Research

Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates

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Accurate predictions of the potential distribution of range-shifting species are required for effective management of invasive species, and for assessments of the impact of climate change on native species. Range-shifting species pose a challenge for traditional correlative approaches to range prediction, often requiring the extrapolation of complex statistical associations into novel environmental space. Here we take an alternative approach that does not use species occurrence data, but instead captures the fundamental niche of a species by mechanistically linking key organismal traits with spatial data using biophysical models. We demonstrate this approach with a major invasive species, the cane toad *Bufo marinus* in Australia, assessing the direct climatic constraints on its ability to move, survive, and reproduce. We show that the current range can be explained by thermal constraints on the locomotor potential of the adult stage together with limitations on the availability of water for the larval stage. Our analysis provides a framework for biologically grounded predictions of the potential for cane toads to expand their range under current and future climate scenarios. More generally, by quantifying spatial variation in physiological constraints on an organism, trait-based approaches can be used to investigate the range-limits of any species. Assessments of spatial variation in the physiological constraints on an organism may also provide a mechanistic basis for forecasting the rate of range expansion and for understanding a species' potential to evolve at range-edges. Mechanistic approaches thus have broad application to process-based ecological and evolutionary models of range-shift.

Humans are increasingly altering the distributions of species by modifying habitat, changing the global climate, and facilitating exotic species invasions (Mack et al. 2000, Parmesan 2006). Successful management of biological resources depends critically on our ability to predict the potential geographic distribution of range-shifting species and to understand the forces that limit them. GIS-based distribution modelling provides a powerful tool for predicting species distributions (Guisan and Zimmermann 2000, Peterson 2003, Elith et al. 2006), yet almost all present approaches depend in some way on associating species occurrence data with spatial datasets ("the correlative approach") (Pearson and Dawson 2003, Ficetola et al. 2007). In range-shifting species, the correlative approach often requires extrapolation to novel environmental conditions, with the risk of erroneous predictions (Davis et al. 1998, Pearson and Dawson 2003, Dormann 2007, Phillips et al. 2008b). Thus, there is a great need for alternative approaches to predicting species' potential distributions that are independent of a species' known geographic range.

Alternative approaches with increased emphasis on the ecology of organisms are beginning to emerge, explicitly considering either population dynamics (Hooten et al. 2007), ecophysiology (Kearney and Porter 2004, Gilman et al. 2006, Buckley 2008), or both (Crozier and Dwyer 2006). Here we present an ecophysiological, traits-based approach to predicting species' distributions that does not use species occurrence data when predicting potential range. We apply it to the case of an invasive species, the cane toad *Bufo marinus*, whose geographic range is still expanding in Australia. Cane toads were introduced to north-eastern Australia in 1935 and have spread extensively along the eastern coastline, as well as penetrating into the arid interior of the continent (Fig. 1a). Established populations occur as far south as 31°S along the east coast, with occasional records as far south as Sydney (34°S). The cane toad is continuing to spread at an increasing rate across far northern Australia (Phillips et al. 2007), and at the time of writing has reached a longitude of approximately 128°E. This toxic species has had a devastating negative impact on native wildlife, and poses a significant management
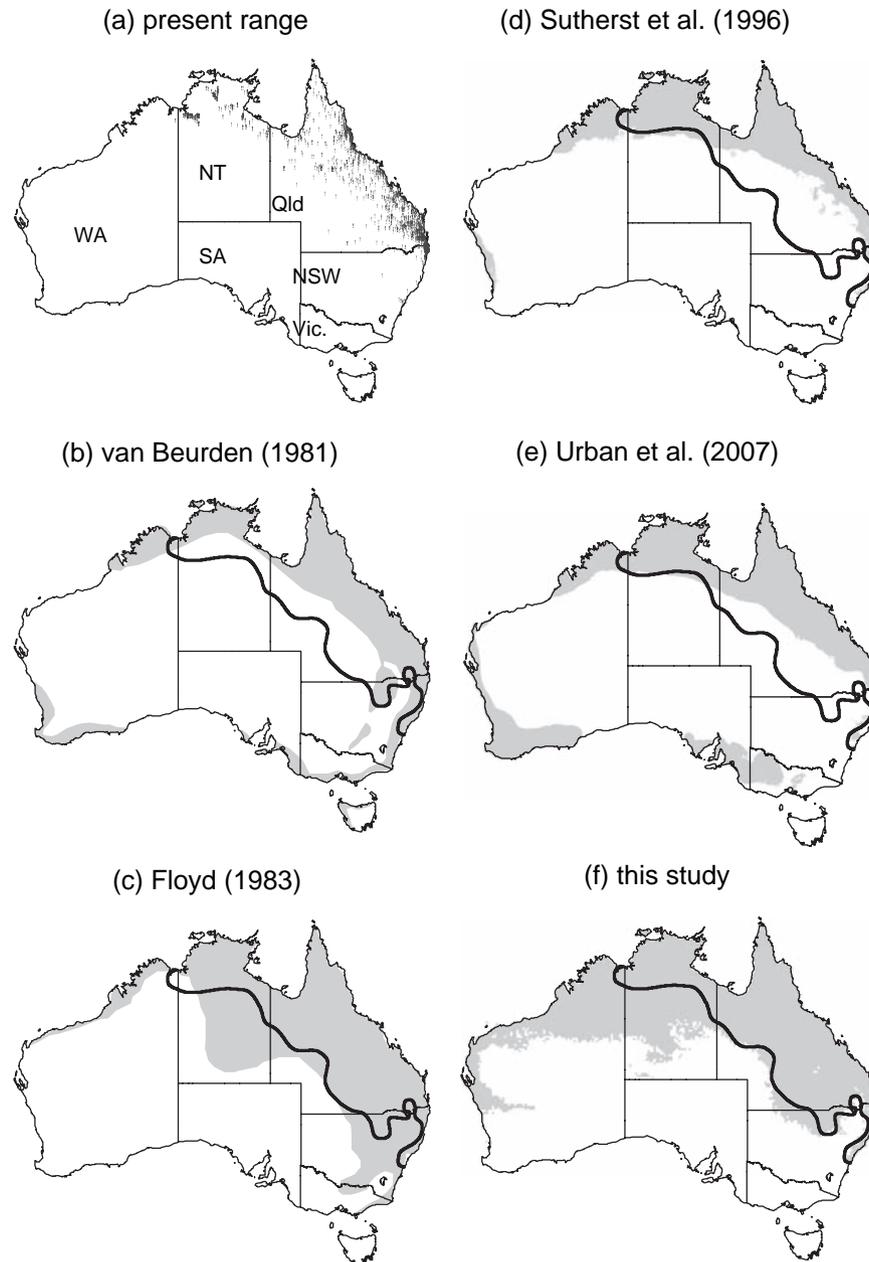
Figure 1. The present distribution of *Bufo marinus* (a) and five predictions of its potential final distribution under average climatic conditions (b-f), including the present study. Figure 1d is a fine-scale (90') re-interpolation of the original analysis. The heavy, black line defines the approximate spatial limit of all toad locality records.

