The toad invasion can be stopped

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Submission to parliamentary inquiry into controlling the spread of cane toads

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Summary

Cane toads have spread across northern Australia unchecked since they were introduced in 1935. An unprecedented opportunity to stop their invasion will present itself in a few years as they reach the region between Broome and Port Hedland. Here the Great Sandy Desert meets the sea, and there is a narrow strip of country that is only suitable for toads because of the artificial waterpoints created by pastoralists. Management of these waterpoints (such that they are still available for cattle but cannot be accessed by toads) can halt the toad invasion and so prevent them from colonising more than 260,000km^2 of their potential range in the Pilbara. The conservation benefits of such an action are enormous: protecting the entire Pilbara bioregion and its many endemic species from the impact of toads. The science behind this idea is very well developed; to the point that we know this waterless barrier can be made to work for an astonishingly small investment of only $5m spent over 50 years. Although implementation potentially provides a win for pastoralists, native title holders, and the environment, the project currently lacks political leadership, and capital; a clear role for government support.

Background

Cane toads are exquisitely sensitive to dehydration. They completely lack the physiological adaptations that allow Australian frogs to survive in dry environments (Schwarzkopf and Alford 1996, Seebacher and Alford 2002). Northern Australia is strongly seasonal, with a wet and a prolonged dry season. In the dry season, very little rain falls, and at this time of year, toads are restricted to permanent water and moist refuges (Child et al. 2009, Tingley and Shine 2011). As we travel south, and into the edges of the arid zone, the availability of water in the dry season becomes the single most important factor limiting the toads' distribution (Kearney et al. 2008).

In arid parts of the country, and in the northern dry season, toads need to rehydrate regularly or they will perish (Brown et al. 2011, Florance et al. 2011, Tingley and Shine 2011, Webb et al. 2014). In arid parts of the country, natural water sources that persist through the dry season are rare. In these regions, toads become increasingly reliant on artificial water sources; ground water brought up to support human settlements and industry (Florance et al. 2011, Letnic et al. 2014). When we map natural and artificial waterpoints across the country it becomes strikingly apparent how important these artificial waterpoint are to the persistence and spread of toads (Figure 1).

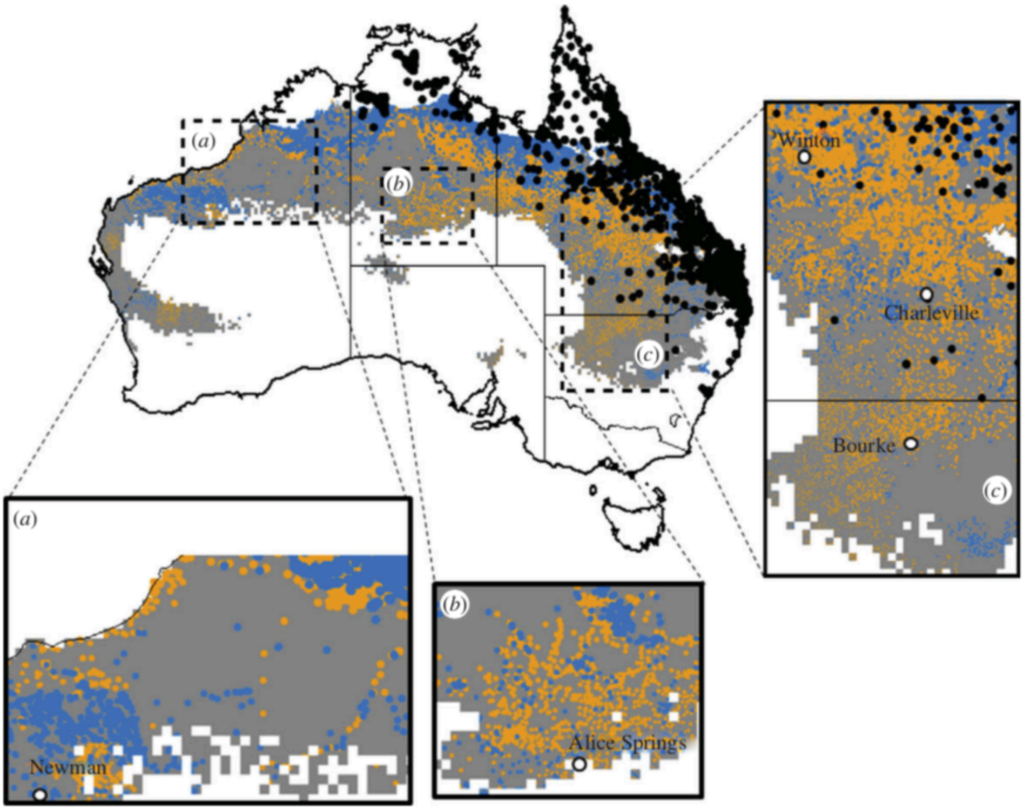

Figure 1. Artificial (orange) and natural (blue) waterbodies within the southern part of the cane toad's range (grey area). Black points are records of cane toads up to 2008. The area shown in inset (a) is the proposed barrier region. The region between Broome and Port Hedland is connected almost entirely by artificial waterpoints. Figure reproduced from Florance *et al.* (2011).

This mapping exercise also reveals an opportunity to prevent the spread of toads. Between Broome and Port Hedland in Western Australia, the Great Sandy Desert meets the coast. This is one of the hottest and (seasonally) driest parts of the country, with temperatures regularly in excess of 45 degrees, and nearly no rain between May and December every year (Figure 2). In this region, pastoralism is only possible along a narrow coastal strip, and along this strip, pastoralists have tapped underground water resources to water their cattle during the dry season. In the dry season, these 566 artificial waterpoints are almost the only source of surface water (Southwell et al. 2017).

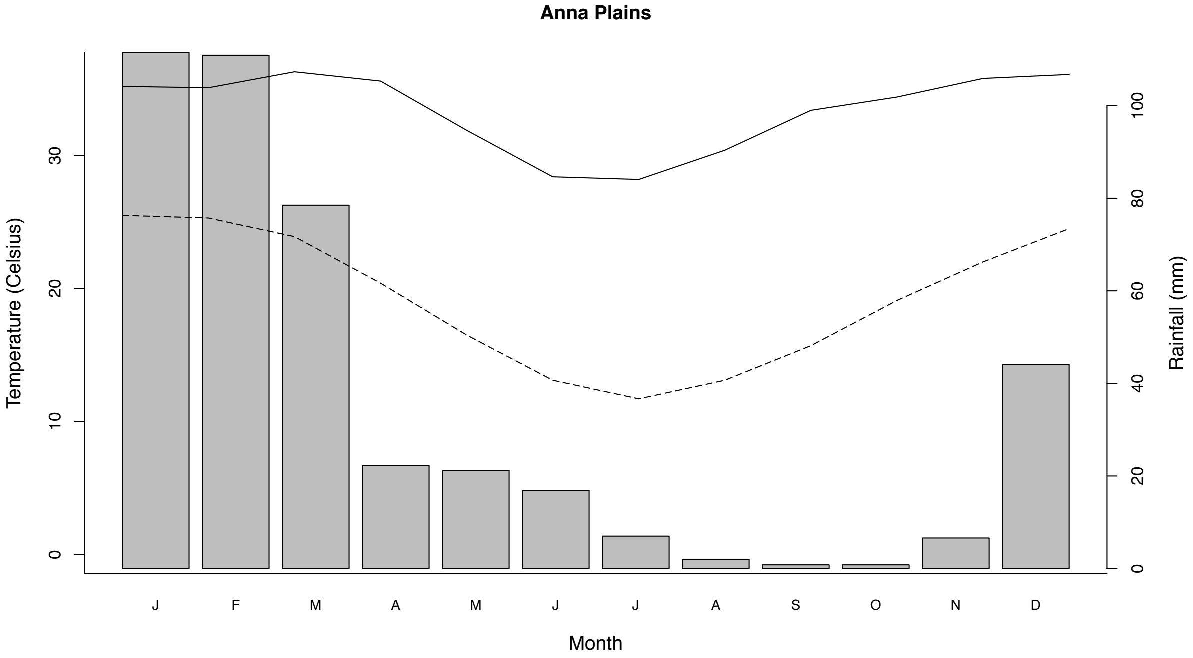

Figure 2. Climate statistics for Anna Plains Station, in the centre of the proposed barrier region. Mean annual rainfall is shown with the bars; mean maximum and minimum temperatures with the lines. The region receives almost no rainfall between August to November, and mean maximum temperatures remain above 30 degrees during this arid time of year. Data from Bureau of Meteorology.

These artificial waterpoints will become critical refuges for toads. Several studies now show that: in dry parts of their range, toads aggregate in vast numbers around these artificial waterpoints; that they do not move between waterpoints in the dry season; and that if they are denied access to these waterpoints, they die within days (Florance et al. 2011, Letnic et al. 2014, Letnic et al. 2015). Finally, a radiotelemetry study of toads in the proposed barrier region showed that, while toads were very good at finding shelter (in burrows and so on), this did not allow them to persist: without access to surface water, all animals were dead within four days (Gregg et al., submitted). All of this suggests that a "waterless barrier" placed somewhere between Broome and Port Hedland could stop the toad invasion.

Modelling a waterless barrier

Thanks to decades of basic research, cane toads are a particularly well understood animal (Shine et al. 2006, Shine 2010, Shine and Phillips 2014). One of the things that is well understood is their rate of movement. Literally hundreds of toads have been radiotracked in various times and places, and under varying conditions (Schwarzkopf and Alford 2002, Phillips et al. 2008, Alford et al. 2009, Brown et al. 2011, Tingley and Shine 2011, Brown et al. 2014, 2015, Jessop et al. 2018). As a consequence, we have good measures of their capacity to move across a landscape. When we combine movement rates with reproductive rates, we can build models of population spread. Such a model has been built with the express aim of investigating potential strategies around the waterless barrier idea (Tingley et al. 2013).

The model clearly shows that, if we do nothing, toads will spread across the waterpoints, between Broome and Port Hedland, and so colonise the Pilbara (an additional 260,000km^2 of the country) (Tingley et al. 2013). The model also shows that, by creating a "waterless barrier" – a region of country about 70 km wide in which we deny toads access to artificial water – the invasion stops, and the Pilbara remains toad-free. The model assumes that toads are free to move (at maximum rates) through the wet season. During this time, there is abundant water in the landscape and they passively spread into the "waterless barrier". Come the dry season, however, they require artificial water to persist, and if we deny them this resource across a 70 km stretch of country, all of these dispersing animals will die, and the invasion is driven back to the near edge of the barrier (Tingley et al. 2013).

These artificial waterpoints are, however, vital infrastructure for pastoralists. We are not advocating the removal of this infrastructure, rather that it be changed to a tank and trough system (inaccessible to toads) and maintained such that it does not leak. This infrastructure is so vital to pastoralists that it is already routinely monitored, thus, the primary cost of implementing the barrier is upgrade of pastoral equipment and ongoing maintenance, rather than monitoring. Applying the above spread model in an economic decision framework, Southwell (2017) show that the barrier could be implemented at surprisingly little cost. Costs vary with where, precisely, the barrier is implemented, but in the optimal locations it could be done for as little as $5m spent on pastoral infrastructure over 50 years (Southwell et al. 2017). Moreover, benefits accrue to pastoralists, because where toads are absent, dung beetles remain common; removing cattle faeces and reducing parasite transmission between cattle around waterbodies (Feit et al. 2015). Relative to other major conservation initiatives, and relative to the size of the benefit (the entire Pilbara kept toad-free), the waterless barrier represents astonishing value for money.

Translation to implementation

The science behind this proposal is unusually well advanced. Decades of field research executed by various independent parties, and sophisticated modelling, all point to this idea as a likely success story. The science has moved on from whether the barrier will work, to how to make it as effective as possible using genetic manipulations (Phillips et al. 2016). The challenge, therefore, now lies in implementation. While a 70 km stretch of country sounds like a lot, in this part of the world this often involves only one or two pastoral leases. Thus, a small consensus of land managers is required to implement the idea. While on-ground leadership could come from the native title holders – Nyangamarta, and Karrajarri – the project currently lacks political leadership, and capital. Thus, there is a clear role for government support.

Political leadership is particularly important at this juncture because we risk losing this opportunity through a) poor planning, and b) lost time. With regard to planning, a major risk to halting the toad invasion is that the proposed barrier region undergoes intensification of groundwater extraction by pastoralists. There has been a push from the State Government in recent years to develop the groundwater in this region for fodder cropping. At this stage only a few of the 11 pastoral leaseholders have invested in fodder cropping, and others have expressed doubts as to its efficacy. Nonetheless, intensification of groundwater extraction will make the waterless barrier substantially more expensive to implement and, in some scenarios, effectively impossible. Thus, leadership is urgently needed to identify priority areas and manage development in these areas in ways that are aligned with the “waterless barrier”. This leadership could come in various forms, but Traditional Owners are an important party.

With regard to time, the toad invasion front is currently 290 kms from the top of the possible barrier region. At current rates of spread, this will see them enter the region of interest within 6 years, around 2023. If they raft down the Fitzroy River, which is a very real possibility (Doody et al. 2019), they will arrive substantially sooner, even within the next year or two. If we are not to be caught unprepared, the time to act is now.

Summary of benefits

- Enormous potential for large-scale and long-lasting conservation benefits for unique Pilbara biodiversity.

- Low annualized-cost implementation enmeshed within existing agricultural practices.

- Improved ground-water resource efficiency for recipient pastoral properties.

- Reduction in the impact of toads on dung beetles; reduced fly numbers and reduced parasite load in cattle around managed waterpoints.

- Integrated land management under multi-stake holder arrangements between traditional owners, pastoralists and key investors.

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Excluding access to invasion hubs can contain the spread of an invasive vertebrate

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Many biological invasions do not occur as a gradual expansion along a continuous front, but result from the expansion of satellite populations that become established at 'invasion hubs'. Although theoretical studies indicate that targeting control efforts at invasion hubs can effectively contain the spread of invasions, few studies have demonstrated this in practice. In arid landscapes worldwide, humans have increased the availability of surface water by creating artificial water points (AWPs) such as troughs and dams for livestock. By experimentally excluding invasive cane toads (*Bufo marinus*) from AWP, we show that AWP provide a resource subsidy for non-arid-adapted toads and serve as dry season refuges and thus invasion hubs for cane toads in arid Australia. Using data on the distribution of permanent water in arid Australia and the dispersal potential of toads, we predict that systematically excluding toads from AWP would reduce the area of arid Australia across which toads are predicted to disperse and colonize under average climatic conditions by 38 per cent from 2 242 000 to 1 385 000 km^2. Our study shows how human modification of hydrological regimes can create a network of invasion hubs that facilitates a biological invasion, and confirms that targeted control at invasion hubs can reduce landscape connectivity to contain the spread of an invasive vertebrate.

Keywords: artificial water; biological invasion; *Bufo marinus*; arid; control strategy; hydrological regime

1. INTRODUCTION

Over the last 500 years, human activities have greatly increased the rate at which animal species are translocated around the Earth [1]. Following their introduction to new environments, invasive species often thrive in the absence of population regulation by predators, parasites and diseases with which they have coevolved, and may undergo rapid range expansions. The subsequent disruption to ecological processes caused by the novel interactions of invasive species has been identified as one of the most serious threats to biodiversity at a global scale [2].

Reducing the economic and ecological impacts of invasive species is a key goal of invasive species management, but requires an understanding of factors that influence the population growth, spread and distribution of invaders. One critical step for managers is to identify the pathways through which invasive species spread [1]. Landscape structure, connectivity and the presence of dispersal corridors can all influence the spread of invasive species. Many biological invasions do not occur as gradual expansion along a continuous front, but result from the expansion of satellite populations that become established at 'invasion hubs' [3,4]. Invasion hubs can result from random dispersal events, or they may occur in habitat patches preferred by the invader or at locations where individuals are directed during the process of dispersal [1,5]. Once invasion hubs are identified, targeted control efforts at such sites can be an effective way of containing the spread of the invader [6,7]. Although the theoretical significance of biological invasions occurring via invasion hubs has long been recognized [5,7,8], few studies have demonstrated functioning invasion hubs [9,10].

