

Does desiccation risk drive the distribution of juvenile cane toads (*Bufo marinus*) in tropical Australia?

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(Accepted 13 November 2008)

Abstract: Immediately after their transition from aquatic to terrestrial life, juveniles of many anuran species are restricted to the margins of natal ponds. Understanding the factors determining the duration of that pondside aggregation has direct management ramifications in the case of the invasive cane toad (*Bufo marinus*) in tropical Australia. Previous work suggests that dispersal confers biotic advantages (reduced risk of cannibalism, enhanced feeding opportunities) to juvenile toads, but desiccation risk constrains these small animals to the moist margins of the pond. If so, juvenile dispersal should be sensitive to fluctuating hydric conditions on a diel and seasonal cycle. We tested this prediction with field observations (monitoring of dispersal to and from the pond) and field experiments (manipulating hydric regimes). Our results support a dynamic model of juvenile distribution, with a primary role for temporal variations in desiccation risk as the primary factor driving dispersal. During the dry season, strong diel cycles in desiccation risk generate a ‘tidal’ flow of juveniles, dispersing out in the moist morning but retreating to the pond margins at midday. Dispersal rates were enhanced by artificial watering during the dry season, and by the onset of the wet season.

Key Words: anuran, dispersal, movement patterns, *Rhinella*, season

INTRODUCTION

Biotic invasions are widely regarded as a major threat to global biodiversity (McKinney & Lockwood 1999, Mooney & Cleland 2001). Thus, there is an urgent need to understand the ways in which invasive species utilize their newly colonized environment (Strayer *et al.* 2006, Willis *et al.* 2007). On a landscape scale, the impacts from an invasive species will be heterogeneous in space and time, owing to varying distributions of the agents of impact (Phillips & Shine 2006). Understanding the factors that influence spatial and temporal heterogeneity in the distribution of the invasive taxon may assist in (1) predicting the magnitude and distribution of ecological impact of the invader; and (2) identifying the times and places where efforts to control the invader should be focused. Additionally, if we understand the causal mechanisms that drive invader dispersal, we may be able to manipulate such factors to reduce invader populations (Bowler & Benton 2005).

The temporal and spatial distribution of recently metamorphosed cane toads in tropical Australia offers an excellent model system for such a study. Cane toads, *Bufo marinus* Linnaeus, 1758, are large toxic invasive anurans that have recently colonized northern Australia (Phillips *et al.* 2007). Recent taxonomic rearrangement places *B. marinus* in the genus *Rhinella* (Pramuk 2006), but for continuity, and until greater taxonomic certainty, we use the old generic name *Bufo* throughout this paper. Juvenile toads are of particular significance for management in this system, because (1) they are small enough to be ingestible by many native predators (with often fatal results for the predator; Phillips & Shine 2005) and thus may be more significant vehicles of ecological impact than are large adult toads; and (2) the small body size of juveniles renders them vulnerable to many sources of mortality, suggesting that we might be able to reduce toad populations by reducing juvenile viability (Child *et al.* 2008a). In previous studies in tropical Australia, we have surveyed the distribution of juvenile toads, examined abiotic and biotic correlates of those distributions, and manipulated selected variables in the laboratory to assess their causal effects on juvenile dispersal (Child *et al.*

