

Mechanisms underlying the occurrence of species in complex modified tropical landscapes: a case study of amphibians in the Osa Peninsula, Costa Rica

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Abstract: The mechanisms underlying occupancy patterns of species in modified tropical landscapes are poorly understood. The presence of adults in a modified habitat may not necessarily indicate the quality of the habitat for sub-adult stages. These issues were addressed by examining patterns in breeding-site use by adult frogs and tadpole performance across a pasture-forest gradient in the Osa Peninsula, Costa Rica. The use of artificial pools by adult frogs for breeding activity was quantified along three transects, with a pool located at the edge (0 m) and 10, 30 and 50 m into forest and pasture. Next, survival, size at metamorphosis and time to metamorphosis were quantified for tadpoles of *Engyptomops pustulosus* and *Dendrobates auratus* in artificial pools at the edge, pasture and forest. Adult frogs used breeding pools non-randomly; two species used pools only in pasture, whereas three species used pools only in forest. In addition, *Smilisca phaeota* used pools in pasture and at the edge while *E. pustulosus* used pools across the pasture-forest gradient. The habitat where adults used breeding pools generally also yielded high performance of their tadpoles, with some exceptions. Tadpole survival to metamorphosis was low in pastures (< 5%) and higher in edge and forest (> 18%) for *D. auratus*; in contrast, survival of *E. pustulosus* was over 80% in each habitat. Metamorphs of *D. auratus* were largest in edges but larval period did not differ among habitats. Metamorphs of *E. pustulosus* were 18% larger and larval period was 27% shorter in pastures compared with forest. These results suggest that modified habitats represent an ecological jackpot for some species, such that offspring performance is enhanced compared with that in forest habitat. Populations of other species may be restricted to forest habitat because of intolerable abiotic conditions in modified habitats. The results of this study indicate that adult breeding site use and tadpole performance contribute to mechanisms that underlie patterns of species occupancy in modified tropical landscapes.

Key Words: anurans, breeding sites, habitat modification, ecological jackpot, forest cover, matrix habitats, mechanisms, tadpole performance

INTRODUCTION

Habitat modification presents new challenges for species, especially those with complex life cycles requiring the use of more than one habitat type. In a landscape mosaic composed of modified and intact habitats, species may encounter habitats that represent an ecological trap (Schlaepfer *et al.* 2002) or an ecological jackpot to different stages in their life histories. An ecological trap can occur when the cues previously associated with adaptive outcomes in an environment are no longer reliable (Schlaepfer *et al.* 2002). In these situations,

species may breed in areas where offspring performance is poor, which can lead to extinction of a population if adaptation to the new environment cannot occur on a similar time scale. In contrast, an ecological jackpot can occur when a modified habitat provides circumstances that result in a demographic benefit for a species. For instance, offspring performance in a modified habitat may be improved due to amenable abiotic conditions leading to population growth. These possibilities can present significant problems or benefits for species living in fragmented landscapes.

Surveys of adult populations are generally the first step to understanding occupancy patterns of species in a mosaic of modified and intact habitats. Most studies investigating frog diversity in modified habitats assume that adult occupancy patterns correlate with overall

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habitat quality (Mendenhall *et al.* 2014, Toral *et al.* 2002, Urbina-Cardona *et al.* 2006). However, this conclusion may be oversimplified for several reasons. First, most amphibians are known to use more than a single habitat type, often migrating from terrestrial to aquatic habitats throughout the year (Semlitsch 2000, Wilbur 1980). Second, the presence of some species in modified habitats may reflect proximity to a suitable habitat with a source population rather than habitat quality (Pullinam 1988). Third, tolerance of abiotic conditions may depend on life-history stage, with adult amphibians more tolerant than sub-adult life stages. If modified habitats do not meet the requirements of a species during each life stage, then we can expect non-random patterns of patch occupancy based on differential fitness across the landscape (Morris 2003). Population surveys that focus solely on the adult life stage do not provide the entire picture of how a species uses resources in a complex landscape mosaic (Cushman 2006).

Landscape-level features, along with species-specific behaviour and ecology, influence breeding-site use in amphibians. Frogs may utilize breeding sites in a matrix habitat near a forest edge even if the matrix habitat is unsuitable for foraging and cover. In contrast, some species may avoid matrix habitats because of physiological or behavioural constraints (Gascon 1993). Breeding-site use has fitness consequences for subsequent life-cycle stages, with possible declines in metamorph and juvenile survival if pools are isolated from suitable terrestrial habitat (Rothermel 2004).