In arid regions, the ability of people to capture and redistribute scarce water has been a key driver of economic growth. However, because water is a limiting resource in arid environments, the modification of hydrological regimes (damming of rivers, depletion of groundwater, and provision of surface water in previously waterless areas) can dramatically alter ecosystems and has facilitated the establishment and spread of non-arid-adapted invasive species [11–15]. Livestock grazing is an important economic activity in arid lands, but is constrained by the scarcity of surface water because horses, cattle, sheep and goats must drink regularly. To increase the livestock carrying capacity of arid rangelands, pastoralists have created artificial water points (AWPs) where water is provided to animals via troughs or dams [11,16].

By providing a reliable water source, AWPs subsidize wildlife with an essential resource for their metabolic homeostasis, growth and reproductive success, and allow 'water-dependent' animal species to persist in numbers that would not otherwise be attainable. For example, the provision of AWPs in arid environments has been linked to range expansions and/or population increases of water birds and wild herbivorous mammals that must drink [16,17] and has provided previously unavailable habitat for aquatic organisms [18,19]. Thus,

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AWPs can influence how arid ecosystems function by facilitating the trophic and competitive interactions of species that need to access water to survive [20,21].

Here, we examine how the redistribution of water in a semi-arid landscape can provide a resource subsidy and subsequently influence the survival and distribution of an invasive species. Our study area was situated in the Victoria River District of the Northern Territory, Australia (electronic supplementary material, figure S1). This semi-arid region has a vast network of bore-holes that supply water to small earthen tanks that in turn supply water to cattle-drinking troughs (electronic supplementary material, figure S2*a*). The region is currently being invaded by the cane toad (*Bufo marinus*), a large anuran from tropical America that is toxic to endemic Australian predators [22,23]. Cane toads lack physiological adaptations to aridity and we tested the hypothesis that AWPs function as invasion hubs for toads by providing them with access to water during the extreme aridity of the dry season. We experimentally fenced AWPs to test our predictions that: (i) cane toads require access to AWPs to survive; (ii) exclusion of toads from water in combination with hand collection of toads confined by fences is an effective way of reducing their populations; and (iii) that the movements of toads are focal around water. Finally, we evaluated the usefulness of excluding toads from AWPs by mapping the distribution of permanent waters in the predicted range of toads across the arid regions of Australia and simulating the extent to which the exclusion of toads from AWPs could reduce the availability of dry season refuge sites for toads and the area over which they are likely to disperse and colonize.

2. METHODS

(a) *Study species*

The cane toad *B. marinus* has spread through more than a million square kilometres of Australia since its introduction to Queensland in 1935 [24]. This spread resulted from both range expansion overland and along watercourses [25] and from inadvertent human-assisted dispersal [26]. Unlike most native Australian desert-dwelling frogs, which possess physiological adaptations (cocoon formation, aestivation, reduced metabolic rate) to survive long dry periods [27,28], cane toads cannot physiologically control evaporative water loss through their skin [29]. Thus, toads are susceptible to dehydration throughout their life cycle, but become increasingly resistant to dehydration as their body size increases owing to a decrease in their surface area to volume ratio [29,30]. To combat dehydration, adult cane toads are active nocturnally and during the daytime they select moist cool microhabitats as shelter sites [29,31]. The arid regions of northern Australia are characterized by distinct wet and dry seasons, with almost all annual rainfall occurring within a brief wet season (December–March). During the dry season, high desiccation rates and limited moisture availability could conceivably restrict cane toads to microhabitats near standing water.

Cane toads are highly toxic, and possess bufogenins which are absent in native Australian frogs [22]. Consequently, most endemic Australian predators lack physiological resistance to bufotoxins [22], and mammalian and reptilian predators can die after attacking or ingesting cane toads [32]. In northern Australia, populations of frog-eating reptiles have declined dramatically in areas invaded by cane toads [33,34]. The cane toad has recently expanded its range into semi-arid regions of the continent, where it poses a serious threat to carnivorous reptiles [34]. Since the 1980s, considerable effort has been expended on developing biological control techniques to reduce toad numbers and hence impacts, however, efforts to date have had little success [35].

(b) *Study area*

Our study area was in the Victoria River catchment (Camfield Station: 17°02′ S, 131°17′ E) in the Northern Territory (electronic supplementary material, figure S1*a*) which experiences a mean annual rainfall of approximately 580 mm. Cane toads first invaded the northern part of the study area in 2007–2008 [34] and are expanding their range westward and southwards into increasingly arid regions. The study area experiences a semi-arid, monsoonal climate characterized by a hot humid wet season (December–March) and a hot dry season (April–November). Temperatures are high year round and on average exceed 30°C on 286.4 days each year at Wave Hill (17°27′ S, 130° 50′ E). During the late dry season, study period of September to November 2009, conditions were hot and dry as is typical for this time of year (mean daily maximum temperature = 37.2°C, mean daily relative humidity = 17%; Australian Bureau of Meteorology). The dominant landforms within the study area are undulating plains that support savannah vegetation dominated by Mitchell grass (*Astrebla* spp.) situated on deep-cracking clay soils.

In most years, no rain falls between April and September, and most stream flow occurs during the wet season (December–March) when monsoonal rains bring more than 80 per cent of the annual precipitation. During the late dry season (September–November), the only sources of natural water are disconnected pools, separated by exposed sand or rock bars in major drainage channels and a small number of permanent natural springs. Discussions with landholders and examination of rainfall records (Australian Bureau of Meteorology) indicated that no rain fell in the study area between 2 March 2009 and the study period in September–November 2009.

Commercial cattle grazing has been conducted throughout the study area since the late nineteenth century. Water is a limiting resource for grazing livestock in this hot semi-arid region. To increase the amount of grazing land available for cattle, pastoralists have established an AWPs at intervals of 5–10 km throughout the landscape.

(c) *Fencing experiment*

We experimentally fenced AWPs during the late dry season to determine if cane toads are dependent on AWPs for survival in this seasonally arid landscape. The purpose of the fences was twofold. The fences prevented toads that were sheltering in AWPs from leaving and thus facilitated collection of these individuals by hand. The fences also prevented toads that were sheltering away from the AWP from accessing the water. If toads require access to AWPs to survive, we would expect that survival of toads would be greater at sites where toads had access to water. If hand collection and exclusion of toads from water is an effective way of reducing their populations, we would expect that population declines following the implementation of the fences would be greater at fenced AWPs than sites where toads were able to freely access and leave the water. The study was located at nine AWPs (electronic supplementary material, figure S1*b*). In each case, AWPs were located more than 4 km from the nearest other source of permanent water. There were three treatments: fenced, unfenced controls and procedural controls, with three replicate AWPs per treatment. Treatments were interspersed to account for any spatial heterogeneity.

We constructed fences made of shade-cloth material, wire and metal posts 2–5 m from the water's edge along the flat crest of the AWP (electronic supplementary material, figure S2*b*). The fences were 600 mm high, to prevent toads from jumping over, and had a soil-covered flange of shade-cloth extending 400 mm outwards along the ground to prevent toads from burrowing beneath the fence. We constructed procedural control fences in the same fashion, but raised the shade-cloth 100 mm above the ground so that toads could access water (electronic supplementary material, figure S2*c*).

Once fences were established, we removed toads by hand from inside the fence at the fenced treatments and euthanazed them. Each morning we recorded the number of dead toads on the outside of exclusion fences that died while attempting to gain access to the water. Toads were left undisturbed at the unfenced control and procedural control AWPs.

(**d**) *Toad survival*

We used radio telemetry to monitor the short-term (72 h) survival of cane toads at fenced, unfenced control and procedural control AWPs. At each AWP, we captured adult cane toads (>90 mm snout urostyle length (SUL) of both sexes 8–10 h after fence installation at night between 20.00 and 22.00 h). All toads were captured within 2 m of water. We then recorded their sex, mass and SUL. We fitted radio-transmitters (Sirtrack, New Zealand, 3.5 g mass) to the toads with a metal chain-link waistband [36]. To ensure that toads were well hydrated prior to release, they were placed in a bucket of water for 20 min. The toads were released approximately 30 min after capture outside of the fences, or 5 m from water in the case of the unfenced controls and procedural control treatments. We released six to seven toads at each of the nine experimental AWPs (total: $n = 19$ unfenced AWP; $n = 20$ procedural fence AWP; $n = 21$ fenced AWP). Each morning following release, we located toads to determine their fate (alive, dead or eaten by a predator). To avoid undue distress to the toads, the animals were not disturbed during tracking. We recorded the mass of toads that died at the fenced dams and the telemetered toads that survived the 72 h tracking period at unfenced and procedural control AWPs.

(**e**) *Toad abundance surveys*

We conducted nocturnal strip-surveys using handheld 12 V spotlights with 25 W halogen bulbs at each AWP to measure the abundance of toads along 4 × 150 m strip transects ($n =$ 4 per AWP) radiating away from the water's edge. All AWPs were surveyed 6 and 3 days prior to fence erection and 1, 3, 6, 12, 20 and 70 days after fence installation. To evaluate if fencing had adverse impacts on native fauna, we recorded the number and species of native fauna found dead on the inside and outside of fences.

(**f**) *The movements and shelter sites of toads*

We used telemetry to examine the movement patterns and identify the diurnal shelter sites of 20 toads at an unfenced control AWP after the cessation of the survival study. These toads were individuals that were not tracked in the survival study. The procedure for fitting transmitters was identical to that described in §2*c*. The location of tracked toads was determined over 12 days both during the day and at night. Toads were not disturbed during tracking. For each shelter site identified, we recorded the habitat type and distance to water (m) using a GPS.

(**g**) *Predicting the broadscale effects of excluding toads from artificial water point*

We used information on the potential range of cane toads in Australia [37], their movement potential and the distribution of permanent natural waters and AWPs to quantify the extent to which the exclusion of toads from AWPs could reduce the number of dry season refuge sites for cane toads and the area over which they are likely to disperse and colonize. We restricted our analyses to areas receiving less than 700 mm annual rainfall because it is in these drier areas where permanent waters are likely to function as invasion hubs for toads by providing them with dry season refuges (see §3). A fundamental assumption of our models was that toads cannot survive without access to water during the dry season and thus must disperse from refuge sites that have permanent water (see §3).

We determined the distribution of potential dry season refuges for toads by mapping all permanent water features within the potential range of toads from data published by the Australian Government (AUSLIG mapping data, http://www.ga.gov.au/mapspecs/250k100k/appendix_a.jsp) in a geographical information system (ArcGIS 9.0). The movement potential of toads is likely to vary geographically owing to physiological constraints imposed by climatic variables [37]. To account for this, we modelled the potential dispersal ability of toads using a model in which the distance that toads were able to move each month was a function of toads' estimated body temperature, curtailed by a spatial dataset on the number of rainy days per month ([37]; see *Methods for calculating toad dispersal potential* in the electronic supplementary material). Rain days were defined as days that received more than 0.2 mm of rainfall. The inter-annual intensity and frequency of rainfall events in Australia is highly variable owing to the influence of coupled oceanic/atmospheric circulation systems, the El Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD), on the continent's climate [38]. Because of this variability, we simulated the movement potential of toads based on the mean annual number of rain days and also the number of rain days from an unusually wet year (2000) when the dispersal potential of toads was likely to be enhanced. Assuming that each permanent water feature could serve as a dry season refuge for cane toads and that toads could disperse in any direction, we used the buffer wizard of ArcGIS 9.0 to map the physiologically constrained distance that cane toads could potentially disperse from permanent natural water and AWPs (electronic supplementary material, figure S3*a*,*b*). We then mapped the connectivity of the landscape for colonizing toads by halving the dispersal distance around each refuge, assuming that toads would only be able to successfully disperse between patches that were spaced at a distance equal to or less than the annual dispersal potential of toads. These predictions assumed that toads experienced the monthly mean temperature, wind speed and cloud cover conditions but high humidity (90%) and hence minimal evaporative cooling. Because rainy nights are often cooler than average and we did not adjust for the dilution of propagules that could be expected to occur with increasing distance from refuges, our predicted distances are likely to be overestimates. We simulated the effect of excluding toads from AWPs by overlaying the predicted dispersal area of toads from permanent natural waters on that from AWP, and then subtracting the area that AWP add to the potential dispersal area of toads from the total area of both layers combined. We conducted these simulations for the average number of rain days per year and the actual number of rain days in a wet year associated with the La Niña phase of ENSO.

(**h**) ***Statistical analyses***

We compared the survival of radio-tracked toads between each treatment using the product-limit method or Kaplan–Meier estimator (JMP 5.0.1 SAS Institute Inc.). To test the effect of fencing on toad density with time, we used a before-after control-impact (BACI) analysis of variance design with time as a repeated measure. Data were log-transformed (log + 1) to reduce variances and correct a skewed distribution [39]. Parametric test assumptions (normality and homogeneity of variances) were evaluated by checking residual plots. Planned pairwise contrasts ($n = 12$ contrasts) investigated differences between treatment means in four time periods: 6 and 3 days before fence installation; 1 and 3 days after fence installation; 6 and 12 days after fence installation; and 20 and 70 days after fence installation. Because of the large number of post hoc tests, a sequential Bonferonni adjustment was applied to reduce the significance levels for the pairwise contrasts [39]. Contrasts were deemed statistically significant at $p \leq 0.005$. We tested the hypothesis that individual cane toads were more likely to be located in the water both during the day and night using Cochran's Q test [40].

3. RESULTS

(**a**) ***The effect of fencing on toad survival***

Radio-tagged toads had lower survival at fenced AWPs than at unfenced control or procedural control AWPs ($\chi^2 = 64.5$, d.f. = 3, $p < 0.0001$; figure 1). All 21 radio-tracked toads at fenced AWPs died within 72 h of release (figure 1). Of the 20 toads radio-tracked at unfenced control AWPs, 19 survived the 72 h tracking period, while one toad was killed by a predatory bird 48–60 h after release. All 19 toads monitored at procedural control AWPs survived the 72 h tracking period.

(**b**) ***Mass loss of telemetered toads***

Over the course of radio-tracking, telemetered toads at fenced AWPs lost more body mass (mean ± s.e. = 46% ± 2.9) than toads at unfenced control (3.2% ± 1.1 body mass loss) or procedural control AWP (0.8% ± 1.7 body mass gain) ($F = 151.0$, d.f. = 2, 51, $p < 0.0001$).

(**c**) ***The number of toads removed and the effect of fencing on toad abundance***

A total of 2016 toads were removed from the three fenced AWPs (table 1). The relative frequency of toads removed from inside and outside of the fences differed between AWPs (table 1; $\chi^2 = 840.6$, d.f. = 2, $p < 0.001$). There was no difference in toad abundance prior to fence installation (figure 2; electronic supplementary material, tables S1 and S2). The abundance of toads at fenced AWPs declined with time since fence installation (figure 2) but varied little at unfenced control or procedural control AWPs (figure 2). No toads were observed on transects conducted at fenced AWPs between 6 and 70 days after fence installation. In contrast, toads were observed on all surveys conducted at unfenced control and procedural control AWPs. Over the course of the study, 16 dead anurans (*Litoria inermis*) and one lizard (*Ctenotus* sp.) were found along the outside perimeter at fenced AWPs.

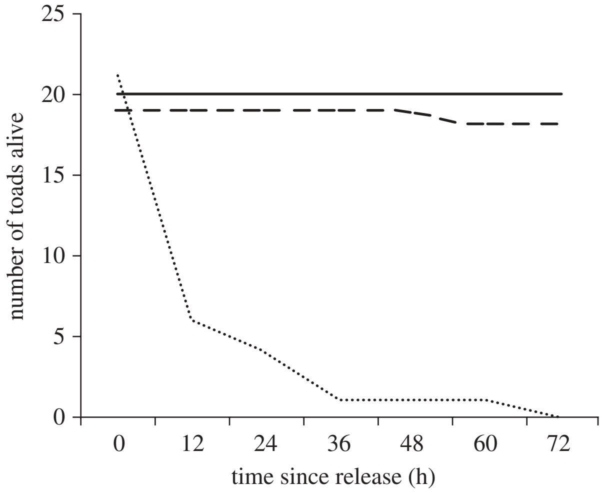

Figure 1. Mean survival time of radio-tracked toads released at fenced (dotted line), procedural control (solid line) and unfenced (dashed line) control AWP ($n = 3$ AWP).