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2008b). Those studies have suggested a new model for the spatial and temporal distribution of juvenile toads around the natal water body. Our model posits that the clustering of juvenile toads around water bodies is driven by desiccation risk. Biotic factors that favour dispersal away from the pond (enhanced feeding opportunities and reduced risk of predation by larger conspecifics; Child *et al.* 2008a, Pizzatto & Shine 2008) are relatively invariant through time and space, so that the major proximate influence on juvenile distribution is likely to be hydric regimes: we predict that these small anurans will disperse whenever they are able to do so without desiccating. This paper describes field studies designed to test two predictions from the model: (1) Increased moisture in the landscape around the natal pond should reduce the level of aggregation at the pond edge and facilitate dispersal. We tested this prediction by artificially watering selected areas, and examining juvenile responses. (2) Previous work has tacitly assumed unidirectional dispersal away from natal water bodies; that is, juveniles emerge from the water when they transform from the tadpole stage, remain near the water's edge for some variable period of time, then leave to exploit the wider landscape (Cohen & Alford 1993). Our model predicts a more complex scenario. Desiccation risk fluctuates strongly on a diel cycle (Child *et al.* 2008a, b), so we predict that juvenile toads will show pulses of immigration and emigration on the same daily timing. Thus, we predict a 'tidal' dispersal of juveniles, spreading out from the pond edge in cooler times of day but retreating as the landscape dries out during midday hours. Such a regular diel dispersal would transform into a unidirectional outwards dispersal when rainy conditions eliminate the diel cycle of substrate moisture levels. To test this prediction, we monitored inwards and outwards dispersal of juvenile toads in detail across the diel cycle.

METHODS

Study species and area

Cane toads are native to Central and South America. Introduced to north-eastern Australia in 1935, these large anurans have since spread widely through the continent (Lever 2001). Cane toads often are regarded as an ecological catastrophe for the native fauna of Australia, although evidence on this point is scarce (Greenlees *et al.* 2006). Female toads in Australia mature at 6–18 mo of age, and produce large clutches (around 15 000 eggs; Lever 2001) in shallow non-flowing water bodies (Hagman & Shine 2006). The eggs hatch in 1–2 d, and the tadpole stage lasts for 2–4 wk before the tiny juveniles emerge at the water's edge. The massive clutch sizes result in high densities of juveniles near pond margins, with Cohen & Alford (1993) recording an

average of >2 individuals m^{-2} . Juvenile cane toads are primarily diurnal in their activity, becoming nocturnal as they grow larger (Freeland & Kerin 1991, Pizzatto & Shine 2008, Pizzatto *et al.* 2008).

We studied cane toads in a recently colonized part of their expanding range at Fogg Dam ($12^{\circ}38'S$, $131^{\circ}19'E$), on the Adelaide River floodplain in the Northern Territory of Australia. Cane toads reached Fogg Dam in the wet season of 2005 (Phillips *et al.* 2007). Our study area is in the wet/dry tropics of northern Australia and experiences a highly seasonal cycle of rainfall and humidity: approximately 80% of the annual average precipitation falls in the monsoonal wet season (December–March). Temperatures are high year-round, with monthly average minima and maxima ranging from 15–34 °C (Shine & Brown 2008).

Field manipulation of habitat quality

We manipulated substrate moisture levels beside a natural water body ($12^{\circ}57'S$, $131^{\circ}31'E$), the edges of which were inhabited by many metamorph and juvenile toads (ranging between 11–27 mm snout-ischium length, SIL). Between 12 July and 17 July 2006, we monitored 1- m^2 quadrats spaced 1 m apart in a rectangular grid with eight quadrats leading away from the water body in four rows running perpendicular to its edge. Thus, we sampled an area encompassing 7 m of pond edge and extending out to 15 m from the pond edge.

To test whether juvenile toads select sites with lower desiccation risk, we manipulated two factors (provision of additional water, and addition of shade) that would affect rates of evaporative water loss. This experiment was only run in the dry season because it was possible to make microhabitat wetter in the dry season, but logistically intractable to make habitat drier in the wet season. The site was chosen to maximize toad visibility: there was no cracking soil and only very sparse vegetation around the pond. Each quadrat was assigned an experimental treatment in an orthogonal design (watered; watered and shaded; shaded; or control). Thus, in a single transect running from the pond edge into higher drier land, the first quadrat (at the water's edge) might be 'control' (no water added, no shelter), the next quadrat 1 m upslope might be 'water added, no shelter', the next 'no water added, but shelter present' and so on.

