The on-ground feasibility of a waterless barrier to stop the spread of invasive cane toads in Western Australia

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Abstract
Modeling suggests that excluding invasive cane toads from artificial water points (e.g., pastoral dams) along an arid coastal corridor in Western Australia would create a “waterless barrier” halting their spread. In this study, we explored one critical assumption of these models: that toads cannot persist in the corridor during the dry season without access to artificial water points. We explicitly tested this assumption by translocating and radio-tracking 78 male cane toads in the proposed barrier region during the dry season. Telemetered toads moved substantial distances (maximum distance >2.5 km/night) and were adept at finding shelter. Nonetheless, toads experienced high water loss rates (1.89%/hr) and rapid mortality in both desert (mean ± SD = 43.6 hr ±1.4) and coastal (24.5 hr ±1.2) habitats. Survival analysis suggested that toads could survive a maximum of 5 days without access to surface water and would move a maximum of 5.35 km in this time. Our results confirm that artificial water points are a critical resource for toads in the proposed barrier region and provide further evidence that the waterless barrier could successfully halt toad expansion in Western Australia.

KEYWORDS
habitat use, invasion, invasion ecology, invasive species, management strategies, pest control, pest management, telemetry

1 | INTRODUCTION

The most cost-effective strategy for combating invasive species is to prevent their arrival (Sharov & Liebhold, 1998), particularly when containment strategies are applied at a landscape scale (Vander Zanden & Olden, 2008). Intensive control of invasion front populations can reduce rates of spread (Florance et al., 2011; Moody & Mack, 1988; With, 2002), but requires ongoing effort. By contrast, natural landscape barriers can provide a powerful advantage: enabling large-scale containment with the potential to halt the spread of the entire invasive population. Such barriers and exclusion zones have been successfully used to halt or slow invasions of insect species (Jessup et al., 2007; Olson, 2006; Sharov & Liebhold, 1998), but have rarely been applied to contain invasive vertebrates.

While landscape barriers are potentially useful, it is difficult to test their effectiveness before they are implemented. Spread models, which integrate dispersal and reproduction to predict the spatial spread of a population, can provide predictions under various management scenarios, but, of course, if models are based on flawed assumptions, they can lead to inappropriate management recommendations. Therefore, wherever possible, we should test assumptions on which arguments for a barrier strategy rest, be they assumptions about a species’ life-history, or about the physical and...
cultural landscapes in which the barrier is to be implemented. In this paper, we test a key model assumption around a landscape barrier designed to halt the spread of one of the world’s most notorious biological invasions: that of the cane toad (*Rhinella marina*) in Australia.

Originally from South and Central America, cane toads rapidly spread across Australia after their introduction in 1935 (Phillips, Brown, Greenlees, Webb, & Shine, 2007). Cane toads often cause declines or local extinctions of native predators that are naïve to the toad’s toxin (Griffiths & McKay, 2007; Shine, 2010; Woinarski et al., 2010). While the southern invasion front (in New South Wales) has travelled slowly (approximately 1 km/year) and is predicted to be halted by cold temperatures (Kearney et al., 2008), expansion on the north-western front (in Western Australia) is rapid (approximately 45–50 km/year) and ongoing (Urban, Phillips, Skelly, & Shine, 2008). Species distribution modeling suggests the toad will continue to expand its range in the Kimberley region of Western Australia—an area prized for its environmental and cultural value—and if left unchecked, will continue to spread into a similarly significant region to the southwest: the Pilbara (Kearney et al., 2008; Tingley, Vallinoto, Sequeira, & Kearney, 2014).

It is too late to prevent the colonization of the Kimberley, but preventing the spread of toads into the Pilbara remains a real possibility: the landscape between the Kimberley and the Pilbara provides that opportunity (Figure 1) (Florance et al., 2011; Southwell, Tingley, Bode, Nicholson, & Phillips, 2017; Tingley et al., 2013). Here, the Great Sandy Desert stretches towards the coast, creating a narrow corridor of suitable habitat from Broome to Port Hedland. This corridor is seasonally arid, but the landscape is scattered with permanent artificial water points (e.g., dams and tanks) that have been installed by pastoralists. During the wet season, we expect toads to thrive in this landscape, even in the absence of artificial water points; however, during the dry season, because of the paucity of natural water bodies, artificial water points will be critical for toad survival. Within their current range, cane toads rely on artificial water points as dry-season refuges, and they focus their movements around them (Letnic et al., 2014; Tingley & Shine, 2011). Indeed, removing access to these refuges during the dry season can be used to eradicate toad populations and restrict movement by reducing water availability and landscape connectivity (Florance et al., 2011; Letnic, Webb, Jessop, Dempster, & Rhodes, 2015).