Table 1. The number of toads removed from the inside and outside of fences at the three fenced AWPs. In : out is the ratio of toads removed from the inside of the fence relative to those removed from the outside of the fence.

AWP	inside	outside	total	in : out
1	62	819	881	0.08
2	716	259	975	2.76
3	61	99	160	0.61

(**d**) ***The movements and shelter sites of toads***

Toads were not restricted to the unfenced control AWPs but their movements were focal around it. We obtained 128 fixes of 19 individual toads over the 12 day tracking period. Toads were located in the water or within 0.5 m of the water for 65 per cent of fixes (59% of diurnal and 41% of nocturnal fixes), but were no more likely to be located in the water than away from the water during the day (Cochran's Q test, $\chi^2 = 4.7$, d.f. = 4, $p = 0.32$) or at night (Cochran's Q test, $\chi^2 = 0.17$, d.f. = 2, $p = 0.92$). All tracked toads were located in the water on at least one occasion during the tracking period. Toads were also located in diurnal shelter sites up to 410 m from the AWP, such as soil cracks (29% of all fixes) and logs (6% of all fixes), frequently with other toads.

(**e**) ***Predicting the broadscale effects of excluding toads from artificial water points***

Under average climatic conditions, simulated exclusion of toads from AWPs reduced the area of arid landscape that

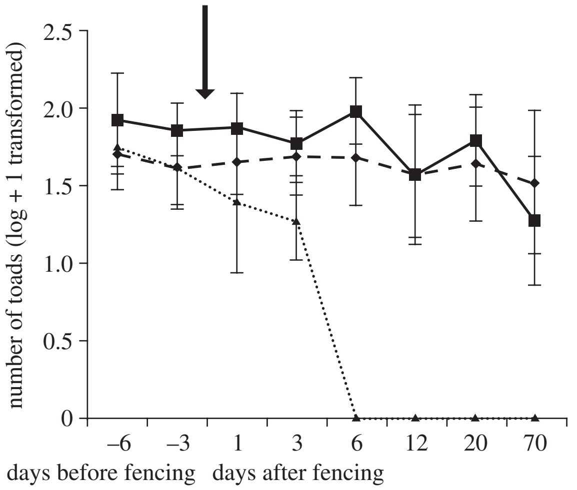

Figure 2. The number of toads observed during nocturnal surveys (log + 1 transformed) before and after exclusion fence installation at fenced (dotted line with filled triangles), procedural control (continuous line with filled squares) and unfenced (dashed line with filled diamonds) control AWP ($n = 3$ in each case). The arrow indicates the time of fence installation. Values are mean ± s.e.

toads are able to colonize by 38 per cent from 2 242 000 to 1 385 000 km^2 (figure 3). Our model suggested that toad exclusion would be more effective during dry years. Under unusually wet conditions, the area available for dispersal and colonization by toads increased to 2 598 000 km^2, and simulated exclusion from AWP would reduce the area available for dispersal by toads by 23 per cent to 1 993 000 km^2 (electronic supplementary material, figure S4).

Mapping indicated three key regions where dry season refuges are naturally sparse and the presence of AWPs provides potential corridors for cane toad dispersal or substantially increase the connectivity of the landscape for toads (figure 3*a*–*c*). Our modelling indicates that exclusion of toads at just 40–50 key AWPs could halt invasion from the Kimberly region to the Pilbara region (figure 3*a*).

4. DISCUSSION

(a) *The effects of excluding toads from artificial water point*

Cane toads at AWPs required access to standing water for survival during the late dry season and their movements were focal around water. Correspondingly, our failure to detect toads between 6 and 70 days after fence installation suggests that we eradicated toads from fenced AWPs and their immediate vicinity. Collectively, these results provide evidence that sites with permanent water serve as dry season refuges for toads and thus act as invasion hubs. Because toads must have access to water during the late dry season, the likely process of invasion in our study area has been gradual range expansion through dispersal from dry season refuges in the wet season following rainfall events. According to this patchy population model (*sensu* [41]), water becomes a limiting resource for toads during the dry season and their distribution contracts to the immediate vicinity of sites with permanent water from which individuals can disperse during the next wet season. Presumably, toads that have not located permanent sources of water by the start of the dry season die from dehydration.

Potentially, toad absence at fenced AWPs could have occurred if toads that were excluded from the water had selected suitable microhabitats (e.g. deep soil cracks) which prevented dehydration and allowed them to survive the observation period without being detected in our surveys [31]. However, we contend that this scenario was unlikely to occur for several reasons. First, toads excluded from AWPs lost on average 46 per cent of their body mass compared to negligible changes in body mass among toads from unfenced AWPs. Presumably, this loss of body mass observed in toads from fenced AWPs was due to dehydration. A previous study has shown that toads are likely to experience fatal dehydration if they lose more than 40 per cent of their body mass [23]. Second, all but one of the toads excluded from AWPs died within 12 h of release and the only individual that survived more than 12 h died within 72 h. In contrast, only one individual at a non-fenced AWP died, due to predation by a bird. Third, although radio-tracked toads at an unfenced dam moved and sheltered in deep cracks away from the AWP, all of the individuals were observed in the water during the tracking period. Together, these results suggest that in the late dry season, cane toads were restricted to the immediate vicinity of sites where standing water was available to avoid dehydration. A similar pattern of water dependency has been documented for adult cane toads during the dry season in the more mesic environments of the wet-dry tropics of Queensland, Australia [29,42].

The massive reduction in toad density following fence installation demonstrates that fencing combined with hand collection can reduce toad numbers around AWPs during the late dry season. The number of dead toads on the outside of fences also decreased with time since fence installation, suggesting that toad densities were reduced as a result of mortality. Moreover, it is likely that any toads that attempted to move to alternative water sources located several kilometres away under the hot and dry climatic conditions prevalent at the time of the study would have died from dehydration.

We recorded negligible mortality of small native anurans at fenced AWPs. In addition, birds, large pythons and large mammals such as dingoes and kangaroos were able to move over the fences unimpeded (authors, September–October 2009, personal observations). Thus, the results show that fencing effectively reduced toad numbers, yet had minimal negative impact on native fauna. 'Wildlife gates' constructed of a mesh size able to be traversed by small native anurans, but not by adult toads, could be incorporated into fences to ameliorate any negative impacts. Metamorph or juvenile toads were not observed at the AWPs, so it appears that the inclusion of wildlife gates would not reduce the effectiveness of the fences as barriers to toads in the late dry season.

(b) *Artificial waters as invasion hubs for toads*

The spatial configuration of landscapes can be an important influence on the dispersal of invasive species [4,43]. For example, the presence of suitable habitat corridors can focus the movements and dispersal of invaders into some habitats, but not others [1,36]. Likewise, the presence of isolated patches of particularly favourable

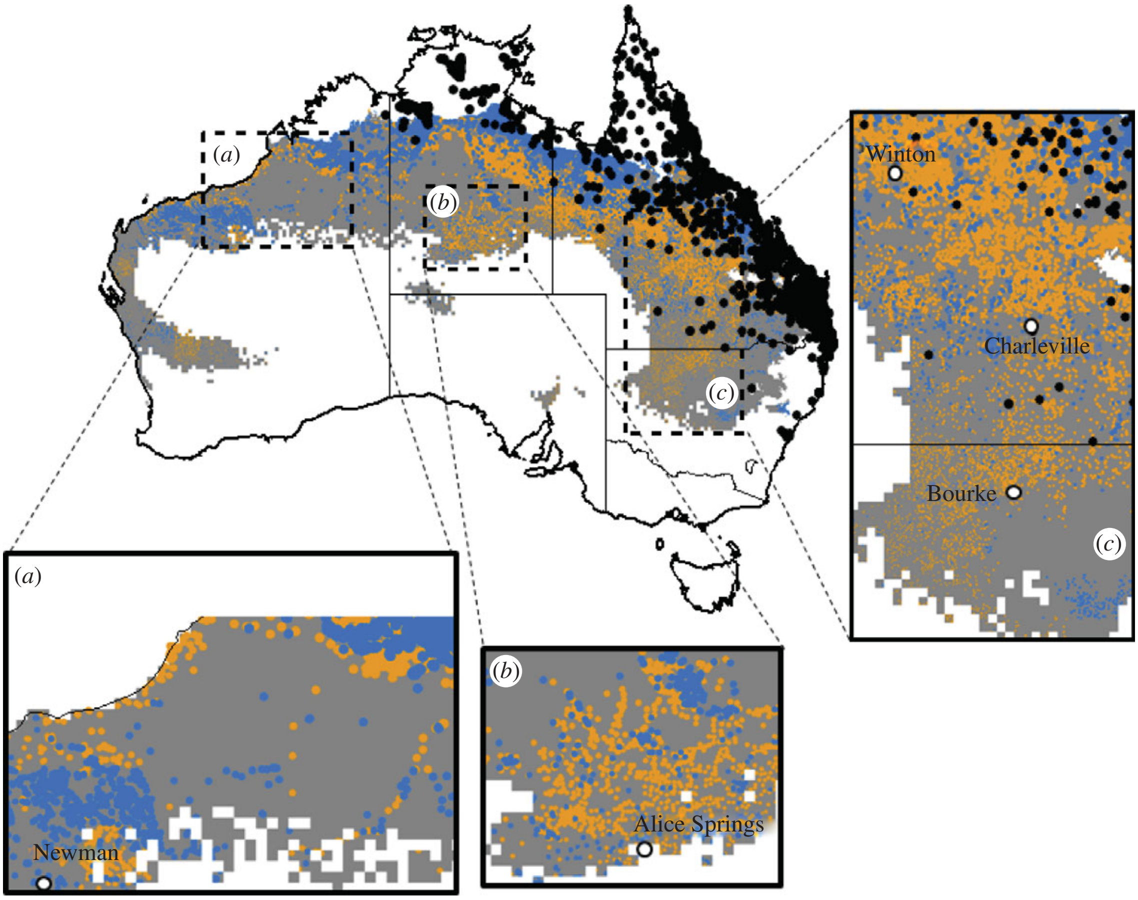

Figure 3. The area available (blue and orange) for dispersal and colonization by toads surrounding potential dry season refuges (sources of permanent water) within the predicted range of cane toads (grey) that receives less than 700 mm of annual rainfall. The orange area indicates the area that our simulation exercise identified could be made unavailable for toads by excluding them from AWPs. The model assumes that each permanent water source could serve as a dry season refuge for toads and that they disperse from such refuges during periods of rain. The annual dispersal potential around water sources has been weighted to reflect the physiological constraints imposed on the movement potential of toads by climatic variables (after [37]). The connectivity of the landscape for toads has been modelled by halving the annual dispersal potential around each refuge, assuming that toads would only be able to successfully disperse between water sources, and thus colonize dry season refuges that were spaced at a distance equal to or less than the annual dispersal potential of toads. The black dots indicate known locality records for toads in 2010. Blue colour, indicates natural water; orange colour, indicates artificial water; grey colour, indicates potential range and black dots, indicate current range.

habitat for invaders, or barriers that prevent successful dispersal can result in invasive species having spatially structured populations [44]. The establishment and subsequent expansion of small satellite populations may allow invaders to colonize new areas faster than through gradual expansion of a larger contiguous population [7]. Both theoretical and field studies indicate that concentrating control efforts on satellite populations, rather than on large focal populations, can be an effective strategy to reduce the rate of spread of invasive plant species [6,7,45,46]. Our study shows that modification of hydrological regimes by humans can create a network of invasion hubs and that targeted control at invasion hubs can be an effective way to contain the spread of an invasive vertebrate.

The presence of AWPs has substantially increased the availability of standing water and spatial distribution of water in the rangelands of Australia and other arid regions of the Earth [11,18,47]. In Australia, the proliferation of AWPs over the last 150 years has generated a landscape where few places are now more than 10 km from water across the approximately 70 per cent of the continent that is used for livestock grazing [16]. Prior to European settlement, surface water was comparatively rare in this low rainfall region and normally occurred only in the channels of major rivers and isolated springs, and was only widespread for brief periods following large rainfall events [47].

By providing a resource subsidy for toads in the dry season, AWPs increase the number of refuges available for adult cane toads, and the connectivity of arid landscapes for toads and potentially other non-arid-adapted wildlife (figure 3; [16]). AWPs probably serve as 'stepping stones' that have facilitated the invasion of cane toads into naturally waterless landscapes where without AWPs toads would be unable to reach or persist owing to scarcity of water. By increasing the number of dry season refuges, AWPs also elevate the regional toad population and may be expected to exacerbate the ecological impacts of toads (e.g. [33]) by increasing their encounter rates with terrestrial predators.

Our experiment shows that excluding adult toads from water coupled with the hand collection of toads confined within the fences can be an effective method for controlling satellite populations at isolated AWPs. Fencing is not the only technique available to exclude toads from AWP. An equivalent approach would be to replace earthen tanks with above-ground plastic tanks that do not allow toads access to water. Despite the success of our exclusion fences, the considerable dispersal potential of toads and the presence of natural waterholes situated on major catchment drainage lines poses a major problem for toad-control programmes. During extended periods of wet weather, toads are likely to re-invade 'treated' dry season refuges from untreated sites and, if they have access to water, re-establish refuge populations. The dispersal abilities of cane toads are evidenced by studies from the wet-dry tropics of Australia, which show that toads move as far as 1 km in a single night and 50 km in a calendar year [25]. No data are available on the annual movements of individual toads in semi-arid Australia. In our semi-arid Victoria River study area, cane toads have colonized AWPs located up to 9.5 km from the nearest source of permanent water (M.L. personal observation). Natural waterholes situated on major drainage lines also function as dry season refuges for toads. Many of these sites are not amenable to fencing because of the length of the waterholes and complexity of their vegetation, and are far too large for hand collection of toads to be feasible. Thus, where they occur, natural waterholes in arid areas will probably be an ever-present source of toads which can then invade surrounding landscapes.

Nevertheless, if toad exclusion devices (e.g. fences, plastic tanks) were strategically established at adjacent AWPs so that the distance between suitable habitat patches was greater than the 'wet-season' dispersal potential of toads, it may be possible to suppress toad populations and prevent their overland spread across vast areas of arid Australia (figure 3). Such a strategy is likely to be particularly effective in regions where natural waterholes are scarce. Our modelling exercise shows that there are several key areas in Australia where excluding toads from AWPs could prevent their overland spread (figure 3*a*–*c*). These areas occur in arid and semi-arid rangelands where natural waters are few and the proliferation of AWPs has increased the connectivity of the landscape for toads.

Rainfall variability will be a key issue affecting the ability to manage toads using water exclusion. Toads' dispersal abilities are enhanced during periods of 'wet' climatic conditions that can be expected during the La Niña phase of ENSO and negative phase of the IOD [38]. During these periods, the capacity to contain the spread of toads using water exclusion would be reduced in comparison with 'average' climatic years, but is likely to remain effective over large areas (electronic supplementary material, figure S4). Moreover, if toads did disperse into areas distant from permanent natural water during unusually wet periods, populations isolated during the inevitable drying out of the landscape would be vulnerable to both dehydration and physical control.

Most research on methods to control cane toads has focused on identifying and developing biological control agents; all have been unsuccessful to date [35]. A growing body of research now indicates that toad populations and impacts can in some areas be managed using physical control and by manipulating the behaviour of predators that attack toads ([48,49]; this study). While we do not propose water exclusion as a 'silver bullet' for toad control, our study shows that exclusion of toads from AWPs can effectively reduce toad numbers and could prevent their overland spread in arid regions.