To artificially water half of the quadrats, a single water source fed four plastic hoses running the entire length of each transect through the middle of each quadrat. The hoses were perforated in quadrats that were assigned to a water treatment, and left intact in non-watered quadrats. All quadrats thus contained a length of hose, but only half the quadrats received water from that hose. Over the course of a day, these hoses piped a total of approximately

1000 litres of water onto the watered quadrats: enough to keep the watered quadrats very moist, but avoid obvious run-off. White, wooden boards (40 cm × 40 cm, elevated on four 3-cm wooden cubes to provide access for juvenile toads) were placed in the centre of quadrats assigned to the shading treatment. We counted toad numbers in each quadrat (including under the shelters) three times each day (at 07h00, 13h00 and 19h00), and then removed (and did not replace until the end of the day) the counted juveniles. We placed pre-weighed agar models (3-cm cubes of 2% agar with an embedded thermochron) in each quadrat to measure rates of evaporative water loss (i.e. desiccation risk: see Child *et al.* 2008b for details). In sheltered treatments, agar blocks were placed under the shelter. We collected the agar models 1 h later, and weighed them to record rates of evaporative water loss. We used percentage mass loss as a measure of desiccation risk.

Field surveys of juvenile dispersal

To test our prediction of 'tidal' diel dispersal of juveniles to and from the pond margins, we set out pitfall traps encircling a pond (12°61'S, 131°30'E) containing toad tadpoles (resulting from natural spawning events). We opened the traps as the toads metamorphosed in November (prior to the onset of monsoonal rains), to quantify toad behaviour under dry conditions, and again in February midway through the wet season. Each trap consisted of a pitfall bucket (24 cm diameter, 26 cm deep) dug into the ground beneath a polyethylene drift fence (2 m long, 30 cm high) that ran parallel to the water's edge and bisected each trap. A polyethylene divider in each bucket (parallel to the water's edge) allowed us to determine the directionality of dispersal (whether juveniles were leaving or returning to the pond when captured). We checked the traps at 07h30, 11h30, 15h30 and 19h30 each day. Concurrent with trap monitoring, we laid out agar models (implanted with temperature-logging thermochrons; Maxim Integrated Products, Sunnyvale, California, USA) in three compass directions and at three distances from the pond margin (0 m, 5 m, 25 m) to measure rates of evaporative water loss.

The designs of these studies differed slightly between dry season and wet season sampling, for logistical reasons. In the dry season we set out 16 traps, comprising eight equally spaced traps in each of two concentric rings 5 m and 25 m from the pond edge. Trap locations were offset so that the traps in the 25 m ring were spaced between the two traps in the 5 m ring. In the wet season, the pond flooded and expanded from its November boundaries and the toads bred in this newly flooded area rather than in the main pond, forcing us to lay additional traps. To approximate the spacing of the dry-season sampling, we

laid four more traps in the inner 5-m ring and six traps in the outer 25-m ring. The total number of traps in the wet season was 24, as two of the original trap-points were submerged by the new pond. Again, we set out thermochron-implanted agar models at three compass directions and at three distances from the pond (0 m, 5 m, 25 m). All juveniles were weighed and measured to the nearest 0.01 g and 0.5 mm in snout-ischium length (SIL). We monitored the traps for 2 d in the dry season and 6 d in the wet season (because of very low capture rates in the latter period).

Statistical analyses

All analyses were conducted with JMP (Version 5.0; SAS Institute, Cary, North Carolina, USA). The assumptions of parametric tests (normality of distributions, homogeneity of variances, etc.) were evaluated prior to testing.

The data on field manipulation of habitat quality were analysed using repeated-measures ANOVA with time of day as the repeated measure, distance from the pond, shelter and moisture as the factors, and number of toads and percentage mass loss of agar models as the dependent variables. Because we were interested in effects over the course of a single day, and because in any given day we had many zero counts in individual quadrats, we pooled our data across days (by summing counts). The numbers of toads were not normally distributed, so the data were fourth-root transformed (Quinn & Keough 2002). Because only one replicate of shelter and moisture was available for each distance, we split the data dichotomously by distance into two nominal categories: 'near' (<7 m from the pond) and 'far' (>7 m from the pond).

We used a similar approach to analyse the data from field surveys of juvenile dispersal. Counts were summed across days and body size was averaged. We then used repeated-measures ANOVA with time of day as the repeated measure, and distance and season as factors to examine changes in body size and the ratio of toads found on the near/far side of the pitfall.