To improve our understanding of how species use habitats within complex tropical landscapes, I examined breeding pool use across a forest to pasture gradient. Then I determined how tadpole performance varies across this forest to pasture gradient. I hypothesized that species would use pools for breeding activities in the habitat where adults are most commonly encountered and where tadpole performance is highest.

METHODS

This study was conducted on private land near Rio Piro in the Osa Peninsula, Puntarenas Province, Costa Rica (8°26'N, 83°22'W). This region is characterized by distinct rainy (May–December) and dry seasons (January–April) with precipitation averaging 4000 to 6000 mm y^{-1} (Sirena Station, unpubl. data). The study landscape is a mosaic of lowland wet forest (Hartshorn 1983) and pasture (60 y old), with a distinct edge separating the habitats. The edge is maintained by local landowners and is abrupt, changing from pasture grasses to mature trees, with variable sunlight hitting the ground depending on edge orientation relative to the sun.

Breeding-site use

Seven plastic pools (10 L; 16 cm depth, 31 cm diameter) were placed at fixed distances from the pasture-forest edge along three transects ($n = 21$ pools). Transects were oriented in different directions with respect to the edge and at least 200 m apart. Along each transect, pools were placed at the edge (0 m), and at 10, 30 and 50 m from that edge into both pasture and forest. Each pool was situated flush with the ground level and surrounded by a barrier to prevent cows from entering. The lower edge of the barrier was elevated 15 cm above the pool, allowing frogs to enter. Frogs could also enter through two openings (30 cm wide) on either side of the pool. Pools contained two fibreglass screen ladders (10 cm wide) to allow metamorphs to escape. Water and leaf litter accumulated within the pools naturally.

Pools were monitored for egg and tadpole presence every 7 d for 20 wk (26 June–6 November 2006). The presence of new cohorts in a pool was based on the life history of the species. In pasture and edge habitats, new cohorts were identified by the presence of eggs or recent hatchlings. In the forest, tadpoles were counted each week and an increase in tadpole population size was used to determine whether a new cohort was present. This conservative approach may underestimate the number of new cohorts in forest pools, for instance, dendrobatids may deposit cohorts of tadpoles on more than one occasion during a week but all were counted collectively as a single new cohort. Although cannibalism and predation could reduce population sizes and/or eliminate cohorts, these issues were expected to have had little influence on the results because only increased population sizes were found over time.

Low sample sizes permitted statistical analysis only for *Engystomops pustulosus* (Cope 1864) and members of the families Dendrobatidae (*Dendrobates auratus* (Girard 1855) and *Phylllobates vittatus* (Cope 1893)) and Aromobatidae (*Allobates talamancae* (Cope 1875)). Data for the latter three species were pooled to permit a test for species with similar life histories. I tested the null hypothesis that the number of clutches deposited in forest pools was no different from the number of clutches deposited in pasture pools using one-tailed t-tests for unequal variance. Edge pools (0 m) were excluded from this analysis.

Tadpole performance study species

Two species, *D. auratus* and *E. pustulosus*, were selected for a study of tadpole performance based on their abundance, contrasting life histories and habitat preferences. *Dendrobates auratus* is a diurnal, territorial, forest specialist that lays eggs in small clutches (5–13)

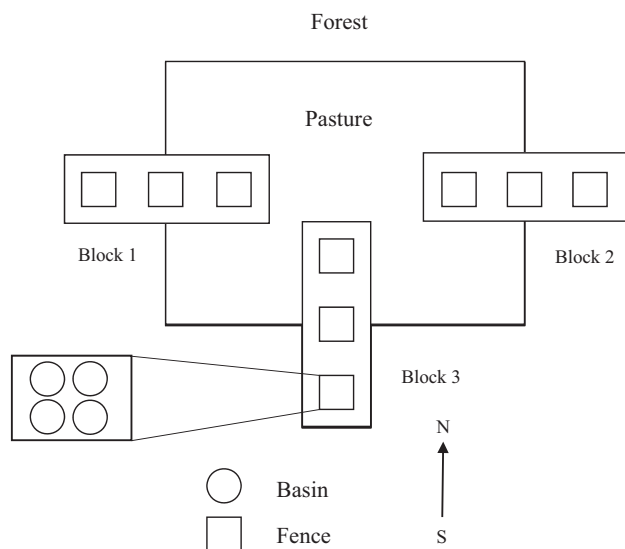


Figure 1. Randomized complete block design used for the tadpole performance experiments conducted in 2005 and 2006 in the Osa Peninsula, Costa Rica. Each block was composed of three sub-blocks, one in forest, pasture and forest–pasture edge. Each treatment had two replicates in each sub-block, for a total of six pools in each block and 18 pools per species in each experiment.