5. CONCLUSION

Understanding the spatial dynamics of invasions can provide key insights into the development of strategic approaches to control invasive species. In arid regions of Australia, human modification of hydrological regimes has created a network of invasion hubs in to which invasive cane toads require access in order to survive through dry seasons. Excluding cane toads from AWPs can effectively reduce their local populations, and if conducted strategically at a large spatial scale, has the potential to prevent toads from using AWPs as 'stepping stones' into arid Australia.

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Identifying optimal barriers to halt the invasion of cane toads *Rhinella marina* in arid Australia

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Summary

1. Spatial heterogeneity in environmental conditions may restrict the spread of invasive species to narrow corridors between extensive patches of suitable habitat; thus, we may be able to curtail invasions by identifying such corridors, and focusing control efforts in these areas. Invasive cane toads *Rhinella marina* have spread rapidly through northern Australia, but to invade further into Western Australia, the toads must traverse a narrow arid corridor where artificial waterbodies may serve as critical stepping stones for range expansion.

2. We focus on the cane toads' imminent expansion into north-western Australia and use stochastic simulation to identify areas in which removal of artificial waterbodies would be most effective at stopping their spread.

3. Our model predicts that toads will spread from the Kimberley to the Pilbara regions of Western Australia through a narrow coastal corridor, but that they will depend upon artificial waterbodies to do so. Importantly, excluding toads from artificial waterbodies is predicted to prevent toads from colonizing *c.* 268 200 km^2 of their potential range in Western Australia.

4. We identified three locations where closure of a relatively small subset of artificial waterbodies is predicted to halt the spread of toads.

5. *Synthesis and applications*. We present a modelling framework that can be used to focus management activities within invasion corridors. Our analyses suggest that strategic removal of potential invasion hubs along such corridors can halt the spread of an invasive species.

Key-words: approximate Bayesian computation, control, corridor, dispersal, eradication, invasion hub, invasive species, simulation model, spread

Introduction

Mitigating the adverse impacts of invasive species requires a detailed understanding of where and when invaders are likely to spread (Andrew & Ustin 2010). Early models of spatial spread (Fisher 1937; Skellam 1951) assumed that invaders disperse through homogeneous terrain with deterministic population growth. Such models produce a smooth invasion front with rates of spread governed entirely by a species' dispersal ability and population growth rate (Skellam 1951). Heterogeneous environments will, however, cause spread rates to vary through both space and time (Neubert, Kot & Lewis 2000). Even in homogeneous environments, stochastic processes such as long-distance dispersal can influence spread rates by facilitating establishment of satellite populations ahead of the primary invasion front, which subsequently coalesce into a larger contiguous population (Fisher 1937; Nichols 1989; With 2002). In fact, a wide variety of stochastic and deterministic processes (e.g. fluctuating or patchy environmental conditions, dispersal along habitat corridors,

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Tingley and Phillips contributed equally to this work.

human-assisted range expansion) can lead to the formation of satellite populations at ‘invasion hubs’ (Cappuccino 2004; Urban *et al.* 2008; Florance *et al.* 2011). When populations are spatially structured in this way, spread rates are not only influenced by stochastic dispersal and population growth rate, but also by the spatial configuration of suitable habitat patches (With 2002).

Range expansion via the fusion of satellite populations has important implications for forecasting the spread of invasive species, because models that ignore this process may significantly under-estimate the rate and extent of a species’ invasion (Fisher 1937; Kot, Lewis & van den Driessche 1996). However, this pattern of range advance may also provide excellent opportunities for targeted eradication of invasive populations. Satellite populations often occur at low densities and thus are subject to environmental and demographic stochasticity (e.g. Allee effects; Cappuccino 2004). Studies of plant invasions have shown that targeting satellite populations can be an efficient strategy to impede rates of spread (Moody & Mack 1988; Cappuccino 2004; Andrew & Ustin 2010). Nevertheless, controlling invasive species remains a formidable challenge, and there are few examples of successful vertebrate eradications on mainland areas (Bomford & O’Brien 1995).

Here we investigate whether it would be feasible to create a barrier to the spread of invasive cane toads *Rhinella marina* L. in an arid region of north-western Australia by preventing the establishment of satellite populations of toads at artificial waterbodies. Cane toads have spread rapidly throughout northern Australia, causing dramatic population declines of many species of frog-eating predators (Shine 2010). In some regions of the continent, the toad invasion front has spread at a rate of greater than 50 km year^{-1} (Phillips *et al.* 2007; Estoup *et al.* 2010). However, toads are also invading regions of Australia that are much more arid than those colonized during earlier phases of their expansion. Desiccation risk is a critical factor determining the survival and dispersal of cane toads in arid landscapes (Florance *et al.* 2011; Tingley & Shine 2011), but this potential constraint has been removed in many places by the construction of numerous artificial waterbodies for pastoralism (Fensham & Fairfax 2008). These artificial waterbodies, which in northern Australia are typically earthen reservoirs for pumped bore water (see Fig. S1, Supporting Information), serve as important breeding sites and dry-season refuges for toads and thus may allow toads to establish satellite populations that subsequently coalesce during the wet season (Florance *et al.* 2011). Importantly, local eradication of toads from artificial waterbodies can be accomplished by excluding toads from water during periods of prolonged dry weather (Florance *et al.* 2011).

We combine data on the dispersal rates of cane toads in northern Australia (Brown, Kelehear & Shine 2011) with a stochastic point process model of spatial spread to address the following questions: (i) would the current configuration of natural and artificial waterbodies allow toads to colonize north-western Australia, (ii) would toads be capable of spreading in the absence of artificial waterbodies, and (iii) could we halt the spread of toads by selectively excluding toads from artificial waterbodies in areas with low densities of natural waterbodies?

Materials and methods

THE MODEL

We use a discrete generation stochastic point process model of contagious spread to identify areas in which removal of artificial waterbodies would be most effective at stopping the spread of cane toads. We define the density D of potential colonizing toads at any point, m, on the landscape, as a function of the distance d_{im} between that point and each colonized point i, the dispersal kernel around each colonized point, $\mathrm{K}_i(d_{im})$, and the number of potential colonizers emanating from each colonized point, C_i:

$$D_m = \sum_{i=1}^{n} C_i \mathrm{K}_i(d_{im}) \qquad \text{eqn 1}$$

where K is a probability density function describing the distribution of toads a given period of time after leaving a waterbody, and n is the total number of colonized waterbodies. The total number of potential colonizers on the landscape in any given generation is then $C = \sum_{i=1}^{n} C_i$. We assume that toads can detect waterbodies from a distance r, and that this detection radius is small relative to the scale of dispersal and the distance between waterbodies. Thus, the proportion of the overall colonizer density falling within the detection radius of a waterbody j is approximately:

$$p_j \approx \frac{\pi r^2 D_j}{C} \qquad \text{eqn 2}$$

and the total proportion of the colonizer density falling within the detection radius of all waterbodies is:

$$p_T \approx \frac{\pi r^2}{C} \sum_{j=1}^{N} \sum_{i=1}^{n} C_i \mathrm{K}_i(d_{ij}) \qquad \text{eqn 3}$$

where N is the total number of waterbodies in the landscape. This approximation is good for relatively flat or constantly sloping parts of the density landscape (i.e. if r is small relative to the scale of dispersal). Introducing a detection radius serves two purposes: ecological realism (we know that toads are capable of detecting breeding sites using a variety of navigational cues, Sinsch 1987) and mathematical necessity (because we modelled toads’ paths on a smooth 2D plane, the probability of a toad finding a waterbody represented by an infinitesimal point is itself infinitesimal).

We can now calculate a realized number of colonizing toads in a given generation as a stochastic process: a draw from a multinomial distribution. To do this, we make a draw of size C from a multinomial with $N + 1$ categories. The probabilities associated with these categories are the vector of probabilities given by $\{p_1, p_2, \ldots p_N, 1\text{-}p_T\}$, the last element being the probability of failing to colonize any waterbody. In the absence of information on the size each waterbody attains in a given year, we treat the number of potential new colonists produced by each colonized waterbody, C_i, as a per-generation, per waterbody draw from a Poisson distribution mean $\hat{C}$.

A waterbody is considered colonized only if two or more toads arrive at that waterbody in a single generation. Once colonized, waterbodies remain colonized thereafter. Population growth is assumed to be instantaneous: a waterbody produces C_i propagules the generation immediately following its colonization. This assumption is based on the biology of cane toads, which can produce 30 000 eggs per year and reach sexual maturity in a single season (Lever 2001). To explore spread, the model is iterated over a number of generations.

THE LANDSCAPE

We focused our analyses on a *c*. 500-km transect across the western margin of the Great Sandy Desert linking the Kimberley and Pilbara regions of Western Australia (hereafter referred to as the *Kimberley-Pilbara corridor*; Fig. 1). The Kimberley-Pilbara corridor lies within the cane toad's fundamental niche (Kearney *et al.* 2008) but has not yet been colonized (in 2010, the toad invasion front was *c*. 565 km north-east of the study area). Importantly, this narrow coastal corridor connects extensive patches of suitable habitat for cane toads to the north and south (see inset of Fig. 1). Natural sources of water are scarce along the Kimberley-Pilbara corridor. However, the establishment of artificial waterbodies for livestock grazing has increased the availability of surface water and potential refuge sites for cane toads. Mean annual rainfall ranges from 466 mm in the north-east to 293 mm per annum in the south-west. The average number of rainy days (>1 mm rainfall) ranges from 35·1 in the north-east to 22·5 in the south-west (Australian Bureau of Meteorology).

Previous analyses of radiotracked cane toads in semi-arid Queensland have shown that precipitation patterns have a marked influence on daily dispersal rates (Tingley & Shine 2011); therefore, we only permitted toads to disperse between waterbodies for three days following rainfall events in our model (Kearney *et al.* 2008; Florance *et al.* 2011). Given this threshold, to determine the total number of days per year that toads could disperse between waterbodies (ndays), we used long-term (1961–1990) average rainfall data for each waterbody adjusted for the probability that days following rain are themselves rainy days (assuming rainfall is independent across days):

$$\mathrm{ndays} = x + 3(x)(1 - (3(d - d^2) + d^3)) \qquad \text{eqn 4}$$

where x = the number of rainy days (>1 mm) at each waterbody and $d = (x\text{-}1)/364$.

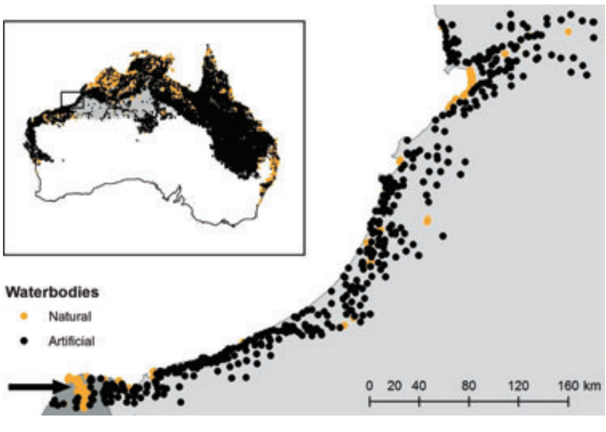

Fig. 1. The study area in Western Australia. The black arrow in the lower left-hand corner shows the location of the De Gray River, which was used as an endpoint in all simulations. The dark grey region below the black arrow shows the extent of the Pilbara region. In the inset, only waterbodies that lie within the predicted distribution of toads (grey shading) are depicted.

The number of rainy days in arid regions of Australia can fluctuate widely from year to year. To explore the sensitivity of our results to periodic floods, we ran additional simulations allowing uncharacteristically wet years every three decades (Florance *et al.* 2011). To estimate the maximum number of rainy days at each waterbody during flood years, we examined weather records from 1961 to 1990 (the same period used to calculate the average number of rainy days above) for a weather station in the middle of the Kimberley-Pilbara corridor (Mindora). The maximum number of rainy days at Mindora over this period was 44. Because this value is 2·431 times the average number of rainy days at Mindora, we multiplied the average number of rainy days at each waterbody along the Kimberley-Pilbara corridor by 2·431 to simulate an unusually wet year once every three decades.

Locations of natural permanent waterbodies (perennial water courses, perennial lakes, waterholes and springs) and artificial permanent water points (bores, canal lines, windpumps, reservoirs, water points and watertanks) were taken from Geoscience Australia mapping data (http://www.ga.gov.au/meta/ANZCW0703008969.html). Our classification of natural and artificial waterbodies follows that of Fensham & Fairfax (2008).

THE DISPERSAL KERNEL

We used data from radiotracked cane toads to estimate the n-wise convolution of the daily dispersal kernel for toads in northern Australia. These data came from a radiotelemetry study conducted on the Adelaide River floodplain in the Northern Territory from 2005 to 2010 (Brown, Kelehear & Shine 2011). We used movement data from 114 adult toads, each of which was tracked for an average of 11 days. We only used data collected during the wet season (between January and March), at which time humidity is sufficiently high, and rainfall sufficiently frequent that toads likely move freely. For each toad, we calculated daily movement distances and turning angles, and then resampled these data 1000 times over ndays to generate a resampled distribution of (scalar) displacements for days of movement between 1 and 160 days. Combining these resampled distributions across all toads gave us the population-level distribution of scalar dispersal distances. This distribution was well described by a 2-dimensional (bivariate) radially symmetric t-distribution (Gosset 1908). The 2D-t-distribution has a shape parameter that allows a smooth transition between Cauchy (thick-tailed) and Gaussian expectations, and a scale parameter analogous to Gaussian variance. To fit this radially symmetric 2D distribution to the scalar resampled displacement data, we first expressed the distribution in terms of absolute displacement, z (as opposed to distances in x and y), and then, bearing in mind this summarizes expectations over increasingly large areas, divided by $2\pi z$ (the rate that the area increases with radius: Lewis *et al.* 2006). The resulting (1D) probability density function for absolute displacement is:

$$K_{1D}(z) = zu^{v}v\sqrt{\frac{v^{v}}{(u^{2}v + z^{2})^{(2+v)}}} \qquad \text{eqn 5}$$

where u and v are shape and scale parameters, respectively. We used maximum likelihood to estimate values of u and v for each n-wise convolution of the toads' daily displacement kernel. These values were then used to parameterized the 2D version of the kernel $[K_{2D}(z)]$ required for the spread model.

ESTIMATING r AND $\hat{C}$

The toad-waterbody detection radius, r, and mean number of potential colonists emitted per waterbody, $\hat{C}$, influence the total number of colonists received by uncolonized waterbodies. These two parameters, along with the spatial configuration of all waterbodies and the scale and shape of the dispersal kernel should therefore determine the spread rate of toads during simulation. As these parameters are difficult to measure directly in the field, we estimated them from observed spread data from a previously colonized region of northern Australia, the semi-arid Victoria River District (VRD) in the Northern Territory, an area that receives a similar number of rainy days to that of our study site. Thirty waterbodies were surveyed repeatedly from 2006 to 2010 (M.L. unpublished data), enabling us to determine which year toads arrived at each waterbody. By seeding this landscape with known toad presences, and then running the model forward in time over the landscape under different values of r and $\hat{C}$, we were able to find values for these parameters that fit the data well. To formalize this process, we estimated these model parameters in an approximate Bayesian framework (Beaumont, Zhang & Balding 2002; Csilléry *et al.* 2010). This involved drawing values of r and $\hat{C}$ randomly from a uniform distribution [for r: U(10^1, 10^3), and for $\hat{C}$: U(10^3, 10^6)], using the drawn value to parameterize the model, calculating the number of sites for which the model correctly predicted the arrival time, storing the parameter values and prediction accuracy, and then repeating this procedure half a million times. Keeping only those values of r and $\hat{C}$ which gave us a close fit to the data, we obtained the approximate posterior probability of different values of r and $\hat{C}$.