Simulation modeling has identified multiple areas within the Kimberley–Pilbara corridor where excluding toads from approximately 100 artificial water points could halt expansion of the toad front indefinitely (Southwell et al., 2017; Tingley et al., 2013). During the dry season, water sources will be crucial to toad survival in the corridor. By managing artificial water points, we could create a “waterless barrier,” protecting the biodiverse Pilbara region and up to 268,200 km$^2$ of mainland Australia from the toad’s impact (Tingley et al., 2013). The barrier need only be wide enough to account for toad movement during the wet season, when toads are not reliant on the artificial water points. In two possible locations the barrier would need to be approximately 70 km wide and, to implement, would cost approximately $4.5 million over 50 years (Southwell et al., 2017). Modeling and sensitivity analyses suggest that such a barrier will hold even under a string of extremely wet years (Southwell et al., 2017; Tingley et al., 2013). But how reliable are our modeled simulations? While the dispersal parameters in the model are well-grounded in empirical work (Tingley et al., 2013), one major assumption of the waterless barrier model remains untested on the ground: that cane toads are incapable of surviving the dry season in the barrier area without access to artificial water bodies. Here, we focus squarely on that question.

This study addresses three major assumptions of the previous simulations, identified through stakeholder workshops (Southwell et al., 2017). First, can we be sure that cane toads will not locate suitable dry-season shelter sites in the corridor? Previous work has demonstrated that the removal of water bodies has a critical impact on toad populations in semi-arid areas (Florance et al., 2011; Letnic et al., 2015). Yet, if available shelter sites in this arid corridor landscape allow toads to survive the dry season without artificial water sources, then the barrier will be completely ineffective. Goanna burrows, for example, are plentiful in the region, and toads use these burrows as refuges throughout much of their current range (Schwarzkopf & Alford, 1996). Second, is it possible that cooler temperatures and heavy dry-season fogs along the coastline will allow toads to survive the dry season regardless of shelter sites (Southwell et al., 2017)? Indeed, are there any other features of the coastal landscape that may assist toad survival (e.g., increased shelter from vegetation)? Third, is it reasonable to assume that there will be no significant dry-season dispersal in the corridor due to poor toad survival? Recent work has shown that novel environments increase toad movement rates (Pettit, Greenlees, & Shine, 2016), and so the stressful climatic conditions experienced in the Kimberley–Pilbara corridor may trigger new behaviors or movement strategies. Through translocating and radio-tracking cane toads in a potential waterless barrier site, we directly address these assumptions.

### 2 | METHODS

#### 2.1 | Study population

We collected 78 adult male cane toads for radio-telemetry from Kununurra and Wijilawarrim (Molly Springs), Western
FIGURE 1 Map of the study area. (a) The study was conducted in the north of Western Australia. Toads were collected around Kununurra, and transported to Wallal Downs Station in the Kimberley–Pilbara corridor. The invasion front was just southwest of Halls Creek during the time of the study (invasion front, as of 2017, shown as solid black line). Predicted cane toad distribution (based on breeding season length) is shown in grey shades. (b) The Kimberley–Pilbara corridor lies along the coast between Broome and the De Grey River near Port Hedland, bordered on the east by the Great Sandy Desert (outlined by dashed black line).
_consecutive allowing consistent tracking of every individual. Each cohort was split in half and released concurrently into two different habitat types (Table S1). Four release sites were used spaced approximately 5–20 km apart: two in the western coastal plains and two in the inland sandy desert (Figure S1), ensuring coverage of the two soil types and vegetation communities which dominate the entire corridor. To mimic a waterless barrier, we selected sites as far as possible from artificial water sources; sites were a minimum of 1.7 km away from an artificial water source. Within release sites there were up to three release points spaced approximately 100 m apart used for different cohorts (see Table S1 and Figure S1).