RESULTS

Field manipulation of habitat quality

Juvenile toads were attracted to moisture but not to shelter ($P = 0.03$ and 0.68 respectively: Table 1, Figure 1). The number of juvenile toads captured was influenced by time of day, and by an interaction between time of day and moisture treatment ($P = 0.03$ and 0.003 respectively; Table 1). Many more toads were found in moist than in dry quadrats at midday, but this disparity was reduced

Table 1. Results of statistical analyses (repeated-measures ANOVA) on the influence of artificial moisture, shelter, distance and time of day on the distribution of juvenile cane toads. Significant values ($P < 0.05$) are shown in bold.

Within subjects (Repeated measure)	Desiccation risk			Juvenile numbers			Between subjects	Desiccation risk			Juvenile numbers		
	df	F	P	df	F	P		df	F	P	df	F	P
Time of day	2,56	135	< 0.0001	2,56	3.57	0.03	Moisture	1,28	45.1	< 0.0001	1,28	5.54	0.03
Time of day × Moisture	2,56	107	< 0.0001	2,56	6.53	0.003	Shelter	1,28	48.4	< 0.0001	1,28	0.178	0.68
Time of day × Shelter	2,56	463	< 0.0001	2,56	0.776	0.47	Distance	1,28	0.555	0.46	1,28	18.4	0.0002
Time of day × Distance	2,56	0.561	0.57	2,56	0.325	0.72							

in the morning and evening (Figure 1). Overall, juvenile densities diminished further from the pond ($P = 0.0002$; Table 1, Figure 1), a result that we would expect simply through the threefold increase in area between near and far annuli (assuming a circular pond).

As we had intended, desiccation rates of agar models were lower in both artificially moistened and sheltered quadrats than in control quadrats ($P < 0.0001$ in both cases; Table 1, Figure 1). Rates of evaporative water loss also varied with time of day, but not with distance from the pond ($P < 0.0001$ and 0.46 respectively; Table 1). Desiccation rates of agar models were highest at midday and lowest in the morning and evening (Figure 1), but artificial moisture and shade also modified the natural diel cycle in desiccation rates (as measured in control quadrats; Figure 1). Both treatments reduced desiccation risk at midday, but had little effect in the morning or evening (interactions Time of day × Moisture and Time of day × Shelter, $P < 0.0001$ in both cases; Table 1, Figure 1).

Field surveys of juvenile dispersal

In the dry season, juvenile cane toads were captured in greatest numbers at morning and midday, with capture rates falling dramatically by the afternoon (Figure 2). Within these samples, the ratio of juveniles leaving vs. returning to the pond varied significantly over the diel cycle (repeated-measures ANOVA with time of day as the repeated measure and average ratio as the dependent variable, $F_{3,15} = 5.72$, $P = 0.008$) and was higher in the morning and evening time periods (0.50 ± 0.02 and 0.61 ± 0.20 respectively) than in the midday and afternoon periods (0.22 ± 0.07 and 0.09 ± 0.06 respectively; post hoc Fisher's PLSD tests show that these two groups differ at $P < 0.05$; Figure 2). Mean body sizes of juveniles varied as a function of distance from the pond (SIL, $F_{1,697} = 12.5$, $P = 0.004$; mass, $F_{1,697} = 11.4$, $P = 0.005$) with larger animals tending to be found further away from the water than were smaller animals. However, the mean size disparity between toads found at 5 vs. 25 m was minor (mean SILs 12.0 vs. 12.1 mm, mass 0.156 vs. 0.157 g).

In the wet season, we captured fewer juveniles, and observed little diel variation in either total numbers or directionality of dispersal. No juveniles were captured

in pitfall traps in the evening period (Figure 2b). More juveniles were caught leaving the pond than returning in the wet season, whereas the reverse was true during the dry season (repeated-measures ANOVA with time of day as the repeated measure, excluding the dusk sampling period, season as the factor, and average ratio as the dependent variable, $F_{1,14} = 39.3$, $P = 0.0004$; Figure 2). This seasonal difference was not significantly influenced by time of day (interaction $F_{2,14} = 0.81$, $P = 0.47$).