RUNNING THE MODEL ON THE KIMBERLEY-PILBARA CORRIDOR

Once we had estimated the n-wise dispersal kernel, r, and $\hat{C}$, we were able to run the forward-time model across the corridor of waterbodies connecting the Kimberley region to the Pilbara. Our initial conditions assumed the Kimberley had been fully colonized and that toads were about to move down into the Pilbara corridor. We considered the corridor to be successfully traversed if toads reached the De Gray River at the southern end of the corridor (see Fig. 1). We first ran the model assuming only natural waterbodies were available, and then allowed both natural and artificial waterbodies to be available. In each case we produced 1000 model runs, each using a value of r and $\hat{C}$ drawn from their estimated distributions. Each model ran until either 100 years had elapsed, or the De Gray River had been colonized.

We then attempted to estimate the extent to which preventing toads from colonizing a subset of artificial waterbodies would halt their spread. Even though the number of waterbodies is relatively small ($n = 430$ artificial waterbodies), the number of potential combinations of these waterbodies is vast. We therefore required a heuristic to determine the likely best places to exclude toads from artificial waterbodies. Assuming that it is impossible (or at least undesirable) to remove natural waterbodies, our first question was where along the corridor we observe the lowest densities of natural waterbodies. To estimate this, we first ran a polynomial smoother through the corridor and then estimated the density of waterbodies (natural, artificial, and combined) along this line using a modified kernel density estimation technique.

This analysis revealed three regions with very low densities of natural waterbodies that might therefore, with the exclusion of toads from artificial waterbodies, act as barriers to the spread of toads (see Fig. 2). Following the identification of these three regions, we removed in a stepwise manner an increasing number of their nearest neighbours to estimate the minimum number of waterbodies that would need to be removed in these areas to halt the spread of toads. At each step, we generated 1000 simulated toad invasions and scored how many of these resulted in colonization of the Pilbara. To account for uncertainty in our estimates of

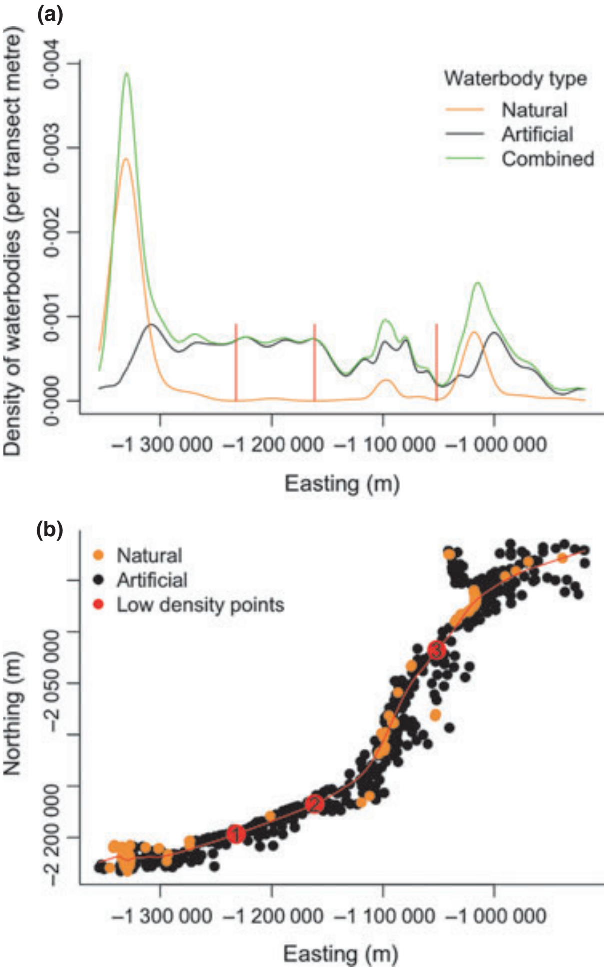

Fig. 2. Densities of natural and artificial waterbodies along the Kimberley-Pilbara corridor in Western Australia (a), and locations of potential barriers to the spread of cane toads (b and red lines in a). In the lower panel, point one corresponds to the 'western barrier', point two to the 'central barrier' and point three to the 'eastern barrier'.

r and $\hat{C}$, each realization used a value drawn at random from the distribution of these parameters estimated using ABC. Simulations were run using R© 2.13.0 (R Development Core Team 2011).

Results

THE DISPERSAL KERNEL

The 2D t-distribution described the resampled dispersal data over varying numbers of days well (Fig. 3), in particular capturing the strong shift in kurtosis with ndays (at small ndays, the kernel is strongly kurtotic, but becomes increasingly Gaussian as ndays increases). While the n-wise convolution has no simple analytical form, it was straightforward to fit the kernel to each n-wise convolution of the resampled data. When daily displacement data were resampled across individuals, the kernel fit steadily increased in scale, and rapidly approached Gaussian shape ($v \rightarrow \infty$), as expected under convolution. However, for the purposes of the current modelling, we wished to take into account the effects of individual variation. When displacements were resampled within each individual's data, the kernel fit to the resulting distribution over individuals asymptoted to a fatter-tailed distribution than Gaussian, close to the Cauchy form at $v = 1$ (Fig. S2, Supporting Information).

ESTIMATING *R* AND $\hat{C}$

Our priors for r and $\hat{C}$ were based on expert opinion: a rough guess as to the range at which toads might be able to detect water (10–1000 m), and a rough estimate of the number of potential colonists that might emerge from a waterbody (10^3–10^6). To express our uncertainty over this expert opinion we used uniform priors within these ranges. Drawing from these pri ors, half a million model runs over the VRD landscape yielded 10 runs in which the observed timing of colonization was perfectly re-created, and an additional 358 runs in which the observed colonization differed by only a single waterbody per year. We took the values of r and $\hat{C}$ from these 368 perfect and near-perfect runs as a sample of the posterior distributions for r and $\hat{C}$. A *post hoc* correction of r and $\hat{C}$ values of the 358 imperfect runs was undertaken following the approach of Beaumont, Zhang & Balding (2002) using linear regression. Given the small variance in our test statistic, we calculated regression coefficients for the correction step from a wider range of our test statistic than that used to define the retained subset (all runs within seven waterbody years of the observed data).

The resulting posterior samples for r and $\hat{C}$ were tightly correlated on a log-log scale (see Fig. S3, Supporting Information), as might be expected given that they co-parameterize the number of colonists received by a waterbody (see Discussion). This correlation precludes us making inference on either of these parameters in isolation (i.e. an increase in r can be countered perfectly by a

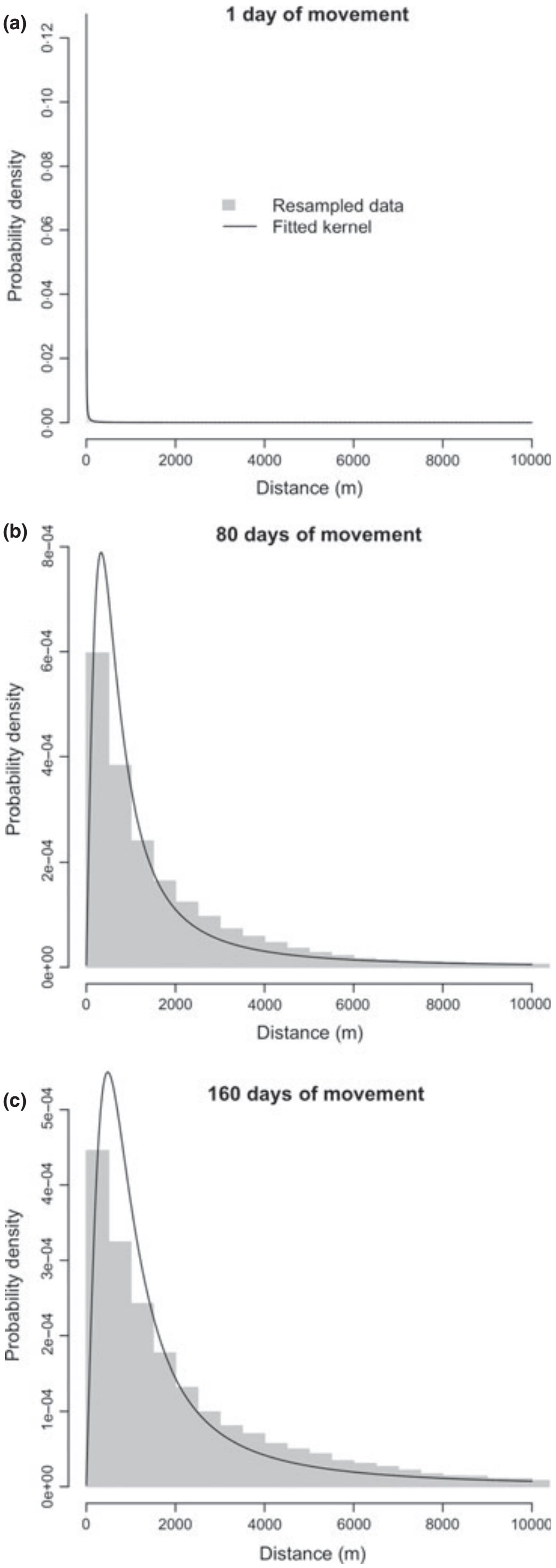

Fig. 3. Resampled distribution of daily displacements of cane toads for 1 (a), 80 (b), and 160 (c) days of movement. The density curves in each panel show the fit of the 2D t-distribution to the resampled distributions.

decrease in $\hat{C}$ to yield an identical rate of spread). It does not, however, preclude us from using the fitted model to estimate invasion dynamics. Thus, for simulations that follow, we fixed r at 100 m, and used the expected posterior of $\hat{C}$ given that value of r.

TOAD SPREAD THROUGH THE KIMBERLEY-PILBARA CORRIDOR

We then used our estimate of $\hat{C}|r$ and the dispersal kernel parameters to address the spread of toads along the Kimberley-Pilbara corridor. This exercise suggested that, unchecked, toads would almost certainly colonize the Pilbara within 100 years (all of 1000 model runs resulted in colonization), and that they would do so in 13–51 years (mean predicted time = 25 years; Fig. 4).

We then asked whether toads would be capable of spreading along this corridor if they could not access artificial waterbodies. To do this, we only included natural waterbodies in the simulated landscape. This exercise demonstrated that toads would be very unlikely to move through the Kimberley-Pilbara corridor if they could only rely on natural waterbodies: none of one thousand replicates resulted in colonization (Fig. 5).

CREATING A BARRIER TO TOAD SPREAD: IDENTIFYING AND TESTING THE REMOVAL OF KEY ARTIFICIAL WATERBODIES

By estimating the density of natural waterbodies along the Kimberley-Pilbara corridor, we identified three potential barrier points. The most eastern of these is near the location at which toads naturally stopped in most simulations where all artificial waterbodies were removed from the landscape (see Fig. 5). The other two localities had an almost equally low density of natural waterbodies (Fig. 2).

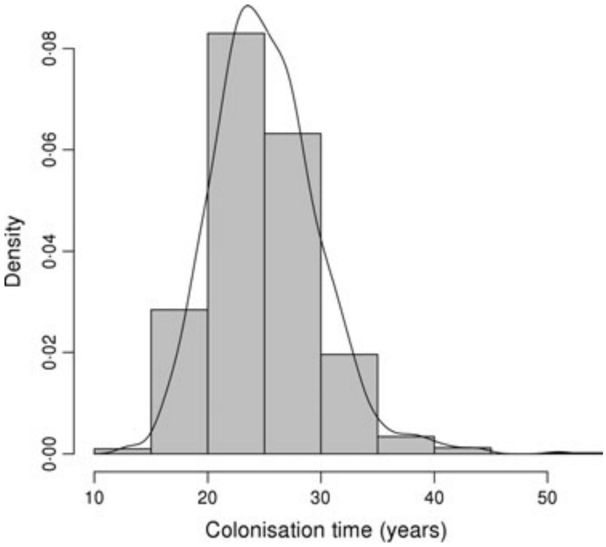

Fig. 4. Distribution showing the estimated number of years that it would take cane toads to colonize the Pilbara across 1000 simulations of spread.

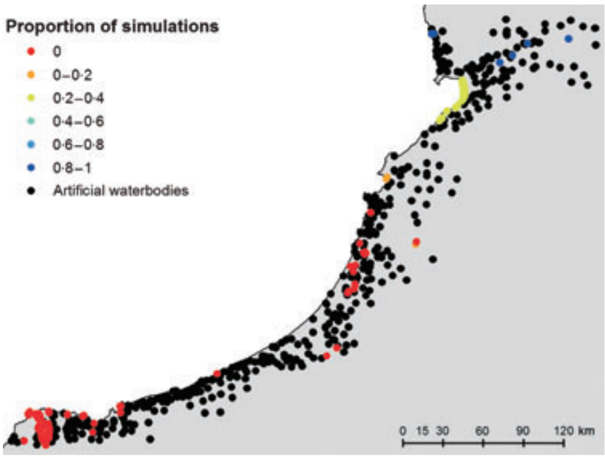

Fig. 5. Map showing the proportion of simulations (n = 1000) in which toads were able to colonize natural waterbodies along the Kimberley-Pilbara corridor in the absence of artificial waterbodies.

Removing artificial waterbodies around each of these candidate barrier points (Fig. S4, Supporting Information) reduced the probability of toads traversing the corridor (Fig. 6). However, the three barriers were not equally effective: some required the removal of a greater number of artificial waterbodies. A central barrier located south of Eighty Mile Beach (Fig. 2) had the greatest effect on colonization probabilities. The western and eastern barrier points required the removal of similar numbers of artificial waterbodies and were generally less effective. Nevertheless, the exclusion of toads from 100 artificial waterbodies at any one of the three barriers reduced colonization probabilities to less than 0·07 (0·065, 0·028, 0·068 for the western, central, and eastern barriers, respectively) over 100 years. Incorporating an uncharacteristically wet year every three decades slightly reduced the effectiveness of all

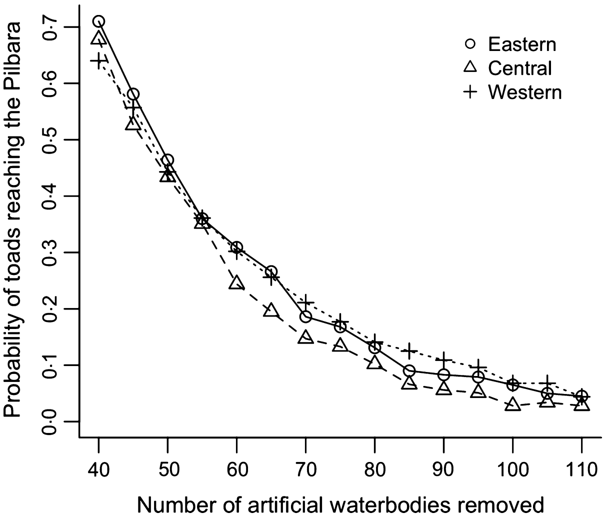

Fig. 6. Probability of cane toads reaching the Pilbara as a function of the number of artificial waterbodies removed at three dispersal barriers. Barriers correspond to those shown in Fig. 2(b).

three barriers, particularly when smaller numbers of waterbodies were removed (Fig. S5, Supporting Information). The effect of wet years on colonization probabilities was also generally greater for the central barrier. However, overall, simulating occasional unusually wet conditions did not qualitatively change any of our conclusions.

Discussion

Our results clearly demonstrate that artificial waterbodies will facilitate the spread of cane toads throughout the Kimberley-Pilbara corridor by allowing toads to establish satellite populations. When artificial waterbodies were present in the simulated landscape, toads were predicted to colonize the Pilbara within decades. In contrast, toads were unable to colonize the Pilbara in the absence of artificial waterbodies in all of our simulations. Excluding toads from artificial waterbodies resulted in the establishment of a stable range limit over 300 km north-east of the Pilbara's De Gray River, and would prevent toads from colonizing *c.* 268 200 km^2 of the range matching their fundamental niche in Western Australia (Fig. 1). A previous analysis that used biophysical predictions of the maximum dispersal potential of toads also suggested that artificial waterbodies could potentially provide greater landscape-level connectivity for toads in arid areas (Florance *et al.* 2011). Here, we modelled the dynamics necessary to test that prediction: we show that a high density of artificial waterbodies can allow a population of toads to spread through a landscape that would otherwise be unsuitable. The corollary is of course that by disrupting this artificial landscape, we can halt the spread of toads.