2.3 | Toad radio-tracking

Prior to release, we attached a radio transmitter around the waist of each toad using a ball chain, a technique used extensively for radio-telemetering cane toads (after Brown, Phillips, Webb, & Shine, 2006, Figure S4). Transmitters were small (approximately 1.5 cm long) and light (mean = 6.0 g) relative to toad body mass (mean = 112.8 g, 5.4% of toad body mass) (PD-2, Holohil, Carp, Ontario, Canada). The ball chain ensured that the belt did not cut into the animal’s waist, and the attachment point ensured that toads did not become caught on vegetation. Toads were placed in a tub filled with approximately 0.5–1 cm of water for 1–2 hr prior to release so they could fully hydrate, and we could measure their fully-hydrated body mass.

We released toads at night (7:30 p.m.–12:00 a.m.) into a shallow (approximately 0.5–1 cm depth) artificial water pool that dried up by the following morning, forcing the toads to disperse. We then radio-tracked and located each toad once to twice a day (6 a.m.–12 a.m.), until they had lost 40% of their body mass or were found dead. We considered any change in body mass as indicative of water loss (or gain) (as in Tingley, Greenlees, & Shine, 2012). A loss of 40%, or more, of initial mass was taken as a sign of severe dehydration; animals in this state were euthanized using the method described by Sharp, Lothan, Munn, and Saunders (2011). Toads can survive losing water up to 52.6% of their body mass (Krakauer, 1970), but a loss of 40% severely compromises locomotor capacity, and in the study area, death would be an inevitable outcome.

Each time toads were located, we recorded their mass (when the toad could be easily moved and returned to the same position in which it was found), behavioral state (e.g., hopping, sheltering, dead), location, and microhabitat (including whether it was a shelter site or not). If a toad was found dead, the microhabitat was not classified as a shelter site, unless the toad had been found sheltering there previously. When necessary, an inspection camera was used to

Australia from October to November 2015 (Figure 1). These collection sites were approximately 350 km behind the toad invasion front at the time and were in the closest accessible area to the invasion front with adequate toad numbers for collection. Toad dispersal rates decline steadily after colonization so these toads will have similar long-distance movement tendencies to those on the invasion front (Lindstrom, Brown, Sisson, Phillips, & Shine, 2013). We caught toads in four groups of 15–23. We only collected male toads, as this was the simplest way to avoid inadvertently establishing a population ahead of the invasion front. Given that juvenile male toads look very similar to females, only adult males were collected, in order to ensure accurate sex determination and to ensure that we considered the dispersal and survival abilities of the largest toads. Toads were transported to the study site in damp cloth bags (maximum two per bag) placed in plastic tubs (maximum 10 per tub). Toads were housed at Wallal Downs Station (see Study area and release sites) in the same bins under cover until their release, which was 2–6 days following collection (Supporting Information Table S1). Only one group was fed insects prior to release, as they were kept for 5–6 days; up to 4 days longer than the other groups.

2.2 | Study area and release sites

We released all 78 toads on Wallal Downs Station (~19.783, 120.645), in the Kimberley-Pilbara corridor in Western Australia (Figure 1). Wallal Downs is within the area identified by Tingley et al. (2013) as one of the optimal waterless barrier locations, and is approximately 550 km from the current toad invasion front at Fitzroy Crossing (as of March 2019). Mean annual rainfall in the area is approximately 376 mm (Australian Government Bureau of Meteorology, 2015). Wallal Downs is characterized by a hot dry season (April–November, mean min−max temperature: 24.0–36.9°C, mean monthly rainfall: 33.9–103.1 mm) and a hot dry season (December–March, mean min–max temperature: 24.0–36.9°C, mean monthly rainfall: 33.9–103.1 mm) and a hot dry season (April–November, mean min–max: 12.5–36.6°C, mean monthly rainfall: 1.0–19.3 mm, see Figure S2 for monthly climate averages). The tracking period was during the hottest and driest part of the year (October–November 2015) in order to test the dependence of the toads on artificial water bodies when natural water sources are limited or unavailable. During tracking, the mean daily maximum temperature was 36.2°C; mean daily rainfall was 0.01 mm. Permanent natural water sources are scarce in the study area, but a long history of cattle grazing has resulted in the construction of numerous artificial water bodies (e.g., bores, above-ground tanks, and troughs), spaced approximately 5–10 km apart (Figure S3).