in terrestrial habitats. After eggs hatch, males carry the tadpoles to small pools (e.g. in palm fronds or tree cavities) and metamorphosis occurs within 5–13 wk (Savage 2002). *Dendrobates auratus* is restricted to lowland forests (Savage 2002) and adults were found to occupy only forests in surveys in the study area (Hawley unpubl. data); however, individuals are known to forage in fields and fence rows adjacent to forest in Panama (Toft 1985). In contrast, *E. pustulosus* deposits large clutches of eggs (80–450) in foam nests in a wide array of aquatic habitats, including small temporary pools, hoof prints and ditches (Savage 2002). Metamorphosis occurs within 5–9 wk (Savage 2002). *Engystomops pustulosus* is nocturnal and common in open and disturbed areas, as well as forest edges (Savage 2002; Hawley unpubl. data). It is associated with forest in other parts of its range (Marsh *et al.* 1999).

Tadpole performance experimental design

A randomized block design was used to reduce variation from genetic and environmental sources, with three blocks each composed of three sub-blocks (enclosed in fences), one in forest, pasture and at the forest–pasture edge (Figure 1). Each block was positioned at a different cardinal angle with respect to the forest–pasture edge. Because of the landscape configuration, pasture sub-blocks were located 65 m from the edge, while forest sub-blocks were 80 m from the edge. Each experimental unit

(10 L; 19 cm depth, 31 cm diameter artificial pool) was randomly assigned to a sub-block and a location in each sub-block. There were two pool replicates per sub-block, for a total of 18 pools per species. The experiment for *D. auratus* was conducted in 2005 and for *E. pustulosus* in 2006.

Each pool was filled with stream water (6 L) and damp leaf litter (150 g). In addition, each pool was inoculated with zooplankton and phytoplankton (1 L water samples filtered through 1.0-mm² mesh) collected from two nearby ponds. All pools were covered with nylon mesh cloth to reduce introductions of insect or frog larvae. Within a block, all pools were prepared on the same day and remained in the edge sub-block until the experiment began. On the day the experiment began, pools were transported to their appropriate position in each sub-block and buried, with 4 cm of the pool top exposed above the soil surface. In 2005, the pools were prepared 3–4 d before introducing *D. auratus* tadpoles. In 2006, pools were prepared 14 d before introducing *E. pustulosus* tadpoles. Tadpoles were placed into the pools in a consecutive manner; in 2005, block 1 was started on 29 May, block 2 on 9 June and block 3 on 18 July. In 2006, block 1 was started on 27 June, block 2 on 3 July and block 3 on 10 July.

The experimental design remained largely the same between species, with a few exceptions. I collected tadpoles of *D. auratus* from natural and artificial breeding sites (~50 plastic cups in tree crevices). Tadpoles were sorted by size class (small, medium and large) and distributed to pools in a standardized manner. Five tadpoles were added to pools in block 1, and four tadpoles to pools in blocks 2 and 3. Tadpoles were digitally photographed and size was determined (mean total length) per pool digitally (Image J, version 1.34s; <http://rsb.info.nih.gov/ij/>; block 1, 1.85 ± 0.06 cm (mean ± SE), block 2, 1.93 ± 0.06 cm, and block 3, 2.00 ± 0.03 cm. All tadpoles of *D. auratus* were in developmental stage 25 (Gosner 1960) at the beginning of the experiment. Three foam nests of *E. pustulosus* laid the previous night were collected as a source of individuals for pools in each block and 10 tadpoles (4 d old; Gosner stage 24 or 25) were added to their respective pools in the late afternoon.

Tadpole survival was determined on day 3 by removing tadpoles and thoroughly searching the leaf litter in each pool. Thereafter, survival was assessed every 5 d. When tadpoles reached stages 40–41 (Gosner 1960), I checked the pools twice daily for metamorphs (at least one emerged forelimb). Metamorphs were removed and held individually until their tail was absorbed, then weighed. The experiment ended on day 103 (in 2005) and day 60 (in 2006) because *D. auratus* require more time to develop than *E. pustulosus*. Any tadpole that did not complete metamorphosis by the end of the experiment was considered to have perished. The response variables were

proportion surviving to metamorphosis, metamorph size (mass) and larval period (time to metamorphosis). Because *D. auratus* suffered high mortality in pasture sub-blocks, the proportion of pools in each treatment with at least 50% of tadpoles surviving over time was also examined.