problem (Lever 2001, Murray and Hose 2005). Three attempts have been made to predict the potential maximum distribution of cane toads in Australia based on occurrence records (van Beurden 1981, Sutherst et al. 1995, Urban et al. 2007) (Fig. 1b, d-e) in addition to one preliminary and unpublished mechanistic model based on larval thermal tolerance (Floyd 1983b) (Fig. 1c). Two of these analyses, including the most recent one (Urban et al. 2007), predict large parts of the densely populated southern regions of Australia as potentially suitable habitat for cane toads.

In this study we extend the analysis of Floyd (1983b) by mechanistically modelling climatic constraints on cane toad eggs, larvae and adults under both current climate and a scenario of climate change. Our approach models the

influence of climate and topography on the energy and water-balance of the different life-cycle stages of the toad, as well as the potential for activity, development, and survival. Thus, it provides an assessment of several dimensions of the toads' fundamental niche; the area in which it can survive in the absence of biotic constraints (Kearney and Porter 2004, Kearney 2006). To make our predictions, we used fine-resolution spatial datasets together with a set of biophysical/ behavioural models collectively called "Niche Mapper™" (Porter and Gates 1969, Porter et al. 1973, Porter 1989, Porter and Mitchell 2006). The models apply principles of physics to calculate how microclimatic conditions interact with an organism's properties to affect mass and energy balances. We use these models to determine 1) the potential

distance that adult toads could move on land as a function of core body temperature throughout the day, 2) the monthly availability of water in ponds of a typical size used by cane toads in nature, and 3) the potential for egg and larval development based on daily thermal cycles and gradients within these ponds.