We radio-tracked one group to completion per week. Four groups were collected in total, each group incorporating between one and three cohorts that were released

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view toads in burrows. When it was difficult to identify the state of a toad, it was prodded to elicit a response. When a toad did not respond to three prods it was assumed dead and dug out of the burrow. Twice we were mistaken, in which case we placed the toads into the closest appropriate burrow. When toads were not visible in burrows, they were assumed dead after 2–4 days in the same location (depending on the number of days since their initial release) and were excavated. All such cases were, in fact, dead.

For survival analyses, we classified whether a toad was alive or dead each time it was relocated. If a transmitter was found without a toad, we defined the toad as “lost,” except in circumstances where it seemed very unlikely that the toad would be alive, in which case it was classified as “dead.” We made this classification of “unseen but dead” only five times: in one instance a transmitter was found in a tree much higher than a toad could climb (likely a predation victim, or the carcass had been scavenged by a bird) and in the others transmitters were found buried under sand on tidal flats approximately 75–100 m below the high tide mark. Whenever a toad was lost, all waterbodies within 5 km were searched over the following two nights. No toad, with a transmitter or otherwise, was located at a waterbody. We specified time of death using an interval bounded by when a transmitter or otherwise was located at a waterbody. We took a sample from the top soil layer, and at 10 and 50 cm depth (where possible) and weighed them immediately in the field. This depth gradient covered the depth of all sampled burrows. Samples were then oven dried for >8 hr and re-weighed to estimate (evaporated) water content.

2.4 | Shelter sites

We anticipated that burrows would provide important shelter sites for toads and so quantified the availability of burrows in each habitat type. We estimated burrow availability by walking six 6 × 100 m transects in each site (n = 12 in each habitat). Transects were walked by two observers, spaced 3 m apart, looking 1.5 m on either side for 100 m. We only counted burrows which were large enough to fit a plaster model of a toad (minimum aperture: 12.5 × 7.0 × 2.5 cm—Figure S5).

To investigate rates of water loss across the landscape, we used plaster models that mimic water loss rates of live cane toads (Tingley & Shine, 2011; Tracy, Betts, Richard Tracy, & Christian, 2007—Figure S5). Models were soaked for approximately 12 hr and subsequently weighed to determine their “fully-hydrated” mass. We placed the models within 22 shelter sites chosen by telemetered toads and placed an additional eight models in the open. Each model was weighed approximately 24 and 48 hr after placement in the field. Thermochron iButtons (Maxim Integrated, San Jose, CA, USA) recorded temperatures within the plaster models over this time period. All models placed in the open reached dry weight (< 0.05% water) within 24 hr, so all mass and temperature measurements taken beyond 24 hr were discarded. Models in burrows were placed as deep as possible, while still being able to be retrieved, resulting in placements at varying depths ranging from approximately 10 to 40 cm.

To further investigate the benefit provided by burrows, we collected soil samples from 10 burrows used by telemetered toads in order to calculate soil water content. We used a sample from the top soil layer, and at 10 and 50 cm depth (where possible) and weighed them immediately in the field. This depth gradient covered the depth of all sampled burrows. Samples were then oven dried for >8 hr and re-weighed to estimate (evaporated) water content.

2.5 | Toad water loss and movement rates

We estimated changes in toad body mass between relocations by calculating the difference in mass since the last time the toad was weighed and dividing this by the initial hydrated weight of the toad. We then calculated water loss rates by dividing this percentage change in body mass by the time since the last weight (discounting observations more than 24 hr since last observed weight). We used a linear mixed effects model to test for fixed effects of habitat type, release site within habitat type, initial toad mass, use of shelter sites (as described above), and time since release on water loss rates (log-transformed to improve normality). Release cohort was included as a random effect.