Differences in experimental design for each species precluded interspecific statistical comparisons. All variables met the parametric assumptions of normality and homogeneity of variance. To examine heterogeneity in larval performance measures between habitats, analysis of variance (ANOVA) was used with habitat as a fixed factor and block as a random factor. When block did not have a significant effect on the dependent variable, the analysis was rerun without the block factor. Tukey's HSD post hoc multiple comparisons tested for differences between treatments and blocks when ANOVA yielded a significant result. Kaplan–Meier survival analysis (Levesque 2007) was utilized to compare tadpole survivorship of *D. auratus* over time in pasture, edge and forest treatments using the proportion of pools in each treatment with at least 50% of tadpoles surviving over time. Survivorship curves were compared among treatments using a log-rank test. All statistical tests were conducted in SPSS Version 24.0 (IBM Corp., Armonk, New York, USA).

Several abiotic characteristics were quantified to describe the environment in each habitat. Air temperature and relative humidity were measured hourly using HOBO data loggers (41 d; 1 June–11 July 2005; Onset Computer Corporation, Pocasset, Massachusetts, USA). A single HOBO logger was placed in forest (85 m from edge), edge and pasture (65 m from edge) habitats. The light environment in each sub-block (Figure 1) was quantified using hemispherical photographs (Nikon Coolpix 4500 digital camera with a Nikon FC-E8 fisheye converter lens; 180° field of view). The camera, mounted on a tripod 30 cm above the ground and oriented with magnetic north at the top of the image, allowed the incorporation of solar tracks in the photo analysis. Four photos in each sub-block were taken on overcast days (19–20 November 2006). The photos were processed and analysed using Gap Light Analyzer, version 2.0 (Frazer *et al.* 1999), calculating global site factor (GSF). Global site factor can range from 0 (complete obstruction) to 1 (open sky) and is the percentage of incident radiation transmitted through a gap to a point below the canopy during a growing season (Canham 1988). Heterogeneity in GSF with habitat as a fixed factor and block as a random factor was tested using ANOVA. In addition, water temperature was monitored hourly in one pool in each sub-block using I-button temperature loggers (Maxim Integrated Products, Sunnyvale, CA) placed in plastic bags at a depth of 18 cm. Mean daily maximum and minimum water temperature was calculated for each sub-block for about 30 d each year (25 July–22 August 2005 and 1–31

August 2006). A subset of the total dataset was used because of logger malfunctions. Relationships between GSF and water temperatures were examined by calculating Pearson product-moment correlation coefficients.

RESULTS

Abiotic environments

On average, the maximum daily water temperature was 10°C higher in pasture than in forest and edge pools (35.2°C, 24.8°C and 26.5°C, respectively), whereas minimum daily water temperature varied little among habitats (25.8°C, 24.0°C, 24.5°C, respectively). In forest and edge pools, water temperature fluctuated by an average of 1–2°C throughout the day; in contrast, it fluctuated by as much as 9°C in pasture pools. Maximum and minimum daily water temperatures in 2005 and 2006 varied little (0.44 ± 0.11 units; mean difference between years in each habitat \pm SE, $n = 3$ habitats). In both years, the daily water temperature range was larger in pasture (24–41°C) than in edge (23–29.5°C) and forest (23.5–26°C). Daily air temperature range varied little in forest (23.9–27.3°C; mean minimum–maximum) and in the edge (23.5–27.8°C), compared with in pasture (23.5–35.0°C). Similarly, daily relative humidity range varied little in forest (96–100%; mean minimum–maximum) and at the edge (94–100%), compared with in the pasture (61–100%).

Global site factor (GSF) was higher in pasture (0.897 ± 0.007 ; mean \pm SE) than in edge (0.117 ± 0.010) and forest (0.130 ± 0.006 ; $F_{2,35} = 5765$, $P < 0.001$), but there was no difference between edge and forest ($P = 0.307$). In addition, GSF differed among blocks ($F_{2,35} = 14.0$, $P < 0.001$); it was higher in block 3 than in block 1 or 2 ($P \leq 0.002$), but did not differ between blocks 1 and 2 ($P = 0.358$). Global site factor was positively correlated with both maximum ($r = 0.983$, $P < 0.001$) and minimum ($r = 0.914$, $P = 0.001$) water temperatures in each sub-block ($n = 9$).