Methods

Modelling adult toads

We modelled hourly core body temperatures (T_b) of toads by solving a standard, steady state energy balance equation including terms representing solar, infra-red, metabolic, evaporative (respiratory and cutaneous), convective and conductive heat exchange

$$Q_{solar} + Q_{IRin} + Q_{metab} = Q_{resp} + Q_{evap} + Q_{IRout} + Q_{conv} + Q_{cond} \,. \qquad (1)$$

Basic elements of the model have been described elsewhere (Porter and Gates 1969, Porter et al. 1973, Porter 1989, Porter and Mitchell 2006). A critical aspect of the model in the context of a wet-skinned amphibian is heat exchange via cutaneous evaporation, Q_{evap}, which is determined by the latent heat of evaporation of water together with the rate of mass transfer

$$m = h_D \cdot A \cdot (\rho w_{skin} - rh \cdot \rho w_{air}), \qquad (2)$$

where m is the rate of mass transfer, h_D is the mass transfer coefficient, A is the area of the skin that acts as a free water surface across which mass exchange occurs, rh is the local relative humidity, and ρw_{skin} and ρw_{air} are the densities of water vapor at saturation at the temperature of the animal surface and air, respectively. See Tracy (1976) and Porter and Mitchell (2006) for further details on the calculation of mass transfer rates.

We modelled a 150 g (medium sized adult) toad, assuming that the surface of the toad acted as a free water surface (Schwarzkopf and Alford 1996); i.e. that the skin was 100% wet. We estimated surface area as a function of body mass using the empirical relationship derived for leopard frogs by Tracy (1976). We assumed that, when active, the toad experienced air temperature, wind speed and relative humidity at 3 cm above the ground (the mid-point of a 150 g active toad), and that the activity posture resulted in a similar fraction (10%) of the animal in contact with the surface as measured empirically in leopard frogs (Tracy 1976, Fig. 2). Thus 90% of the skin surface area of an active toad was involved in cutaneous mass and heat exchange. We tested the sensitivity of the model predictions to changes in body mass as well as postural changes (Supplementary material, Appendix 1).

Only nocturnal activity was allowed in the model, within a core temperature range of 13.7 and 37.4°C (the extrapolated zero points for the temperature vs speed relationship below). When conditions were unsuitable for aboveground activity, the toads were assumed to select a position within the soil profile as close as possible to their preferred temperature (24°C). We assumed toads were active whenever thermal conditions permitted, irrespective of the consequences for water balance. In nature, however, toad activity levels are closely tied to soil moisture levels (Seebacher and Alford 1999). While there are presently no data available on the interaction between body temperature and water loss rates in determining toad activity levels, we have explored this issue in part by including a simulation where toad activity was limited to occur on rainy days only. In these simulations we set the local humidity at 90% and assumed evaporation from 90% of the ground surface area, without altering air temperature (although air temperature is likely to be lower than average on rainy nights).

To estimate the capacity for movement in active toads, we measured mean hopping speed across a 2 m distance at five temperatures between 15 and 35°C (Fig. 3). We used field-collected animals from four different populations that span the invasion front. A quartic function provided the best fit to the data (based on Akaike's information criterion), where hopping speed $S = -25.48396 + 4.51222 \, T_b - 0.29052 \, T_b^2 + 0.0082619 \, T_b^3 - 0.000086431 \, T_b^4$.

For each hour in which the toads were active, we calculated the total distance moved multiplied by the proportion of the maximum potential distance that active toads typically move (median = 0.0384). This proportion was based on estimates of the daily displacement and circular diffusion of 89 radiotracked toads from the same four populations from which our locomotor trial animals were sampled, combined with local weather variables recorded at the time of the radio tracking study (see Phillips et al. 2008a for detailed methodology on radiotracking). To calculate the mean proportion of time a toad spends moving we used the maximum daily displacement observed for each toad and calculated an approximate maximum distance moved on that night based on that animal's mean circular diffusion (see Phillips et al. 2008a for details). For that date's mean nightly temperature we then calculated the maximum distance that toad could have moved if it hopped at maximum speed all night (using the quartic function above). The proportion of time a toad moves was then calculated as the maximum distance moved divided by the potential distance if the toad had moved 100% of the time. Calculating this across all 89 individuals resulted in a skewed distribution with a median of 3.84% and an interquartile range of 1.4–6.8%. We considered the influence of values over this interquartile range as an additional variable in the sensitivity analysis (Supplementary material, Appendix 1).