We used a binomial mixed effects model (logit link) to test whether shelter site use and habitat type influenced whether or not toads moved at all on a particular night, with release cohort as a random effect. We then ran a second analysis on movement rates (distance per hour) in which non-movements were excluded, and movement rates were square-root transformed to improve normality. This analysis assessed the fixed effects of habitat type and shelter site use on movement rates, again including cohort as a random effect.

2.6 | Dry season dispersal kernel

Using the estimated Weibull distribution of survival times (estimated separately for each habitat type), and movement data from radio-tracking (again, split across habitats), we ran a simulation to predict how far a toad population could spread in the dry season in the study area. We calculated distances and angular displacements from our movement data, using the R package “adehabitatLT” (Calenge, 2006), and simulated 10,000 random walks by resampling these values. Given that it was the best model for the survival data, we
used the Weibull model to simulate time to death for each random walk. This produced a naturally bounded dispersal kernel (the distribution of dispersal distances for a given interval of time) showing the distribution of toad movements possible, accounting for survival.

All analyses were performed using R (Version 3.2.3) (R Core Team, 2015), and maps were created using ArcGIS (ESRI, 2012) and R package “ggmap” (Kahle & Wickham, 2013). Unless stated otherwise, all reported values are means ± standard error and p values less than .05 were considered statistically significant.

3 | RESULTS

3.1 | Shelter sites

Telemetered toads were adept at finding shelter sites (59.9% of toad locations; Table S2). Toads used shelter sites more frequently in the desert (70.6% of toad locations) than in the coast (40.0%) \( \chi^2 = 12.67, df = 1, p < .001 \). Burrows were the most common shelter site used by toads in both habitat types (77.8% in desert, 63.6% in coast); *Triodia* grass was the only other shelter site commonly used (15.9% of shelter sites) (Table S2). Burrows were, however, at substantially higher density in the desert \( (11.33 \pm 1.18 \text{ burrows per } 6 \times 100 \text{ m transect}) \) compared to the coast \( (1.33 \pm 0.45 \text{ burrows per transect}) \) \( t = -7.94, df = 14.15, p < .001 \). In both habitat types, toads were found in burrows more often than expected by chance (binomial tests; coast: 14/55 points, null expected <1, \( p < .001 \); desert: 56/102 points, null expected <1, \( p < .001 \); our null in both instances being set to the proportion of ground surface area taken up by burrows, as measured in the transects). Together, these results indicate that burrows were the preferred shelter site in both habitats, but that they were more readily available in the desert.

3.2 | Plaster models and water content

Models placed in burrows had lower water loss rates than models placed in the open (burrows: 3.09% ± 0.28 loss/hr, open: 4.51% ± 0.12 loss/hr, \( t = -3.75, df = 25, p < .001 \), Figure S6), but water loss rates of models in alternative shelter sites were statistically indistinguishable from those in burrows (alternative shelter sites: 3.27% ± 0.2678 loss/hr, \( t = -0.52, df = 25, p = .61 \)) (Figure S6).

Topsoil water content was approximately zero \( (-0.07 \pm 0.30) \). Soil at 50 cm depth was on average slightly moister.
but with high variability (1.13% ± 0.54). Plaster model temperatures (Figure 3) exceeded the critical thermal maximum of toads (CT$_{max}$ = 41.5°C, determined using South American toads) (Zug & Zug, 1979), in the open (30/200 temperature readings; 15.0%), and occasionally even in burrows (5/325 readings; 1.5%), over the first 24 hr of model placement. Plaster models exceeded the toad's CT$_{max}$ under trees and shrubs 32.0% of the time, although this high percentage is likely due to small sample sizes (8/25 readings). Models in rock crevices, under grass, under roots, and under woody debris did not go over the toad's CT$_{max}$.