Breeding-site use

Thirty-seven egg and tadpole deposition events occurred during the study period. Four species (*E. pustulosus*, *Smilisca phaeota* (Cope 1862), *Leptodactylus poecilochilus* (Cope 1862) and *Hypsiboas rosenbergi* (Boulenger 1898)) deposited eggs in pasture and four species (*E. pustulosus*, *P. vittatus*, *D. auratus* and *A. talamancae*) deposited eggs or tadpoles in forest (Table 1). *Engystomops pustulosus* deposited clutches in multiple pools across the forest to pasture gradient (50 m into pasture and 10 m into forest). *Phyllobates vittatus* deposited multiple cohorts in two

Table 1. Number of cohorts deposited by different species in artificial pools in pasture, edge and forest at different distances from the edge, along three transects in the Osa Peninsula, Costa Rica from June to November 2006 (species abbreviations: At = *Allobates talamancae*, Da = *Dendrobates auratus*, Hr = *Hypsiboas rosenbergi*, Lp = *Leptodactylus poecilochilus*, Ep = *Engystomops pustulosus*, Pv = *Phyllobates vittatus* and Sp = *Smilisca phaeota*).

Transect	Pasture			Edge	Forest		
	50 m	30 m	10 m	0 m	10 m	30 m	50 m
1	1 Lp	0	0	0	0	0	4 Pv, 4 At
2	0	1 Hr	2 Ep	1 Ep	1 Ep	0	0
3	1 Ep	4 Ep, 1 Sp	5 Ep, 1 Sp	1 Sp	1 Da	0	9 Pv

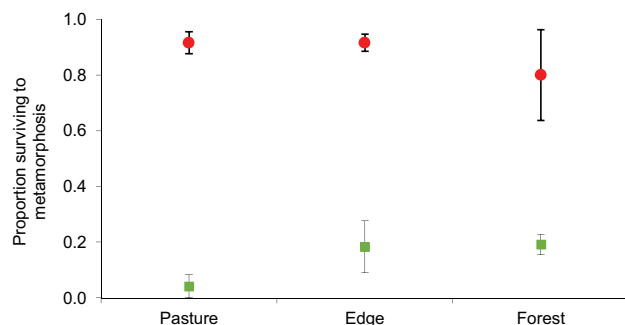


Figure 2. Proportion of tadpoles surviving (mean \pm SE) to metamorphosis for *Engystomops pustulosus* (red circles) and *Dendrobates auratus* (green squares) in pasture, edge and forest in the Osa Peninsula, Costa Rica.

50-m forest pools on two transects. A single cohort of *L. poecilochilus*, *H. rosenbergi* and *D. auratus* was found in different pools. Multiple cohorts of *A. talamancae* were found in one 50-m forest pool and single cohorts of *S. phaeota* were observed in three pasture pools (Table 1).

The majority of egg and tadpole depositions occurred in pasture pools near the forest edge and at two 50-m forest pools, with no depositions occurring in 30-m forest pools (Table 1). The number of depositions in pasture decreased on two transects with distance from forest. *Engystomops pustulosus* used marginally more pools in pasture than in forest ($t = 1.87$, $df = 8$, $P = 0.050$), while members of Dendrobatidae and Aromobatidae used pools only in forest, almost exclusively 50 m from the edge, although the statistical results did not meet the conventional standard for significance ($t = -1.74$, $df = 8$, $P = 0.061$).

Tadpole performance

Survival to metamorphosis for *Engystomops pustulosus* was high (greater than 90%) in all pools with the exception of one forest pool in block 3 (Figure 2). In this pool, no tadpoles survived, creating large variation in survival in forest pools. Tadpole survival to metamorphosis did

