alford, 2007; Tracy et al., 2010). Along with identification and prioritization of at-risk habitats (Baldwin and deMaynadier, 2009), anchoring estimates of functional connectivity in an understanding of animal behavior at relevant spatial scales (Van Dyck and Baguette, 2005) is therefore an important goal for amphibian conservation in future.

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Appendix A

See Fig. A.1.

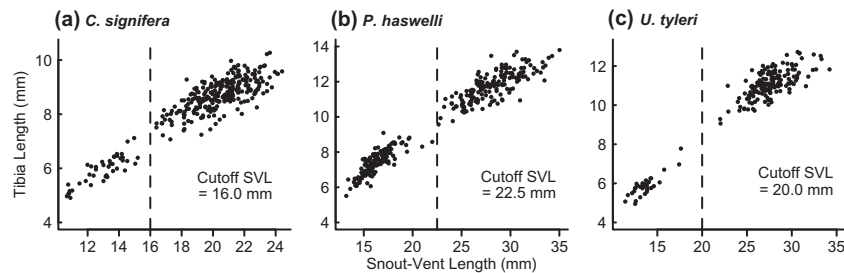


Fig. A.1. Tibia length (TL) versus Snout-Vent length (SVL) for the three most abundant species in our study. Dashed lines give 'cut-off' SVL's used to differentiate adults from juveniles in this study.

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