DISCUSSION

Our field studies were designed to test two major predictions of the model that spatial and temporal variation in the distribution of juvenile cane toads is driven by the risk of desiccation. Our results support both predictions. First, juvenile toads were attracted to artificially moist – and therefore, low desiccation-risk – habitats in an otherwise dry and desiccating environment. Second, the dispersal patterns of juvenile *B. marinus* responded to natural variation in substrate moisture levels, exhibiting a diel cycle in immigration and emigration from the pond as predicted by the desiccation-risk model. In dry season conditions, the juveniles utilized moist windows of opportunity for activity, resulting in a tidal dispersal away from and back to the pond edge over the course of each day. The timing of those dispersal events was synchronized, at least broadly, with the diel cycle in desiccation risk. Under wet-season conditions, desiccation risk was low and homogeneous through space and time, and dispersal thus unconstrained by this factor. As predicted by the model, wet-season juveniles simply emigrated from the pond soon after they transformed from the tadpole stage.

By creating low-desiccation 'havens' in an otherwise desiccating environment, we created a spatial mosaic of rich- and poor-quality habitat patches. The fact that juveniles were more abundant in moistened quadrats supports two major assumptions of population distribution theory: (1) that organisms can assess differences in habitat quality; and (2) that organisms should occupy high quality habitat because this confers fitness benefits (Rosenzweig 1991, Tokeshi 1992). One counter-intuitive result was that although artificial shelter reduced desiccation rate – which should therefore make sheltered sites