### 3.3 | Toad water loss rates

No telemetered toad gained water mass. On average, toads lost 1.89% ± 0.17 of their body mass per hour ($n = 38$ observations, limited to observations less than 24 hr since last observed weight, groups = 5, range = 0.37–5.84% loss per hour, Figure S7). We detected no effect of habitat type ($t = 1.50$, df = 3, $p = .23$), shelter site use ($t = −3.37$, df = 1, $p = .18$), or time since release ($t = −2.12$, df = 1, $p = .28$) on water loss rates. Plaster models (including those placed in the open and in toad shelter sites) had a higher mean water loss rate (3.50% ± 0.18 per hour, $n = 28$ observations, limited to first 24-hr point observation) than radio-tracked toads, indicating that toad behavior reduced water loss expected by chance in this environment.

### 3.4 | Movement rates

We observed substantial variation in nightly movement rates (range = 0–2,541 m/night, Figure S8). Toads did not relocate on 19.7% of occasions. Toads were more likely to move in the coastal habitat compared with the desert habitat ($z = −2.64$, $n = 152$, groups = 8, $p = .008$, Figure 4a). Shelter site use had a weaker, and non-significant effect on whether a toad moved or not, where toads using shelter sites were less likely to move ($z = −1.45$, $n = 152$, groups = 8, $p = .15$).

Removing instances in which individuals did not move between relocations, toad movement rates were 718 m ± 49 per night (range = 2–2,541 m per night). Movement rates were lower in toads that used shelter sites compared to those found in the open (shelter sites: 653 ± 58, in open: 885 ± 86; $n = 122$, groups = 8, $t = −2.10$, df = 112, $p = .038$, Figure 4b). Habitat type was not significantly associated with movement rate ($t = −0.75$, df = 112, $p = .46$).

### 3.5 | Survival analysis

All located toads were dead by the end of the tracking period, most presumably from dehydration and/or heat stress ($n = 64$ out of 78). Of these, five were euthanized during tracking: three individuals reached critical levels of dehydration (40% of hydrated weight), and two were found alive in the open unmoving and covered in an unknown species of diurnal ant (and so were euthanized). Eight toads lost their...
transmitters. Of these transmitters, four were found buried under sand (approximately 5–75 cm deep) on tidal flats, one was found on top of a tall *Triodia* clump, and another was found approximately 1.5 m up a tree. These were treated as mortalities due to being found in places where it was extremely unlikely the toads had survived (due to the harsh tidal flats landscape, or predation). The other two transmitters were found in piles of woody debris (treated as lost toads). We failed to relocate the remaining six toads, or their transmitters, by the end of the study (treated as lost toads).

A Weibull model including habitat type and shelter site use was the best fit to the survival data, according to the Akaike's Information Criterion (AIC). A Weibull model including only habitat type had less support (delta AIC = 14.32). The Weibull model is an age-dependent hazard model, where the threat of death (i.e., due to high temperatures and water loss) increases over time, so is mechanistically what we would expect in this system. All toads followed to the end of the study died, surviving a predicted 34.3 hr ±1.4 hr (predicted survival range = 18.2–47.9 hr, Figure 5a). Mean time to death in the desert sites was almost twice that of the coastal sites (desert: 43.6 hr ± 1.4 hr, coastal: 24.5 hr ± 1.2 hr, \( t = 3.00, n = 78, p = .002, \) Figure 5b). Across both sites, shelter site use

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**FIGURE 4** Movement of telemetered toads. (a) Proportion of toad relocations. (b) Density plot (smoothed histogram) showing movements rates of toads from both habitat types, split by use of shelter sites and discounting toads that did not relocate.

**FIGURE 5** Kaplan–Meier survival plots showing survival (i.e., proportion of individuals alive) over time. (a) Overall survival. Dashed lines indicate 95% confidence intervals. (b) Effect of habitat on survival. * indicates censored points where a lost toad was last seen alive.
increased survival (shelter sites used: $42.9 \pm 1.0$ hr; not used: $20.4 \pm 0.7$ hr, $z = 4.54$, $n = 78$, $p < 0.001$).

3.6 | Dry season dispersal kernel

Simulations of toad dispersal in the dry season revealed maximum dispersal distances of 5.35 km in the coastal habitat and 3.97 km in the desert habitat before animals perish (Figure 6).