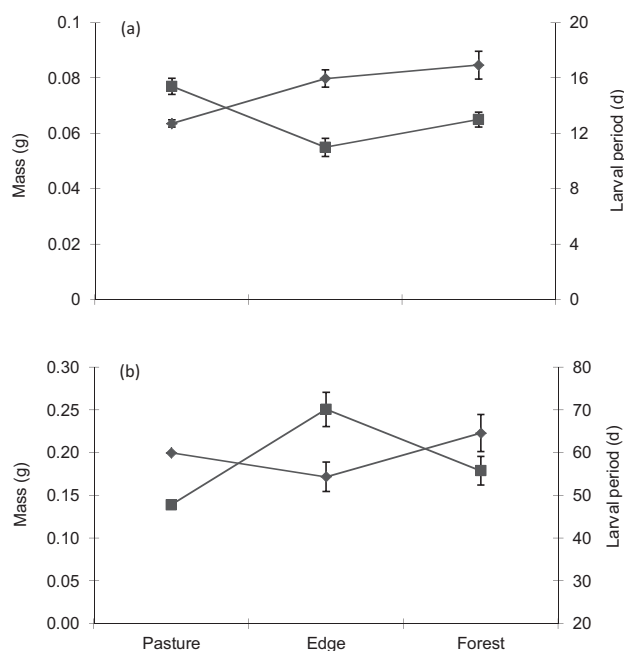


Figure 3. Metamorph mass (mean \pm SE; squares) and larval period (mean \pm SE; diamonds) for *Engystomops pustulosus* (a) and *Dendrobates auratus* (b) in pasture, edge and forest in the Osa Peninsula, Costa Rica.

not differ among habitats ($F_{2,17} = 0.466$; $P = 0.636$); but, metamorphs from each habitat did differ in size ($F_{2,16} = 13.0$; $P = 0.001$) and larval period ($F_{2,16} = 11.4$; $P = 0.001$; Figure 3). Post hoc comparisons showed that pasture metamorphs were 29% larger than those from the edge ($P < 0.001$) and 16% larger than those from the forest ($P = 0.043$) but edge and forest metamorphs did not differ ($P = 0.113$; Figure 3).

Additionally, *E. pustulosus* completed metamorphosis in pasture in 12.7 d, 3–4 d faster than those in edge or forest (Figure 3). Larval period was shorter in pasture than in edge ($P = 0.008$) and forest ($P = 0.001$) but did not differ between edge and forest ($P = 0.570$).

Survivorship curves of *D. auratus* differed by habitat type ($\chi^2 = 33.6$, $P < 0.001$, $df = 2$, $n = 18$; Figure 4). By 50 d, at least 50% of tadpoles in over half of pasture pools had perished (Figure 4). In all edge and forest pools, over 50% of tadpoles survived to the end of the experiment