Although the results of our simulations with and without artificial waterbodies are encouraging, excluding toads from every artificial waterbody along the Kimberley-Pilbara corridor is likely financially unfeasible. Where then might we most efficiently allocate limited resources to control the spread of toads? By estimating the density of natural waterbodies along the corridor, we identified three regions where 'waterless' barriers could be created to halt the spread of toads into the Pilbara. Importantly, excluding toads from only 100 artificial waterbodies at any one of these three barriers substantially reduced colonization probabilities. Our analyses thus provide strong evidence that excluding toads from a subset of artificial waterbodies could be sufficient to halt the toads' invasion of the Pilbara. Our uncertainty around estimates of $\hat{C}$ together with our assumption of contiguous rainfall means that it is likely that removal of fewer than 100 waterbodies would, in fact be very effective, but more accurate data on toad spread rates and rainfall patterns would be needed to assess this possibility.

Most artificial waterbodies in the study area reside on leasehold lands used for pastoralism, and thus complete removal of even a subset of waterbodies would involve the closure of productive rangelands, requiring financial compensation for land owners. Given this constraint, how could we prevent toads from accessing artificial waterbodies? One option would be to manually remove toads in the dry season when toads are concentrated at waterbodies. However, this method is unlikely to be a feasible long-term solution given the dispersal ability (Phillips *et al.* 2007) and reproductive potential of toads (Lever 2001), as well as the failure of community efforts to stop toads using manual removal (Shine 2010; Somaweera & Shine 2012). A more effective strategy might be to enclose waterbodies with toad exclusion fences that do not prevent livestock from accessing drinking water (Fig. S1a, Supporting Information). Florance *et al.* (2011) demonstrated such fences could be used to eradicate satellite populations of toads at artificial waterbodies with negligible impacts on native species (see also Wingate 2011). Alternatively, existing artificial waterbodies could be replaced with above-ground tanks (Fig. S1b, Supporting Information) that provide livestock with water via gravity-fed troughs (Florance *et al.* 2011). Above-ground tanks made of plastic or steel are also more cost-effective reservoirs for bore-pumped water than earthen dams because they lose less water through seepage and evaporation. Thus, long-term savings could more than recoup the initial investment necessary to switch from dams to tanks. Finally, it should be borne in mind that because toads do not adversely impact pastoralists, the implementation of toad exclusion systems would necessitate finance in perpetuity from conservation agencies and/or government.

Unfortunately, exercising any of these management strategies with complete effectiveness is likely to be impossible. For example, small numbers of toads can persist by rehydrating from the small quantities of water that are released from improperly sealed pipe joins and the leaks that frequently occur along the seams of tanks. Clearly, a cost-benefit analysis would be necessary before choosing amongst all possible strategies, which might also include temporary eradication of populations, or imposing dispersal barriers around specific sites; however, we stress that complete and permanent removal of key artificial waterbodies, coupled with monitoring around key natural waterbodies, will be the best strategy to prevent toads from colonizing the Pilbara.

Our modelling framework can be applied to any organism that relies on a critical resource with a patchy spatial distribution; however, further refinements to our approach would, of course, be possible. For example, an optimization algorithm might also be used that takes into account other variables, such as cost of closure of each waterbody, so as to optimize the problem on both biological and economic grounds. Both natural and artificial waterbodies could also be used to identify candidate barrier regions, either by pooling the two types of waterbodies, or by considering them sequentially. The latter strategy is particularly appealing because it could shift the focus from areas with a small number of natural waterbodies to those that would require the least management effort (because there are also few artificial waterbodies to remove). For example, the eastern barrier used in our simulations could be moved north-eastwards to capitalize on an area with a particularly low density of all waterbodies (Fig. 2). Here, however, our primary goal was to investigate the theoretical feasibility of excluding toads from waterbodies as a management strategy to halt their spread. It is clear that the globally optimal strategy for implementing this idea would require an analysis that incorporates societal, ecological and economic values as well as toad dispersal modelling. For example, from a purely ecological point of view, the strategy which excludes toads from as large a range as possible would be favoured, but the total balance of forces may dictate allowing spread to whichever front is most likely to be defensible.

Our model, although taking into account the spatial distribution of waterbodies, assumes that the quality of these waterbodies for toads is equal, on average. This assumption seems reasonable for artificial waterbodies given their reasonably homogenous size and design. However, in instances where environmental conditions are more heterogeneous, our approach could be extended to incorporate the suitability of habitat patches (e.g. the size of waterbodies, or habitat suitability estimated using species distribution models: Engler & Guisan 2009). The structure of the matrix surrounding habitat patches may also be important, not only in influencing occupancy, but also in determining rates of dispersal (Palmer, Coulon & Travis 2011). In our model, we accounted for the strong influence of precipitation on dispersal rates of toads by only allowing toads to disperse between waterbodies under humid conditions (Tingley & Shine 2011). Incorporating such environmental constraints on dispersal will be particularly critical for forecasting spread rates of invasive species in regions that lie outside of their native climatic envelopes (Phillips, Chipperfield & Kearney 2008). Our model also assumed that rainfall patterns were temporally clustered, and thus that toads could move continuously for the total number of wet days at each waterbody. This assumption was necessary because we lacked data on temporal variability in rainfall, but seems like a sensible approximation given that rainfall patterns along the Kimberley-Pilbara corridor are strongly seasonal (being monsoonal). Nevertheless, including temporal variation in rainfall in our model would reduce the number of contiguous days in which toads could disperse between waterbodies, resulting in lower colonization probabilities. Our estimates of the number of artificial waterbodies needed to be removed to create a dispersal barrier are therefore likely to be over-estimates and, thus, conservative.

Interestingly, in the process of estimating the posterior distributions of our key unknown parameters (the detection radius, r, and the mean number of colonists per waterbody, $\hat{C}$), we observed a clear correlation between these parameters on the log–log scale. This correlation suggested that the value of $\hat{C}r^2$ drives the spread rate, so large values of $\hat{C}$ can be offset by low values of r and *vice versa*. In situations where populations tend to grow from even very small numbers of colonists (as is certainly the case with cane toads), colonization can be described by a pulled ('Fisherian') wave in which the rate of spread is determined by a diffusion constant (describing dispersal) multiplied by the growth rate of the population (Fisher 1937; Barton & Turelli 2011). In our model, the population growth rate is driven entirely by the number of potential colonists multiplied by the detection radius (i.e. $\hat{C}r^2$). Thus, when applied to the landscape of the VRD, our model appears to approximate a classic pulled wave spread dynamic. This might be expected where the (stochastic) spatial distribution of waterbodies is sufficiently uniform. It is therefore reassuring that this emergent property of our stochastic model matches the deterministic expectation.

It is important also to note that the dispersal ability of toads has shown rapid evolution during their invasion across northern Australia. Toads from the invasion front disperse between 5 and 10 times faster than their conspecifics from old, long-established populations (Phillips *et al.* 2008; Alford *et al.* 2009). In fitting our model, we used dispersal data from invasion front toads given these are the toads that will first move down the Kimberley-Pilbara corridor. However, high dispersal is traded-off against other fitness traits, and so, once the invasion halts, dispersal rates should evolve back to much lower levels (as slower, fitter genes eventually catch up; Brown *et al.* 2007; Phillips 2012). Thus, if a barrier can halt the high dispersal phenotype of toads for a hundred years, and if we assume that toads will not adapt to a completely arid landscape, it will likely act as a barrier indefinitely.

The provision of artificial water sources for pastoralism, energy, recreation, and human consumption has dramatically transformed arid and semi-arid landscapes across the globe, allowing numerous invasive species to expand their geographic ranges (Havel, Lee & Vander Zanden 2005; Fensham & Fairfax 2008; Banks & Duggan 2009; Russell, Letnic & Fleming 2011). Our results suggest artificial waterbodies will facilitate the range expansion of invasive cane toads into the arid Pilbara region of Western Australia by enabling toads to establish satellite populations in an otherwise inhospitable landscape. More importantly, our findings provide compelling evidence that selective removal of a subset of artificial waterbodies along the Kimberley-Pilbara corridor would halt the spread of toads into the ecologically unique and environmentally sensitive Pilbara region. This would help secure populations of numerous endemic (e.g. *Varanus panoptes rubidus*, *Acanthophis wellsi*) and endangered (e.g. *Dasyurus hallucatus*) anurophagous predators that are extremely vulnerable to the toad's toxin (Shine 2010) and should therefore be considered a top management priority.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Examples of an artificial waterbody and plastic water tank found throughout northern Australia.

Fig. S2. Parameters of the resampled distributions of daily displacements of radiotracked cane toads.

Fig. S3. Relationship between r and $\hat{C}$ from model runs in which the observed timing of colonization of waterbodies in the Victoria River District, Australia was closely re-created.

Fig. S4. Map of the Kimberley-Pilbara corridor in Western Australia illustrating the 100 artificial waterbodies surrounding each of three potential barrier points that were removed in our simulations.

Fig. S5. Difference between the probabilities of cane toads reaching the Pilbara under unusually wet versus average conditions as a function of the number of artificial waterbodies removed at three dispersal barriers.

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Cost and feasibility of a barrier to halt the spread of invasive cane toads in arid Australia: incorporating expert knowledge into model-based decision-making

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Summary

1. Active engagement with practitioners is a crucial component of model-based decision-making in conservation management; it can assist with data acquisition, improve models and help narrow the 'knowing–doing' gap.

2. We worked with practitioners of one of the worst invasive species in Australia, the cane toad *Rhinella marina*, to revise a model that estimates the effectiveness of landscape barriers to contain spread. The original model predicted that the invasion could be contained by managing artificial watering points on pastoral properties, but was initially met with scepticism by practitioners, in part due to a lack of engagement during model development.

3. We held a workshop with practitioners and experts in cane toad biology. Using structured decision-making, we elicited concerns about the original model, revised its structure, updated relevant input data, added an economic component and found the most cost-effective location for a barrier across a range of fixed budgets and management scenarios. We then conducted scenario analyses to test the sensitivity of management decisions to model revisions.

4. We found that toad spread could be contained for all of the scenarios tested. Our modelling suggests a barrier could cost \$4·5 M (2015 AUD) over 50 years for the most likely landscape scenario. The incorporation of practitioner knowledge into the model was crucial. As well as improving engagement, when we incorporated practitioner concerns (particularly regarding the effects of irrigation and dwellings on toad spread), we found a different location for the optimal barrier compared to a previously published study (Tingley *et al*. 2013).

5. *Synthesis and applications*. Through engagement with practitioners, we turned an academic modelling exercise into a decision-support tool that integrated local information, and considered more realistic scenarios and constraints. Active engagement with practitioners led to productive revisions of a model that estimates the effectiveness of a landscape barrier to contain spread of the invasive cane toad *R. marina*. Benefits also include greater confidence in model predictions, improving our assessment of the cost and feasibility of containing the spread of toads.

Key-words: artificial waterbodies, containment, cost-efficiency, engagement, knowing–doing gap, point process, *Rhinella marina*, spread model, stakeholders, structured decision-making

Introduction

Humans are poor at making unsupported decisions about complex problems (Kahneman & Tversky 1984), particularly when those problems are highly dimensional, probabilistic, stochastic and/or dynamic (Tversky & Kahneman 1974; Sternberg 2003). Conservation decision-making is always complex, involving trade-offs between social, economic and environmental values, each interacting, uncertain and individually complex elements (Ludwig, Mangel & Haddad 2001; Burgman, Lindenmayer & Elith 2005). Given this inherent complexity, humans can be poor at making sensible unsupported decisions around conservation management.

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Quantitative modelling and decision analysis can, however, provide important decision support. These tools help avoid common biases that undermine human judgment, and can explicitly incorporate uncertainty and constraints into decision-making (Akcakaya, McCarthy & Pearce 1995; Burgman 2005). Quantitative models aim to provide predictions about how an environmental system might behave in the future in response to competing management alternatives (Akcakaya, McCarthy & Pearce 1995; Burgman 2005). Models can simulate outcomes of management when on-ground experiments are difficult due to economic, social, ethical or ecological constraints; they can improve transparency, defensibility and repeatability of conservation decisions (Starfield 1997; Burgman & Yemshanov 2013); and they can identify important knowledge gaps for further research.

Advances in computational power, data availability and ecological theory have enabled evermore complex models of ecological systems. Despite this enhanced capacity, an important exercise often neglected by modellers during model development is practitioner engagement (Fulton *et al.* 2013; Wood, Stillman & Goss-Custard 2015). Practitioner engagement can benefit conservation decision-making by: (i) reducing conflicts between modellers and practitioners (Elston *et al.* 2014); (ii) facilitating a collective understanding of management problems, objectives and constraints (Sandker *et al.* 2010; Biggs *et al.* 2011); (iii) improving the representation and conceptualization of the study system (practitioners often have greater knowledge of the system being modelled; Nichols *et al.* 2007); and (iv) providing modellers with access to the most relevant data (practitioners generally have knowledge of unpublished data and literature).

Close collaboration also gives practitioners an increased awareness of, and trust in, model predictions. However, quantitative models remain underutilized by practitioners (Cowling *et al.* 2003; Knight *et al.* 2008), who often rely on unstructured subjective judgment, intuition or personal experience to make conservation decisions (Pullin & Knight 2005; Cook, Hockings & Carter 2010). This ‘knowing–doing gap’ (Knight *et al.* 2008) is partly the result of practitioners’ perceptions of models as expensive, unrealistic, or poorly constructed, parameterized or validated (Wilkerson, Wiles & Bennett 2002; Hajkowicz 2007), or due to lack of communication by modellers during or after model development (Addison *et al.* 2013). As a result, conservation lags behind other fields such as fisheries and marine ecosystem-based management (Fulton *et al.* 2013) in adopting participatory, quantitative decision-making methods.

In this study, we actively engaged with landowners and practitioners to revise an existing model (Tingley *et al.* 2013), which predicted the effectiveness of a landscape barrier to halt the spread of one of Australia’s worst invasive species, the cane toad *Rhinella marina*. Cane toads rely on artificial watering points (AWPs) during the dry season to spread across arid regions of Australia (Florance *et al.* 2011). Tingley *et al.* (2013) suggested that managing AWPs to construct a ‘waterless barrier’ might halt the invasion front and prevent toads from invading an additional 268 000 km^2 of their potential range. However, the model was met with scepticism from some practitioners, in part due to a lack of engagement between modellers and practitioners during model development. Debate centred on whether a barrier would be feasible given the assumptions in the model, undermining support for the best locations identified by Tingley *et al.* (2013).

The aim of this study was to identify and address landowners’ and practitioners’ concerns relating to the science, assumptions and data underpinning the model, to enable improved, model-based decision support. To achieve this aim, we sought to: (i) actively engage with landowners and practitioners to elicit concerns towards the Tingley *et al.* (2013) model; (ii) update model parameters using more relevant data agreed upon by both modellers and practitioners during engagement; and (iii) use a revised model to identify the most cost-effective barrier location, and assess whether that location is robust to ecological and economic uncertainty. By engaging with practitioners, we sought to improve their understanding of the model and its assumptions, gain feedback and incorporate their expert knowledge, and test the sensitivity of management decisions to this knowledge, while improving our assessment of the cost and feasibility of a cane toad barrier.

Materials and methods

STUDY SYSTEM AND SPECIES

Cane toads are one of Australia’s most ecologically destructive invasive species. Since their introduction in 1935, they have spread rapidly across more than 1·2 million km^2 of Australia (Urban *et al.* 2007), causing declines in populations of many native predators (Shine 2010). The toads are predicted to continue spreading throughout coastal regions of tropical and subtropical Australia (Tingley *et al.* 2014), and have now reached the Kimberley region of north-western Australia (Fig. 1). Biophysical and dispersal modelling suggests that toads will continue to spread south into Western Australia (WA; Kearney *et al.* 2008; Florance *et al.* 2011; Tingley *et al.* 2013), threatening numerous endangered and endemic species that are naïve to the toad’s toxin.