4 | DISCUSSION

This paper tests whether toads can survive in a proposed “waterless barrier” area without access to artificial water points. A major concern raised by stakeholders in an earlier workshop was whether cane toads could persist throughout the dry season by sheltering in burrows (Southwell et al., 2017). Indeed, studies of cane toad behavior suggest that toads are excellent at finding appropriate shelter sites even in very dry environments. Our results illustrate that toads were certainly adept at locating goanna burrows, regardless of habitat type and shelter site availability. In agreement with earlier work (Schwarzkopf & Alford, 1996), our plaster models show that burrow shelters provide reduced rates of water loss. Despite this benefit, however, toads in our study lost water at a mean rate of 1.89% per hour. At this rate, we would expect an average toad to reach critical water loss (50% of body weight) within 30 hr. Our sample size for toad water loss rates was limited and somewhat biased ($n = 38$, due to toads deep in burrows being irretrievable for weighing), but this time course for survival is very similar to the observed survival times. It remains possible that there may be deeper burrows in the landscape that our toads did not find (e.g., mammal burrows), but even so it seems unlikely that toads will be able to limit their water loss sufficiently to survive this environment without daily access to water. Our results, in the proposed barrier region, echo earlier results from the toads’ current semi-arid range in the Northern Territory. There, when free-ranging toads were excluded from artificial water points, all excluded toads all died within 72 hr (Florance et al., 2011), a survival time-line similar to that observed here.

Telemetered toads exhibited highly variable movement rates. Many toads did not move at all, particularly in the desert site, whereas some toads moved remarkable distances. The highest movement rate was 2.54 km in one night, one of the largest single-night movements ever recorded in an anuran (Pettit et al., 2016; Phillips et al., 2007). The surprisingly high dispersal rates observed here likely reflect not only highly dispersive phenotypes of toads from the invasion front (Perkins, Phillips, Baskett, & Hastings, 2013; Phillips, Brown, Webb, & Shine, 2006), but also behavioral plasticity: toads translocated to novel environments show sharply increased movement rates (Pettit et al., 2016). Therefore, since toads reaching the waterless barrier will be naïve to its novel environment, we can expect this study is a good representation of the expected movement behavior of frontline toads.

Most toads survived only 2–3 days, and the maximum predicted survival time was 5 days. Despite concerns that heavy coastal fogs would render the coastal habitat more suitable for toads than locations further inland, instead we found that survival was lowest along the coast, and toads moved around more often. Transects suggest that burrow availability was responsible for this difference: higher burrow densities in the desert presumably drove lower dispersal and greater survival times in this habitat compared with the coast. The short survival times we observed place a natural restriction on maximum dispersal distance during the dry season. Using our estimated distributions of survival and movement, we predict a maximum dry-season dispersal distance of approximately 5.5 km. Therefore, an increase of the barrier width by approximately 7 km would compensate for dry season dispersal. The Weibull survival model (in which hazard increases over time) will always place strong limits on survival time, and this model was well supported by the data.
4.1 | Management implications

This study provides further support for the waterless barrier strategy, demonstrating that cane toads are unable to persist in the waterless barrier area during the dry season without access to artificial water sources. Toads appeared to take one of two strategies; use shelter sites and disperse only short distances, or do not use shelter sites and disperse long distances. The latter strategy usually resulted in shorter survival times. These results suggest a trade-off between lowering water loss rates by sheltering in burrows versus increasing the likelihood of finding water by dispersing long distances (Chuang & Peterson, 2016). A waterless barrier should negate any benefit of dispersing long distances in search of water, placing a selective pressure on toads to disperse shorter distances (Phillips, Shine, & Tingley, 2016). Therefore, in time, long-dispersing toads are likely not to be a threat to the barrier. Initially, however, the barrier must be approximately 80 km wide in order to account for toad dispersal during the wet season (up to approximately 60 km) (Tingley et al., 2017). Releasing short-dispersing toads preemptively in front of the barrier area may also reduce the risk of hyperdispersive invasion front toads ever moving into the barrier region (Phillips et al., 2016). Invasion front toads have evolved to be highly dispersive compared to toads within long-established populations, providing potential for genetic backburning by introducing less dispersive toads on the nearside of the waterless barrier. While further modeling work on genetic backburning is warranted, research so far suggests that this relatively inexpensive strategy would greatly increase the effectiveness of the waterless barrier.