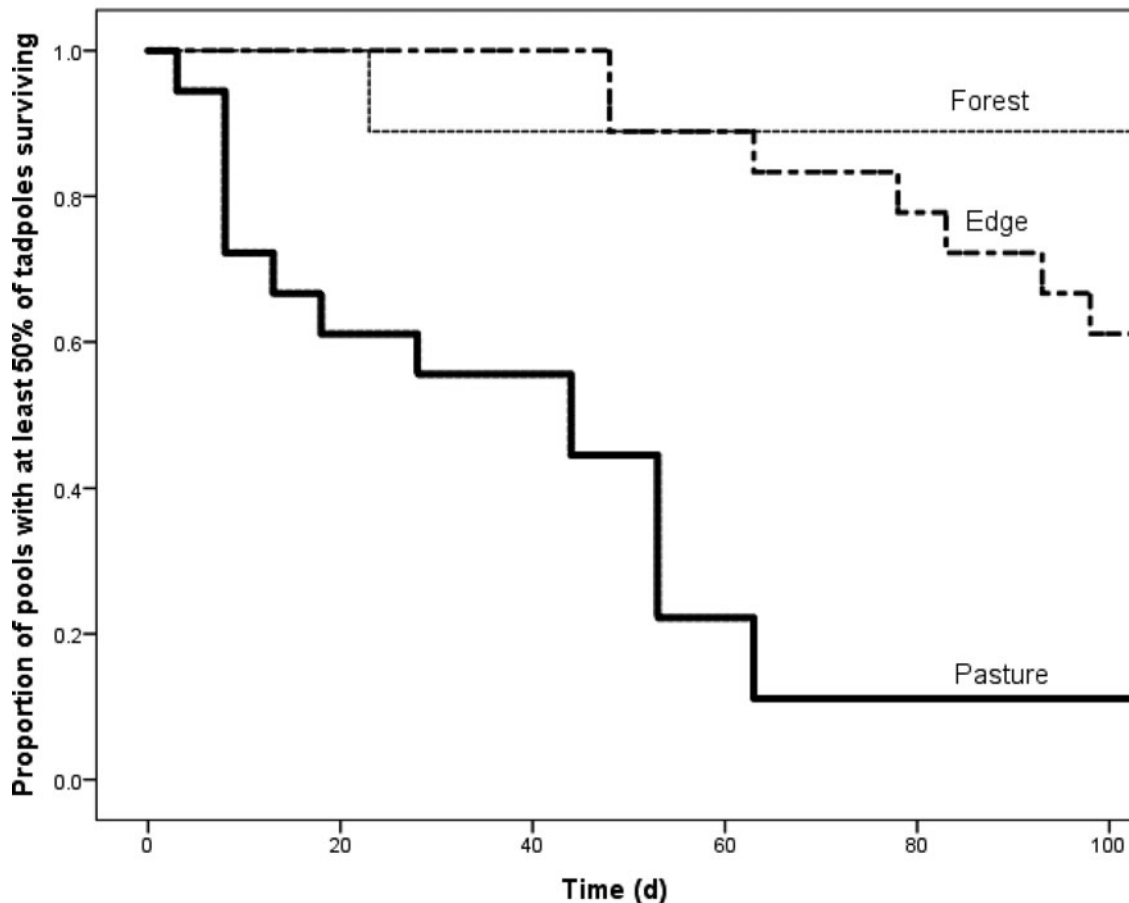


Figure 4. Kaplan–Meier survival estimates for the proportion of basins with at least 50% of tadpoles of *Dendrobates auratus* surviving until the end of the experiment in the Osa Peninsula, Costa Rica.

but many did not complete metamorphosis. Survival to metamorphosis at the end of the experiment was less than 20% in each habitat type (Figure 2), with only one tadpole surviving to metamorphosis in pasture, and survival differed by habitat type ($F_{2,17} = 4.19$; $P = 0.039$). Yet these differences were not clarified by post hoc analysis comparing survival to metamorphosis in pasture to forest ($P = 0.056$), edge to forest ($P = 0.989$) and pasture to edge ($P = 0.072$). Metamorph mass differed by habitat ($F_{2,9} = 5.45$; $P = 0.037$) with individuals from edge pools 29% larger than those from forest pools and 45% larger than the single metamorph from a pasture pool (Figure 3). Larval period was long (46–78 d) and did not differ among habitats ($F_{2,9} = 1.280$; $P = 0.336$; Figure 3).

DISCUSSION

By linking habitat use by adults with tadpole performance, my study provides quantitative fitness measures of habitat quality in forest and pasture. Adult breeding

site use was non-random and somewhat consistent with tadpole performance across the pasture-forest gradient, with some exceptions. *Engyptomops pustulosus* deposited clutches in pools in pasture and near the edge, whereas *D. auratus* and species with similar life-histories used pools only in forest. Although tadpoles of *E. pustulosus* survived equally well across the pasture-forest gradient, tadpoles developed faster and metamorphs were larger in pasture than in edge and forest. In contrast, tadpoles of *D. auratus* had higher survival and metamorphs were larger in edge and forest than in pasture. For both species, adults concentrated breeding efforts where their tadpoles attained the highest fitness.

High performance during the tadpole stage can lead to improved fitness during later life stages. Individuals that spend less time as tadpoles or become larger metamorphs may attain reproductive status faster and produce more offspring at a younger age (Semlitsch *et al.* 1988). Additionally, individuals that develop faster decrease risks of mortality from predation and desiccation by spending less time in pools (Skelly 1996). Therefore, beneficial tadpole performance can result in higher adult fitness,

with positive consequences for population growth in that habitat.

Surveys of adult populations in the region (Hawley unpubl. data) and habitat preferences of species (Savage 2002) are consistent with my results for breeding site use and tadpole performance for species occupying forest, but not as clear for those occupying pasture. In summary, species that occupy and use pastures for breeding activities may also occupy adjacent forest, but species occupying and using forests for breeding activities are not likely to use pastures. *Engystomops pustulosus*, *S. phaeota* and *H. rosenbergi* deposited eggs only in pasture pools in my study, with the exception of one clutch at the edge and at 10 m in forest for *E. pustulosus*. In addition to open habitats, these species are also known to occupy forest (Savage 2002), suggesting that they may migrate to pasture habitat for breeding activities because of higher offspring performance in pasture compared with forest. In contrast, my results indicate that species reported to occupy forest habitat (*D. auratus*, *P. vittatus* and *A. talamancae*) will not use breeding pools in a pasture matrix. However, in Brazilian pastures, many forest specialists are encountered (Tocher *et al.* 2001); yet, it is not known whether pastures meet the resource needs of those species or how far these species are found from the pasture–forest edge.