In the Australian arid zone, cane toad activity during the dry season is restricted to permanent waterbodies such as springs, perennial water courses and AWPs (Florance *et al.* 2011; Letnic *et al.* 2014). AWPs are constructed by pastoralists to make the landscape more suitable for cattle, and include circular dams (~30 m in diameter) and tanks fed by bores. Excluding toads from AWPs by erecting toad-proof fences around their perimeter or by replacing AWPs with toad-proof tank/trough systems may limit the establishment of populations (Florance *et al.* 2011; Letnic *et al.* 2015) and halt further spread of the invasion front if conducted across a large enough area (Tingley *et al.* 2013).

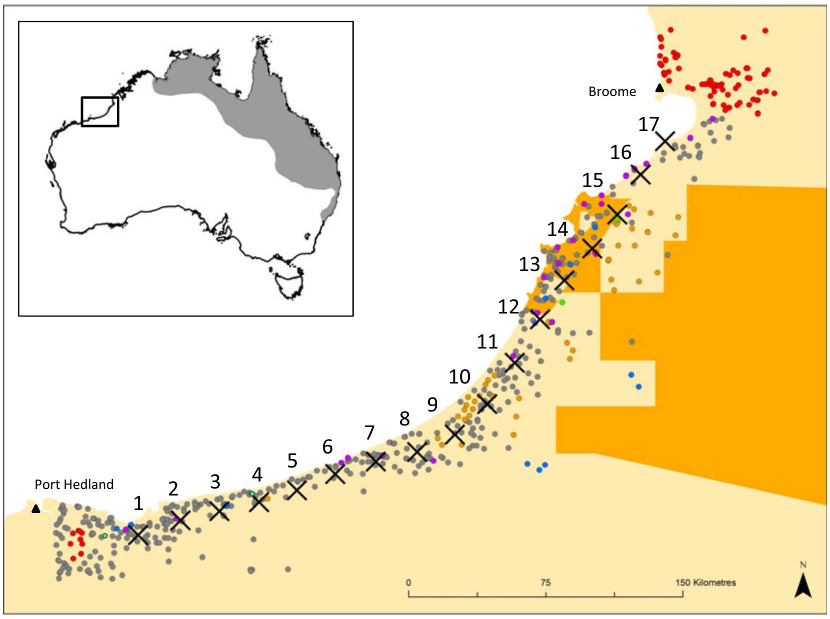

Fig. 1. Locations of dams (orange dots), tanks (grey dots), permanent natural waterbodies (blue dots), dwellings (purple dots) and irrigation (green dots) in the Kimberley–Pilbara corridor in north-western Australia. Waterbodies assumed to be colonized at the start of simulations are shown as red dots in the north of the corridor near Broome. The De Grey River (red dots near Port Hedland in the south) was used as the endpoint of all simulations. The Indigenous Protected Area (IPA) is shown with orange shading, within which AWPs will likely be decommissioned independently of the barrier. Barriers were simulated at 17 equally spaced locations within the corridor (black crosses). Insert map shows the location of the corridor in Australia and the approximate current distribution of toads (grey shading).

MODELLING A TOAD BARRIER

Tingley *et al.* (2013) tested the theoretical feasibility of a 'waterless barrier' to contain the spread of cane toads using a spatial spread model. Their model assumed that toads disperse freely during wet periods when conditions are humid and temporary waterbodies are numerous. Come the dry season, however, toads need to take refuge at permanent waterbodies, or perish. The model simulated the spread of toads using information about the locations of permanent waterbodies and data on the dispersal ability of toads in response to rainfall. The density D of potential colonizing toads at any location m depended on: (i) the toads' rainfall-dependent dispersal kernel $K_i(d_{im})$ and the distance between the location and each occupied waterbody d_{im}; and (ii) the number of potential colonizers emanating from occupied waterbodies C_i, given by:

$$D_m = \sum_{i=1}^{n} C_i K_i(d_{im}) \qquad \text{eqn 1}$$

where n is the total number of occupied waterbodies. Tingley *et al.* (2013) assumed that toads can detect waterbodies within a radius r_d of 100 m; that a waterbody is colonized if two or more toads arrive in a single generation; that the population at a colonized waterbody reaches carrying capacity instantaneously; and that toads disperse from colonized waterbodies the season following colonization.

The total number of days per year that toads could disperse from each waterbody (N) was a function of the number of rainy days at that location, based on the rate at which surface water is likely to evaporate in this landscape:

$$N = x + 3(x)\left(1 - \left(3(w - w^2) + w^3\right)\right) \qquad \text{eqn 2}$$

where x is the average number of rainy days (>1 mm between 1961 and 1990) at each waterbody and $w = (x - 1)/364$. To determine the dispersal kernel for toads at each waterbody, data on the movement of 114 radiotracked toads were used to generate a resampled distribution of scalar displacement for days of movement between 1 and 180 days. Dispersal was well described by a two-dimensional t-distribution:

$$K_{ID}(z) = zu^v v\sqrt{\frac{v^v}{(u^2 v + z^2)^{(2+v)}}} \qquad \text{eqn 3}$$

where z is absolute displacement and u and v are shape and scale parameters of a t-distribution, respectively.

Using this model, Tingley *et al.* (2013) predicted the effectiveness of a barrier positioned at three locations in an arid region between the Kimberley and the Pilbara in north-western Australia, approximately 650 km ahead of the invasion front where there is a natural 'bottleneck' in the availability of surface water (hereafter referred to as the corridor; Fig. 1). They found that the spread of toads through this area could be contained by managing as few as 110 AWPs. Further details and justifications are described in Tingley *et al.* (2013).

UPTAKE OF THE MODEL

Several NGOs and state and federal government agencies expressed interest in the idea of a barrier, but some practitioners were concerned about the reliability of model predictions. This scepticism impeded any further assessment or implementation of a barrier, and was partly because the model was developed by experts in cane toad biology without consultation with practitioners and land managers at the proposed barrier locations. Below we describe how we actively engaged with local practitioners to elicit and address concerns towards the model, and how we used a revised model to assess the cost–benefit of a proposed barrier scheme.

ELICITING EXPERT AND LOCAL KNOWLEDGE

We held a 1-day workshop in Broome, WA (Fig. 1), to: (i) discuss the feasibility of a toad barrier; (ii) better understand practitioners' concerns towards the model; and (iii) incorporate their knowledge of toad biology and of the corridor into the model.

The workshop was attended by 24 practitioners and experts in cane toad biology from universities, state and federal government agencies, indigenous ranger groups, community groups and NGOs.

We ran the workshop using structured decision-making, which involved systematically evaluating the problem, management objective, alternative actions and sources of uncertainty (Gregory *et al.* 2012). There was widespread agreement that a barrier is the most promising strategy to contain toad spread in the corridor. We presented the model, explaining its capabilities, assumptions and limitations using visual aids. We then elicited all of the concerns towards the model and asked practitioners to identify which three concerns should be addressed to improve predictions (three votes were assigned to the most important concern, two to the second-most important and one to the third-most important). In order of importance, workshop attendees ranked the following concerns:

1. verifying the accuracy of waterbody data and modelling other potential refuges (35 votes);
2. incorporating a cost component, particularly incorporating ongoing costs (14 votes);
3. incorporating more recent rainfall data with temporal and spatial variation (11 votes).

Following the workshop, we updated the original model to address these concerns, described in detail below.

REVISING THE MODEL

Improving the accuracy of waterbody data

Workshop participants were concerned about the accuracy of waterbodies (both artificial and natural) in the original model, collated from a single source (Geoscience Australia mapping; http://www.ga.gov.au/meta/ANZCW0703008969.html). To improve the reliability of waterbody locations, we augmented the original data with data from the Department of Water, WA, and the Department of Agriculture and Food, WA. Data are available upon request from these two agencies. We screened our augmented data set for duplicates and classified each waterbody as a dam (an open man-made reservoir), tank or permanent natural waterbody.

To verify our augmented waterbody data set, we then conducted face-to-face interviews with 10 of the 12 private land managers in the corridor (two were unavailable). We presented each manager with a map of their property and asked them to verify the location, type and status of each waterbody. This process identified 566 waterbodies in the corridor (0·037 per km^2), 44 fewer than identified by Tingley *et al.* (2013).

Workshop attendees and land managers were concerned that toads may seek refuge at locations in the corridor other than permanent waterbodies, such as irrigated areas and dwellings (e.g. homesteads, resorts, roadhouses). We therefore mapped all dwellings (n = 26) and irrigated areas (n = 4) in the corridor after consulting land managers. Irrigated areas were grouped into two categories: horticulture (n = 1) and hay production (n = 3). The detection radius and number of colonists emanating from these points were modified to account for their larger area compared with AWP (see Appendix S1 in Supporting Information).

The workshop also identified AWPs that, although mapped, may not contribute to the future spread of toads. In particular, an Indigenous Protected Area (Karajarri IPA) was recently established in the north of the corridor (Fig. 1). An IPA is a class of protected area formed in agreement with, and managed by, Indigenous Landholders. We consulted the Kimberley Land Council to identify which AWP within the Karajarri IPA will likely be decommissioned and thus not contribute to the future spread of toads.

Incorporating cost

Practitioners viewed cost as a crucial factor influencing the feasibility of a barrier, believing the cost of the barrier to be prohibitive. We therefore added a cost estimation component to the model using information from published reports and local experts (Table 1). Further model assumptions of our revised model included the following:

- Toads could be excluded from AWPs but not from natural waterbodies or dwellings (we call this the 'most likely' scenario, although we tested the sensitivity of these assumptions). To exclude toads from AWPs, we assumed existing dams and tanks would be replaced by leak-proof tanks.
- Toads could be excluded from the single horticultural area by erecting a permanent fence around its perimeter; erecting fences around waterbodies results in toad death within 3–4 days during the dry season (Florance *et al.* 2011; Letnic *et al.* 2015).
- For the three hay production areas, toads could be controlled by foregoing one harvesting cycle each year, preventing toads from accessing water for a period that exceeded their dehydration tolerance.
- The surveillance cost for AWPs is negligible because tanks are already checked by pastoralists every 1–3 days.
- Waterbodies managed as part of a barrier had a small chance of failing in each time step; those that failed were assumed to contribute to one generation of spread before being detected and repaired by the start of the next time step. No information was available on the failure rate of managed AWPs. We therefore chose a conservative failure rate of 5% and conducted a sensitivity analysis on this parameter (Fig. S3).

The cost C (net present value) of managing n waterbodies in the corridor was given by:

$$C = \sum_{i=1}^{n} \left(I + \sum_{t=1}^{T} \left(M + \frac{R}{L} \right) (1 - \delta)^t \right) \qquad \text{eqn 4}$$

where I is the installation cost, M incorporates ongoing annual maintenance and surveillance costs (visiting AWP to monitor and repair leaks), R is replacement cost, L is the life span of the infrastructure, δ is the rate of time-discounting (set at 2·5%) and t is time. The length of the management programme, T, was set to 50 years. Installation, maintenance and replacement costs were functions of travel costs, labour and materials (Table 1). All costs are given in 2015 Australian dollars.

Refining dispersal data

Tingley *et al.* (2013) assumed that toad dispersal was a function of the average number of rainy days (>1 mm) recorded at waterbodies from 1961 to 1990. Workshop participants were concerned that this did not account for the higher and more variable rainfall experienced in recent years. To account for both temporal and spatial rainfall variability, we extracted the number of rainy days (>1 mm) at each waterbody for each year between 1990 and 2009

Table 1. Summary of cost parameters. All monitoring and maintenance costs are subject to a 2·5% interest rate

Waterbody type	Action	Installation (I) and Replacement (R)	Monitoring and maintenance (M)	Life span (years)	Source
Artificial (AWP)	Install leak-free tank	Travel costs ($1·50/km from Broome or Port Hedland) Labour (32 h at $100/h) Materials ($8500)	Travel costs ($1·50/km from Broome or Port Hedland) Labour (8 h at $100/h) Materials ($500)	50	Workshop attendees Land managers
Horticulture	Erect fence	Travel costs ($1·50/km from Broome or Port Hedland) Labour (32 h/100 m at $100/h) Materials ($3000/100 m × perimeter)	Labour (8 h at $100/h × 26 weeks) Materials ($100)	10	Brook, Whitehead & Dingle (2004) Shane Sercombe, Central Outback Contracting (pers. comm.)
Agriculture (Hay production)	Compensation	NA	$1650/ha × area (ha)	NA	Christopher Ham, Department of Agriculture and Food, WA (pers. comm.)

using 5-km gridded rainfall data from the Australian Water Availability Project (AWAP; Raupach *et al.* 2009) and cycled through this 20-year period during simulations (Fig. S1).

The dispersal kernel K_i used in the original model is long-tailed, which allowed toads to disperse infinite distances from colonized waterbodies (albeit with a small probability). Workshop participants identified this assumption as unrealistic, concluding that there is an upper limit to the distance toads can disperse in a given year. We therefore truncated and then renormalized the kernel at a distance of 55 km, the estimated annual advance of the invasion front in the Northern Territory between 2001 and 2006 (Phillips *et al.* 2007). While more accurate, this distance is still likely to overestimate the rate at which toads would spread through the corridor, as it was derived from the toads' advance through tropical Australia where environmental conditions are much more favourable (Tingley *et al.* 2014).

COST-EFFECTIVENESS AND SCENARIO ANALYSES

We first simulated the spread of toads through the corridor assuming no management using the revised model. We assumed that toads had colonized the Kimberley at the start of simulations (Fig. 1). We ran the model for 1000 iterations until either 50 years had elapsed or the De Grey River, located at the southern end of the corridor, had been colonized (Fig. 1).

We then found the most cost-effective location for a barrier across a range of fixed budgets. To do this, we centred a barrier at 17 equally spaced locations along the corridor (~20 km apart; Fig. 1). At each location, we created a barrier by sequentially removing the closest AWPs until a fixed budget was exhausted. Thirty budgets were tested, ranging from $200,000 to $6 M over 50 years. For each budget and barrier location, we assessed two management objectives: (i) minimize the probability that toads reached the De Grey River; and (ii) minimize the number of colonized waterbodies at the end of 50 years.

We ran the simulations described above using what workshop attendees considered the 'most likely' scenario, that is with an active IPA, with spatial and temporal variation in the number of rainy days at each AWP, a dispersal kernel truncation distance of 55 km, a failure rate of 5% and when only AWPs are managed. Workshop attendees agreed that while detection of toads at dwellings will likely be higher than at remote locations such as AWPs, eradication or even restricting their access to water at these locations would be next to impossible (Wingate 2011).

We also ran the model for a range of alternative landscape and management scenarios to test the sensitivity of barrier locations to key model revisions. Specifically, we ran three additional management scenarios: (i) both AWPs and dwellings were managed (although managing dwellings did not incur a cost); (ii) AWPs and irrigation were managed (with a cost for managing irrigation areas); and (iii) both irrigation and dwellings were not included in the data set.

Further sensitivity analyses were also conducted with an inactive IPA, on alternative failure rates (0%, 2·5%, 10%), on the truncation distance of the dispersal kernel and on the number of days that toads could disperse from waterbodies (Figs S2–S4). For example, we tested the robustness of a barrier location to extremes in rainfall by modelling a very dry landscape (toads could disperse from occupied waterbodies for 50 days each year), a very wet landscape (toads could disperse from occupied waterbodies for 180 days each year) and alternative truncation distances (30 and 78 km).