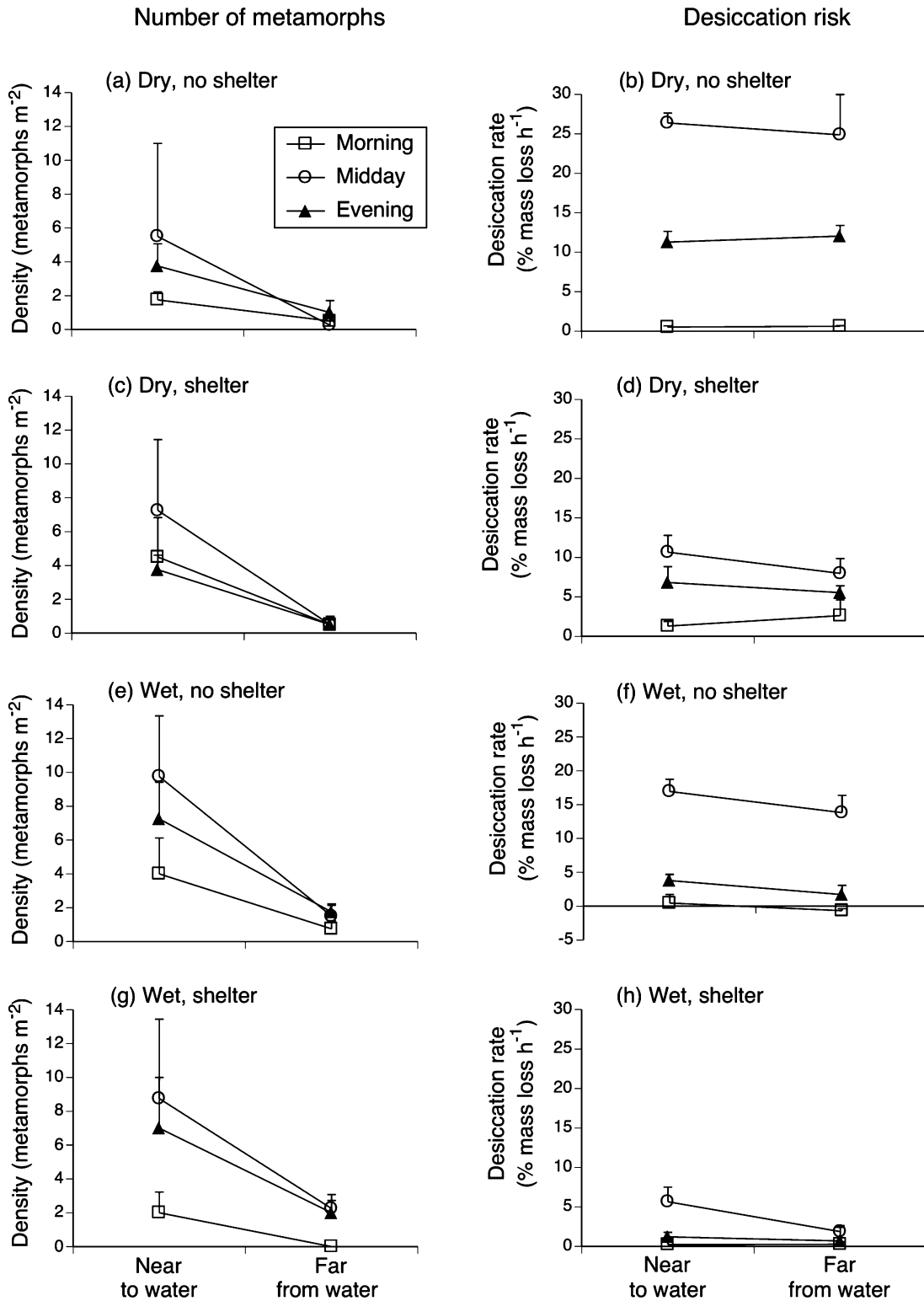


Figure 1. Abundance of juvenile cane toads (number m⁻²) and desiccation risk (% mass loss of agar models h⁻¹) either near (<7 m) or far (>7 m) from the pond edge at three times of day (morning, midday and evening). Data were obtained for four different experimental treatments involving manipulation of shelter and moisture as follows: dry, no shelter added (a, b); dry, shelter added (c, d); water added, no shelter provided (e, f); water and shelter both added (g, h). The figure shows mean values and associated standard errors.

