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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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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):

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

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

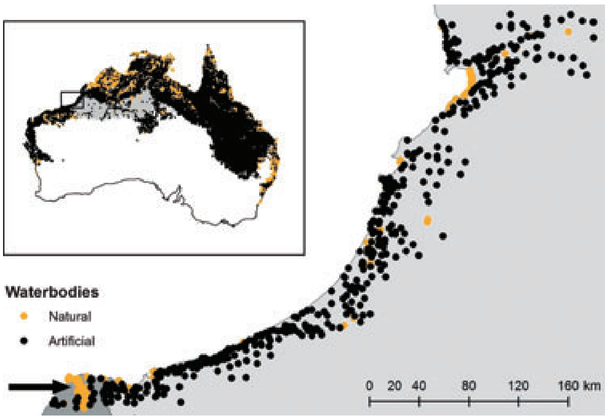

Fig. 1. The study area in Western Australia. The black arrow in the lower left-hand corner shows the location of the De Gray River, which was used as an endpoint in all simulations. The dark grey region below the black arrow shows the extent of the Pilbara region. In the inset, only waterbodies that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

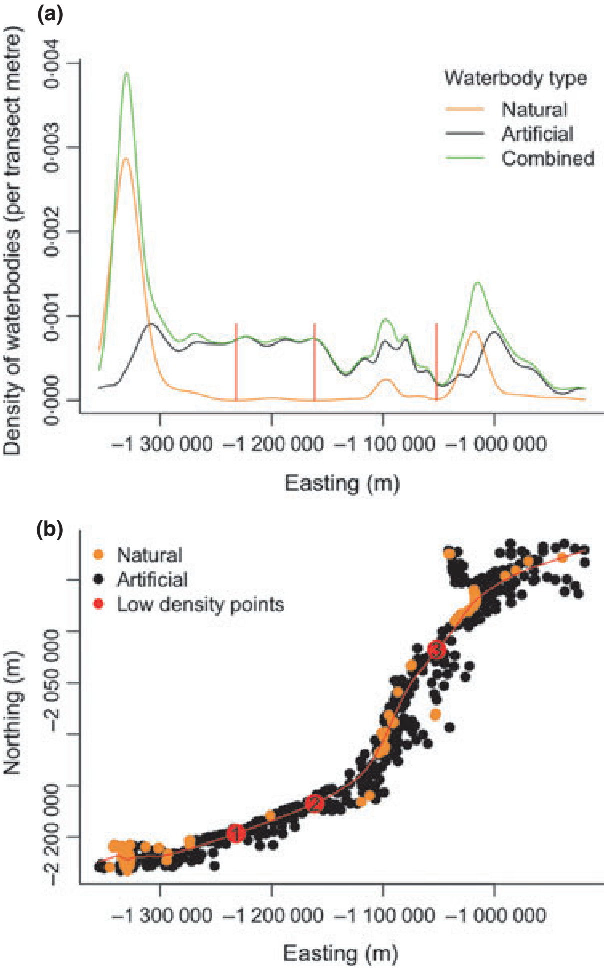

Fig. 2. Densities of natural and artificial waterbodies along the Kimberley-Pilbara corridor in Western Australia (a), and locations of potential barriers to the spread of cane toads (b and red lines in a). In the lower panel, point one corresponds to the 'western barrier', point two to the 'central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