To ensure the waterless barrier remains secure over time, we also need to consider dispersal and survival capabilities of later established populations on its edge. Previous work has demonstrated behavioral and physiological differences between invasion-front toads and toads from long-established populations (Alford, Brown, Schwarzkopf, Phillips, & Shine, 2009; Phillips et al., 2007; Phillips, Brown, & Shine, 2010; Phillips, Brown, Travis, & Shine, 2008). For example, invasion front toads have greater locomotor ability than toads from long-established populations, and their movements tend to be more direct (Lindstrom et al., 2013). Is there a chance that the shorter-dispersing phenotype in long-established populations may be better equipped for survival in the barrier area? Clearly this is an important question to address, particularly if plans to pre-emptively introduce short-dispersing toads on the near side of the barrier are to be considered.

4.2 | Limitations

There are two main limitations to this study. First, we were logistically limited to testing the assumption in one potential barrier location, with 78 individuals. It is possible that as greater numbers of toads move into the corridor, there will be rare events that pave the way for further spread. Here we used estimated distributions of survival time and movement rate to predict population-level spread, but rare events (e.g., human-mediated transport, cyclones) remain a concern and will require ongoing monitoring and management.

Second, we released toads into a shallow body of water that dried within ~24 hr, but it is possible that as the corridor begins to dry at the end of the wet season, toads at the invasion front will have more time to select appropriate shelter sites (e.g., deep crevices, underground springs) than they were afforded in our experiment. It seems unlikely, however, that toads will be able to limit their water loss to an extent where they could maintain adequate hydration levels in this environment without daily access to water. An alternative approach to the one used here would be to record toad responses in the waterless barrier region as the landscape dries near the end of the wet season, when surface water is more readily available. Such an approach is logistically challenging but would allow toads more time to locate suitable shelter sites. Another approach could be to release toads into artificial or natural burrows that have been artificially wet to depth to simulate and test best case scenarios for burrow mediated survival. Nonetheless, in our study area—the most promising location for establishing the waterless barrier—we found no shelter sites that would allow toads to persist for more than five days in the dry season.

5 | CONCLUSION

Our results illustrate that it is important to understand fine-scale refuges in the landscape when managing invasive species. We expected survival along the coast to be higher than in the desert (due to coastal fogs and vegetation differences) yet the greater availability of burrows in the desert led to greater survival in that environment. Therefore, when exploring the feasibility of barrier areas or exclusion zones for invasive species, vital life history requirements, such as shelter sites, must be considered alongside physiological requirements. More broadly, while it may not always be possible to test the effectiveness of a barrier prior to its implementation, this study shows that on-ground testing of key assumptions can provide important insights into how a species will respond to a barrier environment. Understanding landscape structure and physiological requirements of a target species can inform distribution predictions, but we cannot know for certain how a species will respond to a landscape without directly observing individuals within it. By translocating and tracking a species in a novel environment, we were able to directly observe survival rates in a
potential barrier area, and determine preferred shelter sites within the landscape.

Our results show that cane toads cannot survive in the proposed barrier area for more than five days during the dry season. Rapid mortality also places strong constraints on their capacity to move to alternative locations. Despite heavy coastal fogs, the coastal plains habitat is an unsuitable environment for cane toads, providing little to no adequate shelter sites. In the desert habitat, shelter sites are readily available, but burrows only extended survival by a mean of 19 hr. In addition, we found that toads were less likely to move long distances when using shelter sites, and therefore the toads surviving the longest moved shorter distances. Our results demonstrate the importance of considering the interaction of landscape structure and species life history traits when determining habitat suitability for an invading species. From an applied perspective, our results provide further support for the waterless barrier idea, indicating that this management strategy could successfully halt cane toad expansion in Western Australia.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHORS’ CONTRIBUTIONS

Field work was conducted by E.G. and R.T. Statistical analyses were conducted by E.G. under the guidance of B.P. and R.T. B.P. assisted with the dispersal kernel simulation. E.G. led the writing of the manuscript, with substantial inputs from B.P. and R.T.

DATA ACCESSIBILITY

Data are accessible on Figshare (doi: 10.6084/m9.figshare.8187824).

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