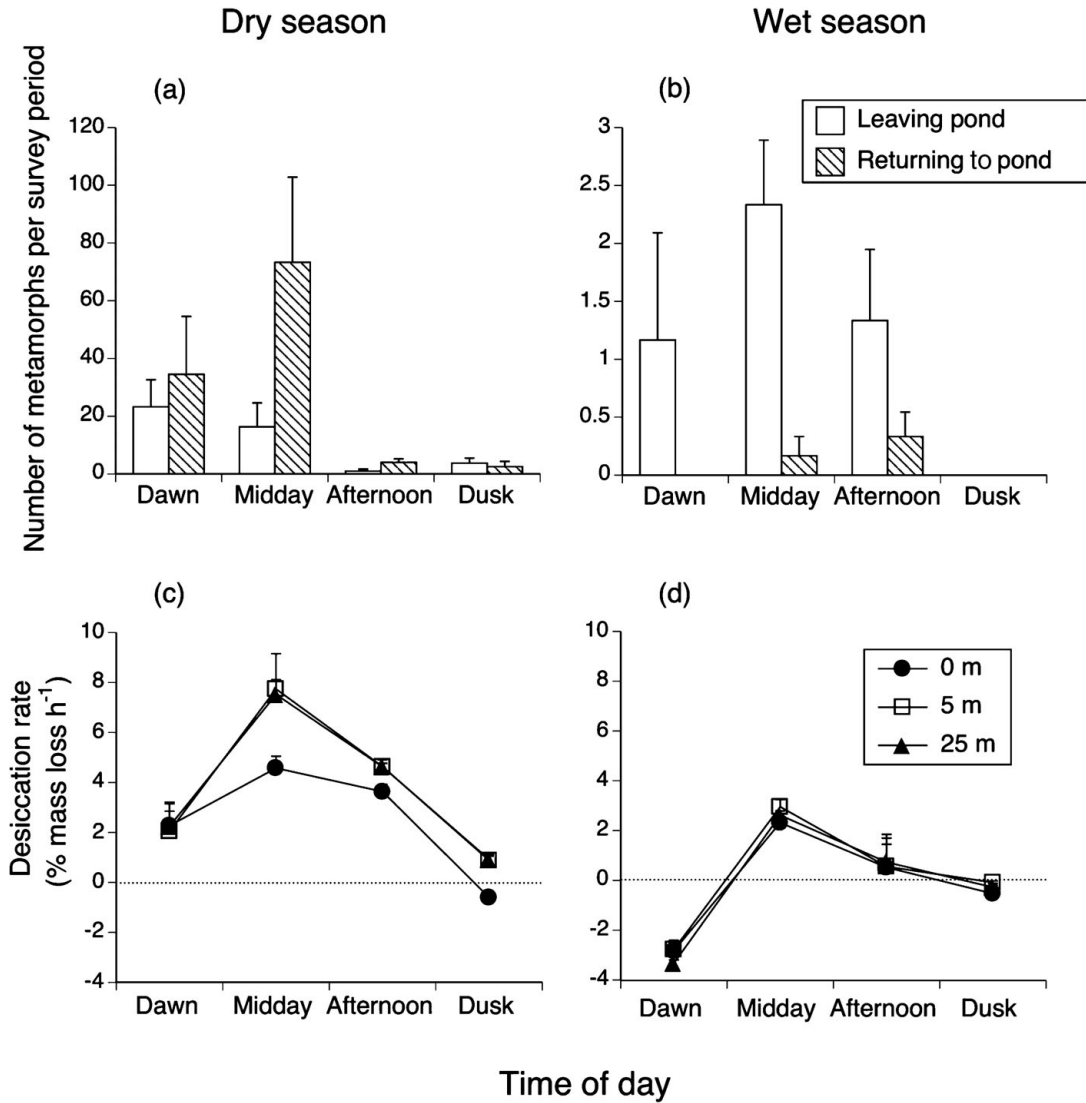


Figure 2. Numbers of juvenile cane toads captured either leaving or returning to the pond edge, based on pit-traps 5 m from the pond in (a) the dry season and (b) the wet season. The graphs also show corresponding desiccation rates at 0 m, 5 m and 25 m from the pond edge in (c) the dry season and (d) the wet season (mean ± 1 SE).

high-quality habitat – juveniles were no more abundant under shelters than they were in control quadrats.

Given the benefit of a greater food supply and fewer competitors and cannibalistic conspecifics away from the pond (Child *et al.* 2008b), we would expect most juveniles to move away from the pond edge unless there is a desiccation cost of doing so. Our studies support this prediction both in an artificially moistened habitat and under natural variation in hydric conditions. First, juveniles were attracted to moistened quadrats in a matrix of low and high desiccation-risk patches. Second, the details of movement patterns within the dry-season pond edge environment further support a causal role for desiccation risk in driving juvenile dispersal. Surveys

show that juveniles are more intensely aggregated at the pond edge at midday than in the morning and evening (Child *et al.* 2008a). What behavioural mechanism causes this changing distribution? Many juveniles leave the pond edge in the morning while desiccation risk is low, travelling up to at least 25 m from the pond in our survey. As desiccation risk increases to midday levels, the juveniles return to the pond to find moister habitats (Figure 2a,c). In the afternoon, few juveniles are caught in traps because their activity is reduced. During this most desiccating part of the day juveniles are largely restricted to moist microhabitats such as cracks in the soil, shadows formed by displaced mud from bird footprints, and even the shade of single blades of grass. Despite a decreased

desiccation risk in the late afternoon, juveniles tend not to leave the pond edge at this time, although more are found leaving than returning (Figure 2a).