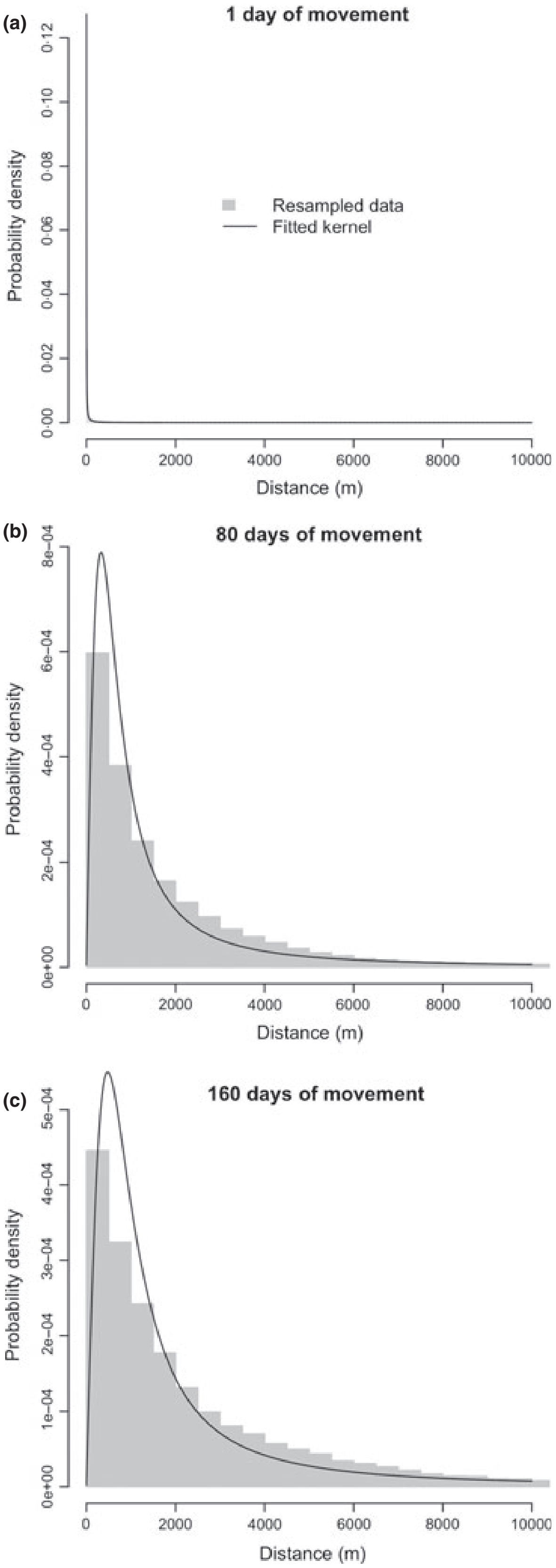

Fig. 3. Resampled distribution of daily displacements of cane toads for 1 (a), 80 (b), and 160 (c) days of movement. The density curves in each panel show the fit of the 2D t-distribution to the resampled distributions.

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).

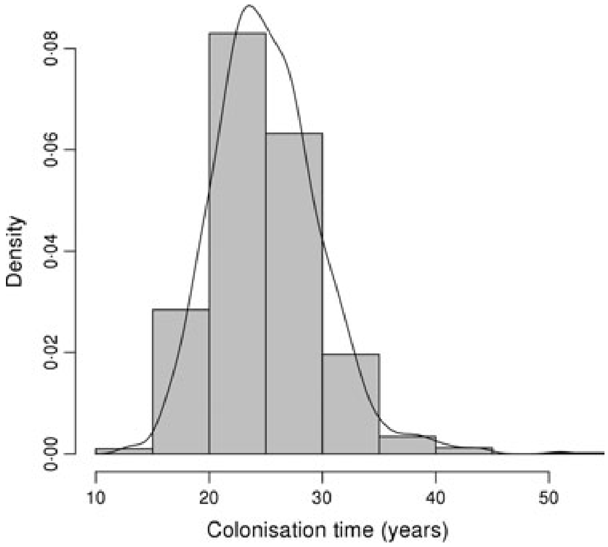

Fig. 4. Distribution showing the estimated number of years that it would take cane toads to colonize the Pilbara across 1000 simulations of spread.

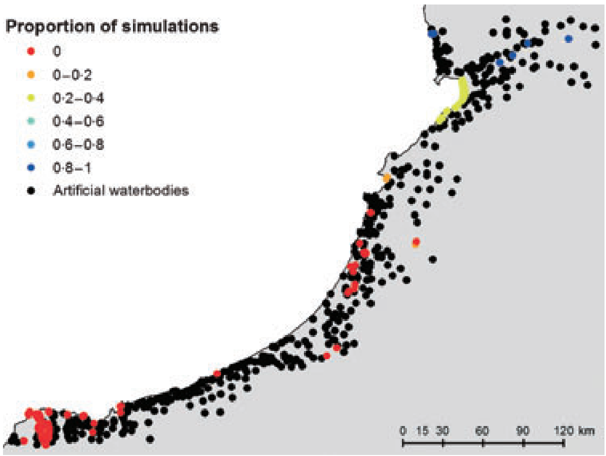

Fig. 5. Map showing the proportion of simulations (n = 1000) in which toads were able to colonize natural waterbodies along the Kimberley-Pilbara corridor in the absence of artificial waterbodies.

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

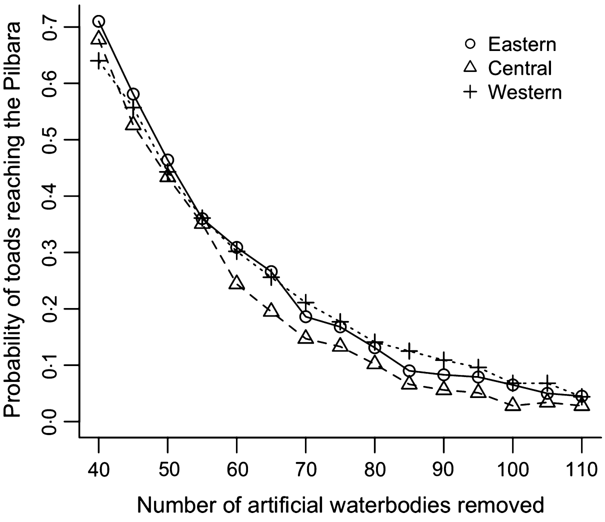

Fig. 6. Probability of cane toads reaching the Pilbara as a function of the number of artificial waterbodies removed at three dispersal barriers. Barriers correspond to those shown in Fig. 2(b).

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.