The presence of a species in matrix habitat may be influenced more by proximity to a suitable source habitat rather than the ability of the matrix to meet the resource needs of that species (Pullinam 1988). Intermediate habitats, edges between forest and a matrix habitat, may provide useful resources for species and with time will likely compose an increasingly larger proportion of habitat in complex tropical landscapes (Mendenhall *et al.* 2014). If the pasture did not meet the requirements of species in my study, I would expect my data to show an isolation effect, i.e. fewer clutches deposited in pasture pools distant from forest edge than near forest edge. There was an indication of an isolation effect on transect three, where *E. pustulosus* used more pasture pools near the forest edge. Other studies have shown an isolation effect; for example, grey treefrogs prefer to oviposit in pools located close to forest edges (Hocking & Semlitsch 2007). In pastures in south-eastern Brazil, Silva *et al.* (2012) found greater species richness and abundance at artificial breeding sites within 50 m of forest edges compared with those located 100 or 200 m away from a forest edge. Future studies should examine how species use matrix habitats further than 50 m from a forest edge.

By integrating abiotic heterogeneity among habitats with interspecific variation in breeding site use and tadpole performance, my study identifies specific mechanisms influencing patterns of species occupancy in a pasture-forest mosaic. The abiotic environment in pasture is characterized by greater light availability, higher

air and water temperature, and lower relative humidity, compared with edge and forest environments, which are similar to one another. It is likely that pasture pools also had improved food quality and quantity for tadpoles, as has been documented in other open-canopy ponds (Schiesari 2006). These pasture pool characteristics probably resulted in improved tadpole performance for *E. pustulosus* compared with forest pools.

Physiological limitations probably impact the ability of *D. auratus* and other members of the Dendrobatidae and Aromobatidae to use the pasture matrix. In addition to already high rates of evaporative water loss (Shoemaker *et al.* 1992), small body size and diurnal activity may deter these species from moving through pasture. If adults were able to deposit tadpoles in a breeding pool in pasture, my data suggest that those pools would be an ecological trap for these species. Water temperatures likely exceed the critical thermal maxima of *D. auratus* tadpoles in pasture pools, resulting in high tadpole mortality observed at the beginning of my experiment. Most mortality events occurred during periods when water temperatures reached or exceeded 38.5°C. Surprisingly, one *D. auratus* tadpole survived to metamorphosis in pasture, indicating potential for broad plasticity in ability to tolerate high temperatures, yet this occurrence is likely extremely rare. My data are consistent with a laboratory study showing that *D. auratus* tadpoles reared at 30.4°C have lower survival (10%) and longer larval periods (> 100 d) than those reared at 26.2°C and 29.4°C (Korbeck & McRobert 2005). Because of poor survival to metamorphosis in my experiment, it would be useful to repeat my study for a longer time period in smaller-sized pools. Regardless, my results raise concern for the persistence of *D. auratus* in fragmented landscapes. Local extinctions in forest fragments are inevitable (Vandermeer & Perfecto 2007) and the recolonization of areas where populations have been extirpated is dependent on dispersal events (Fahrig & Merriam 1994). If a population of *D. auratus* in a forest fragment goes extinct, my results suggest that it may not be recolonized if the fragment is surrounded by a pasture matrix.

My data suggest that pasture matrix habitats represent an ecological jackpot for *E. pustulosus* and species with similar life histories. In the pasture, water temperatures are tolerable and directly as well as indirectly (through increased food quantity and quality) confer benefits of faster growth and development to tadpoles of *E. pustulosus*. My results suggest that *E. pustulosus* has behavioural and physiological flexibility and when adults concentrate their reproductive efforts in pasture, fitness advantages will be gained.

Quantifying amphibian vital rates in modified and intact habitats can aid land managers in improving management strategies (Armstrong 2005) by identifying the specific life stages vulnerable to land-use change. My

results suggest that some species use breeding sites in pastures because their tadpoles have higher performance than in adjacent forest habitat. My results cautiously support the assumption that adult occupancy patterns reflect the overall habitat quality for a species. However, patterns of abundance along modified-intact habitat edges may underestimate the resource needs of some species and the flexibility of others. Adult behaviour and tadpole performance influence frog occupancy patterns across a landscape mosaic of forest and pasture. I suggest that species with life histories similar to *E. pustulosus* may maintain large populations in modified habitats because they thrive in abiotic environments in open canopy habitats. Those species may also be capable of surviving in forest, but with reduced performance compared with individuals in pasture. However, the reverse pattern is not supported by my data. Species with life histories similar to *D. auratus* are probably incapable of sustaining viable populations in abiotic environments similar to that of a pasture matrix habitat. It is necessary to consider options for repopulating fragments where species become extirpated in highly modified landscapes.

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