We observed this tidal dispersal pattern over 3 d of sampling, implying that it is a repeatable daily pattern related to the daily cycling of desiccation risk. While we only ran our manipulative experiment at a single pond, our observational (pitfall) experiment was run at a different pond and also provided support for our tidal movement hypothesis. Thus, while this study should be interpreted with caution (with only two ponds sampled) our current results strongly support the tidal flow model. Narrow temporal windows of opportunity make dispersal possible, and juvenile toads take advantage of those windows. However, the young toads still rely on the pond edge for refuge and rehydration every afternoon in dry conditions. If the daily cycle and spatial gradient of desiccation risk are disrupted (e.g. by rainfall), the tidal dispersal probably transforms into uninhibited emigration. In the wet season, for example, conditions are more benign and desiccation risk is low and homogeneous through both space and time (Figure 2d). These conditions facilitate emigration, because juveniles are no longer constrained to the moist pond edge (Figure 2b). This pattern explains why quadrat sampling in the wet season records few juveniles (Child *et al.* 2008a): the young toads simply disperse soon after they emerge from the pond.

Interestingly, the spatial extent of this tidal dispersal tended to increase with juvenile body size. Our previous laboratory trials showed that larger individuals tend to move further between rehydration bouts (Child *et al.* 2008b), and this behaviour is reflected in our field surveys where larger juveniles were found furthest from the water.

In summary, our studies provide strong empirical support for the model that variation in desiccation risk drives the spatial and temporal distribution of juvenile cane toads. One consequence of that support is that alternative hypotheses are challenged. For example, Taigen & Pough (1981) and Pough & Kamel (1984) – who worked on an almost identical size-range of toads as we do here – suggested that juvenile bufonids aggregate around their natal pond margins until they have developed the metabolic (and especially, locomotor) capacity to disperse. Our data do not support this hypothesis. Although body size influenced dispersal potential in dry conditions, this correlation is likely to be due to the greater desiccation resistance of larger individuals than to metabolic competence. Both from our laboratory trials (where immediately post-metamorphic toads often travelled long distances: Child *et al.* 2008a) and from our field observations (where young toads move out from the pond in the morning, return in the middle of the day, then disperse out again in the evening), the picture that emerges is of a physiologically competent organism able to move about the landscape. The metabolic constraints

(from heart size, lung development, etc.) identified by Pough and his co-authors do not seem to constrain the distribution of juvenile cane toads for long after metamorphosis. Instead, young cane toads are restricted to pond margins for much of the year because desiccation risk away from the pond is too high for survival.

This hydrically driven model of juvenile toad dispersal patterns has significant implications both for understanding the impact of cane toads on native fauna, and for approaches to control toad populations. First, the immediacy of response by juvenile toads to artificial watering means that even a brief localized shower during the late dry season (as commonly occurs in the wet-dry tropics: Brown & Shine 2006) would almost immediately distribute juvenile toads through the wider landscape, and hence might bring them into contact with small predators. Thus, we predict that rainfall will rapidly and dramatically increase the spatial extent of ecological impact from small toads. Second, the immediacy of response suggests that juvenile toads may disperse from the natal pond in response to brief rain – and then, be trapped in a drier landscape when the rain ceases. Although these small animals may be able to find moist microhabitats, such places may be vanishingly scarce in some landscapes (especially in the Kimberley area of north-western Australia, where ambient temperatures often exceed those in the Northern Territory). Hence, entire cohorts of juvenile toads may be eliminated by premature dispersal from water bodies following sporadic rainfall at the critical (late dry season) time of year. It would be of great interest to test whether or not such events do indeed occur, and if so whether it might be feasible to increase their frequency by providing cues that the juveniles use to initiate dispersal. The most obvious such cue is the animal's desiccation rate, or the water content of the substrate on which it sits; but scent cues produced by rainfall might also be involved. If so, application of the appropriate cues might elicit dispersal prematurely, and reduce juvenile numbers within the landscape. Lastly, our work identifies the times and places of greatest aggregation, and hence the optimal situations to focus control effort on juveniles (i.e. midday during dry periods).

ACKNOWLEDGEMENTS

We thank the members of TeamBufo (especially M. Crossland, H. Bowcock, G. P. Brown, S. Dusty, M. Greenlees, D. Nelson, L. Pizzatto and C. Shilton) and the staff of Middle Point Farm (especially E. Cox and J. Stevens) for their encouragement and assistance. Approval for research was given by the University of Sydney Animal Ethics Committee.

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