Results

DO NOTHING SCENARIO

Our model predicted that it could take 20·29 years (SD = 1·92) for toads to spread from the Kimberley to the De Grey River in the Pilbara in the absence of a barrier, which is approximately 4 years (16%) faster than predicted by Tingley *et al.* (2013). Toads spread faster in our model because we used updated rainfall data (with spatial and temporal variation) and incorporated dwellings and irrigation in the landscape. More recent rainfall data, in particular, allowed toads to disperse faster through the northern half of the corridor, where it was significantly wetter than assumed in the original model (Fig. S1). Modelling irrigation and dwellings also increased the rate of spread because these points produced more dispersers, were more easily detected by colonists compared with AWP (due to their larger area) and were relatively evenly distributed throughout the corridor. Toads reached the Pilbara in <32 years in the absence of a barrier for all of the scenarios tested (Fig. S4).

THE MOST COST-EFFECTIVE BARRIER LOCATION

The most cost-effective location for a barrier under the 'most likely' landscape scenario (where only AWPs are managed, but not dwellings or irrigation areas) was relatively insensitive to the available budget (Fig. 2a,c). Managers would have to spend ~$4·5 M over 50 years developing and maintaining a barrier ~80 km wide at location 10 or 11 to reduce the probability of toads reaching the Pilbara to <0·05. A barrier at these locations also minimized the number of waterbodies colonized after 50 years (Fig. 2e). A barrier positioned north of location 12 had little effect at containing the invasion front because toads could still spread via dwellings and/or irrigation.

In the scenario where toads were excluded from *AWP*s *and dwellings*, location 8 was the most cost-effective at containing the invasion front, followed by locations 7 and 9 (Fig. 3b,d). Again, managers would have to spend ~$4·5 M over 50 years to reduce the probability of toads colonizing the Pilbara to below 0·05. Barriers positioned north of location 11 or south of location 7 were relatively ineffective for this scenario because toads could still spread using irrigated areas as stepping stones.

When *AWP and irrigated areas* were managed, locations 9, 10 and 11 were most cost-effective, at a cost of, again, ~$4·5 M over 50 years (Fig. 3a,c). Location 11, followed by locations 10 and 9, minimized the number of waterbodies colonized after 50 years. When *both irrigation and dwelling*s were removed from the data set, the most cost-effective location for a barrier was location 17 in the far north of the corridor, followed by locations 16 and 5 (Fig. 2b,d).

Decommissioning AWPs *within the IPA*, changing the number of rainy days at each waterbody and truncating the dispersal kernel had a slight effect on the most cost-effective location for a barrier (Figs S2–S4). However, the absolute cost of a barrier was sensitive to changes in these parameters: a more expensive barrier was required when we assumed a wetter than expected landscape (180 days of movement), or a larger than expected truncation distance (78 km).

Similarly, the most cost-effective barrier location was insensitive to the choice of failure rate, unless management was assumed to be 100% effective (Fig. S3). The overall cost of a barrier did, however, increase with failure rate. For example, the model predicts that managers would need to spend ~$3·5 M on a barrier if the failure rate is 2·5%, but this amount increased to ~$9 M if 10% of managed AWPs failed each year.

Discussion

Decisions regarding the optimal location, size and configuration of barriers are complex and entail uncertainties (Bode & Wintle 2010). Our modelling, as a result of extensive practitioner consultation, suggests that toad spread through the Kimberley–Pilbara corridor in north-western Australia can be contained, even for scenarios with extremely high rainfall (180 days of toad movement) or a large truncation distance (78 km). A barrier positioned in the middle of the corridor (locations 10–12) was most cost-effective for scenarios including the revised AWPs, dwellings and irrigation. Our results confirm the importance of practitioner engagement during model development and analysis because local knowledge overlooked in the original incarnation of the model – specifically knowledge about irrigation and dwellings – influenced the best barrier location. Excluding these points from the analysis shifted the most cost-effective barrier location from the middle of the corridor to the far north (locations 16 and 17). The most cost-effective locations for all of our scenarios also differ to those reported by Tingley *et al.* (2013), partly because they tested a barrier at fewer locations, and partly because they did not explicitly incorporate expert knowledge of the corridor into the model.

Our results suggest that for the most likely scenario where only AWPs are managed, an investment of ~$4·5 M would reduce the probability of toads reaching the Pilbara to < 0·05 over 50 years. This is considerably less than the amount spent on other invasive species management programmes in Australia. For example, the Australian government recently spent $19 M on feral camels in central Australia over 4 years, and $35 M on the fox eradication programme in Tasmania over 8 years (Newsome *et al.* 2015). A toad barrier is relatively cost-effective (~$90,000 per year), because we found that most pastoralists have already converted open dams to tanks (due to aridity and soil drainage conditions), and because they already check their watering infrastructure every 1–3 days. These factors would substantially reduce upfront installation and ongoing maintenance costs. A toad barrier is not only cost-effective, but also has the potential to create a win–win situation for pastoralists and conservationists, because installing leak-proof tanks improves farm productivity, while simultaneously mitigating a key threatening process for biodiversity.

Practitioner engagement not only validated and refuted important data, but also led to more realistic model assumptions. For example, we truncated the dispersal kernel to eliminate long-distance dispersal. Although cane toads occasionally hitchhike on vehicles (White & Shine 2009), the probability of such dispersers establishing viable populations south of the barrier is extremely small because: (i) toads have external fertilization, making it impossible for lone dispersers to establish populations ahead of the invasion front; (ii) if more than one individual jumps ahead of the invasion front, they are likely to be of the same sex because sex ratios are highly skewed in

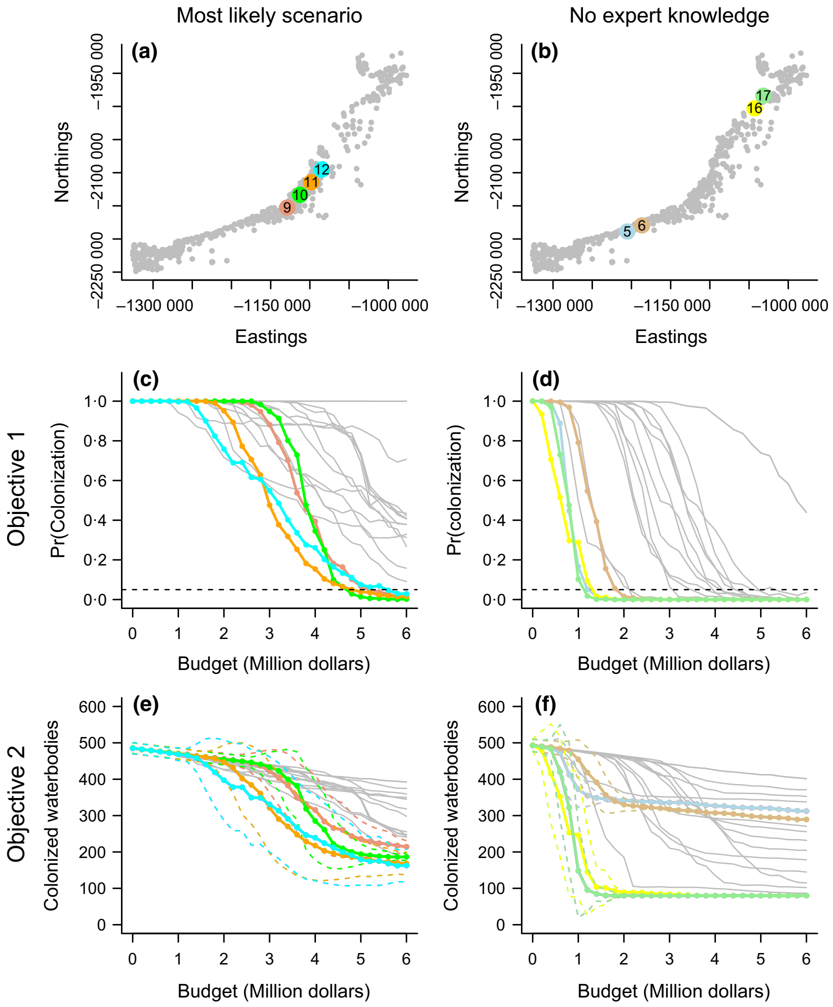

Fig. 2. The most cost-effective locations for a barrier in the Kimberley–Pilbara corridor with a truncation distance of 55 km, our best estimate of the number of rainy days, a 5% failure rate, and assuming only AWPs are managed. The left column (a,c, e) assumes the most likely management scenario with expert knowledge (irrigation and dwellings are modelled but not managed); the right column (b,d,f) ignores expert knowledge (irrigation and dwellings are not included in the waterbody data set). The top row (a,b) shows the locations of the best four barrier locations under objective 1. The probability of toads reaching the Pilbara for each of the 17 potential barrier locations across a range of fixed budgets is shown in the middle row (c,d). The number of waterbodies colonized after 50 years is shown in the bottom row (e,f). In figures (c–f), coloured lines represent the first four locations to fall below a 5% chance of toads colonizing the Pilbara. The corresponding position of these locations is shown in the top row (a, b). Dashed lines (e,f) represent standard errors from 1000 simulations.

space and time; and (iii) dispersal following transportation makes it unlikely that transported toads would find each other to breed. These arguments are backed up by the observation that despite billions of toads being present in Australia for over 80 years, and the relatively common detection of transported toads in densely trafficked parts of the country (i.e. major cities; White & Shine 2009), there have been very few accidentally seeded populations that have successfully established ahead of the front (Lever 2001). Nonetheless, post-barrier surveillance, quarantine and community education would obviously play important roles in minimizing the chance of long-distance dispersal across the barrier.

While there are various ways to engage practitioners, to date, there is little understanding of which approaches achieve and maintain collaboration (Wood, Stillman & Goss-Custard 2015). We adopted a structured decision-making approach, which is advocated in the conservation literature for explicitly acknowledging uncertainty, facilitating relationship building and revealing hidden agendas (Addison *et al.* 2013). There is no doubt that in this case, the engagement process, facilitated by structured decision-making, helped all parties agree on the problem and objective, while improving practitioners' understanding of the model's capabilities and limitations, as well as modellers' understanding of the landscape. The effect of engagement with practitioners on decision-making is often unclear: they may change their mind when provided with relevant information (Walsh, Dicks & Sutherland 2015) or maintain their original belief (McConnachie & Cowling 2013). An avenue of further research, although outside the scope of this study, would be to quantify how engagement influenced trust towards the model and its use as a decision-support tool.

Finally, engaging with practitioners revealed a number of practical considerations that could further clarify the feasibility of a barrier strategy. First, our model relies on the assumption that toads cannot survive between mapped waterbodies during the dry season. Fine-scale on-ground mapping of waterbodies and radiotracking toads at candidate barrier locations would provide useful tests of this assumption. Secondly, the failure rate had little effect on the most cost-effective barrier location unless managed AWPs can be kept completely leak-free. However, the failure rate did influence the overall cost of a barrier. Thus, further research is required to better understand how often managed AWPs leak enough water to sustain at least one toad throughout the dry season. One option to reduce the failure rate, should it be high, is to also erect toad-proof

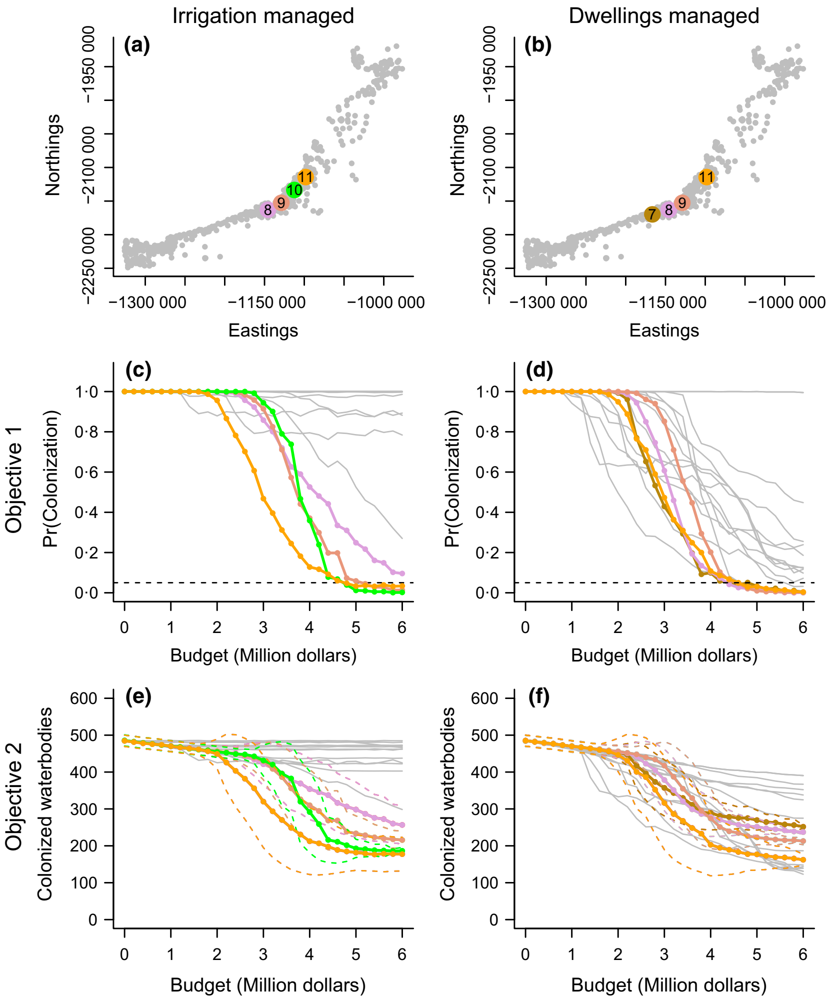

Fig. 3. The most cost-effective locations for a barrier in the Kimberley–Pilbara corridor with a truncation distance of 55 km, our best estimate of the number of rainy days, a 5% failure rate, an active Indigenous Protected Area (IPA), and assuming AWP are managed. The left column (a,c,e) assumes irrigation is managed and that toads cannot be excluded from dwellings. The right column (b,d,f) assumes dwellings are managed and that toads cannot be excluded from irrigation. The top row (a, b) shows the locations of the best four barrier locations under objective 1. The probability of toads reaching the Pilbara for each of the 17 potential barrier locations across a range of fixed budgets is shown in the middle row (c,d). The number of waterbodies colonized after 50 years is shown in the bottom row (e,f). In figures (c–f), coloured lines represent the first four locations to fall below a 5% chance of toads colonizing the Pilbara. The corresponding position of these locations is shown in the top row (a,b). Dashed lines (e,f) represent standard errors from 1000 simulations.

fences around managed AWPs. However, while this additional measure would reduce the chance of toads accessing water, it would substantially increase installation and maintenance costs. Finally, our optimization procedure ignored potential social opportunities or constraints a barrier may present. Further research could parameterize a penalty for barriers that span multiple land tenures, incorporate incentives or include a reward for barriers that present social opportunities such as the involvement of indigenous ranger groups.

We modified a previously published model of cane toad spread across an arid region of north-western Australia to find the most cost-effective location for a barrier through participatory modelling and scenario analysis. Our findings are broadly in agreement with those of Tingley *et al.* (2013): that a barrier can stop toads reaching the Pilbara. However, the results of our refined analysis indicate that the best location is sensitive to local knowledge of the corridor, particularly the locations of dwellings and irrigated areas. By eliciting and addressing concerns with the Tingley *et al.* (2013) model, we involved practitioners in the model-building process. Although this does not guarantee adoption, an ongoing dialogue not only establishes trust, but benefits both modellers and practitioners. As such, ongoing dialogue should be routine in model-based conservation decision-making.

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Data accessibility

Waterbody data are available upon request from Geographic Information Systems at the Department of Agriculture and Food, WA (samantha.vanwyngaarden@agric.wa.gov.au), and the Spatial Data Exchange section of the Department of Water, WA (timothy.fardon@water.wa.gov.au). Rainfall data are available from the Australian Water Availability Project (AWAP) (http://www.csiro.au/awap/).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detection radius for irrigation and dwellings.

Fig. S1. Rainfall variability across space and time.

Fig. S2. Barrier locations with an inactive Indigenous Protected Area (IPA).

Fig. S3. Barrier locations with alternative failure rates.

Fig. S4. Barrier locations with alternative number of rainy days and truncation distance.