We estimated required feeding rates and annual water balance by calculating environmental impacts on metabolism and water loss (Kearney and Porter 2004). We estimated metabolic rate (M) as a function of hourly body temperature (T_b) according to a standard equation for ectotherms $M = 0.0056 \times 10.0(0.038 \times T_b - 1.771) \times mass^{0.82}$, where metabolic rate is in watts and mass is in grams (Bennett and Dawson 1976). We determined required feeding rate assuming a diet of crickets (composition 67% protein, 18% fat, 10% carbohydrate dry mass) (Kearney and Porter 2004), and a digestive efficiency of 85%. There are few data available on field metabolic rates of amphibians and no data for *B. marinus*, but lizard field metabolic rates range from 1.1 to 5.1 times standard (resting) metabolic rate (Christian et al. 1997). We thus
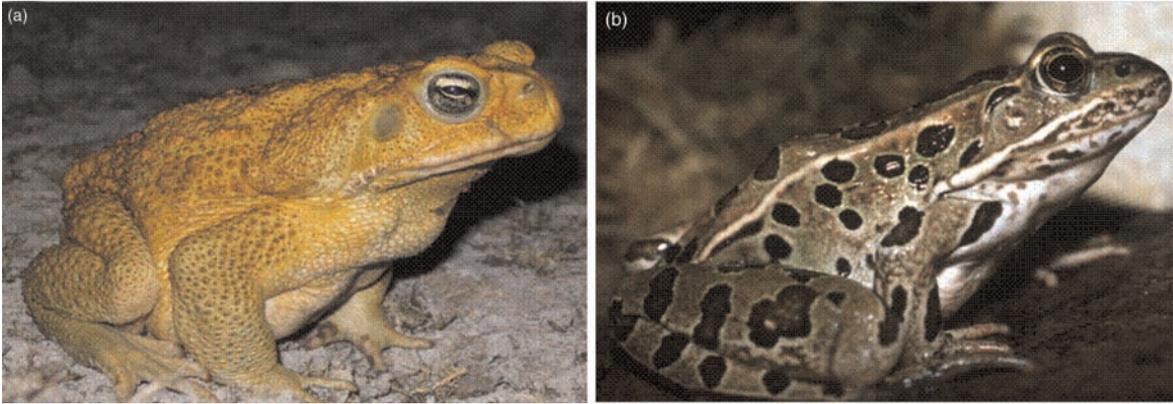
Figure 2. The cane toad *Bufo marinus* and the leopard frog *Rana pipiens* in activity postures. We used surface area relations derived for *R. pipiens* by Tracy (1976) to parameterize our model for *Bufo marinus*. *Bufo marinus* photo credit: B. L. Phillips. *Rang pipiens* photo credit: Cindy Hitchcock.

approximated field metabolic rate by assuming it was 2.5 times resting.

We assumed the retreat was a humid burrow, although we recognize that in nature toads may also use more superficial retreat-sites where water loss can be an important issue (Seebacher and Alford 2002). Water balance in our simulations was thus a function of cutaneous and respiratory water loss during periods of above-ground activity only, as well as metabolic water, water input from the metabolically driven food requirements (assuming 69% water in food), and water excreted with faeces and urine assuming 25% faecal water and 20% urea in urine (Kearney and Porter 2004). The parameterisation of the model with respect to feeding rate and water balance was necessarily tentative at this stage due to a lack of empirical data; while we did not base our final predictions of potential range on our inferences of feeding rates and water balance, we include them to illustrate how they might be included in future predictions

Modelling eggs and larvae

We modelled the availability and temperature of water in ponds across the landscape by solving transient-state energy and mass balances for cylindrical bodies of water under different microclimates, and then calculating the consequences for the survival and development of eggs and larvae based on published data on temperatures lethal to eggs and larvae, and on development rate as a function of temperature (Floyd 1983a, b, 1984).

Cane toads preferentially spawn in large, shallow water bodies with little surrounding vegetation (Evans et al. 1996, Hagman and Shine 2006). We used a pond dimension of 90 m diameter $\times$ 0.3 m deep, corresponding to typical ponds used by toads in northern Australia (Hagman and Shine 2006). We also considered a smaller, deeper pond of 10 m diameter $\times$ 1 m deep. The ponds filled according to the rainfall each month, with a portion entering the pond directly and a portion entering as runoff. Since there are no data on the catchment sizes of ponds used by cane toads, we considered two catchment sizes of 7 and 15 times the pond area (5 and 10 ha for large ponds, 0.6 and 1.3 ha for small

ponds). We reduced runoff from the catchment area according to an empirically derived pattern for clay pans (<http://pandora.nla.gov.au/pan/57998/20060412/LC0084. pdf>: yield fraction = 0.00016989 $\times$ annual rainfall (mm) + 0.00738137) with a maximum threshold set at 20% for annual rainfall above 1100 mm. We included all four pond configurations in our sensitivity analyses of adult traits (Supplementary material, Appendix 1).

Initial pond depth was determined by the monthly rainfall entering the pond. The transient-state energy and water balance was then modelled for the resulting pond mass and dimensions across a 24 h period for each month subject to the environmental conditions at 10 cm height in full sun, with conduction according to the deep soil temperature (60 cm). A stable daily periodic in pond temperature was obtained after three iterations of each day. The transient-state energy balance subroutines solve a standard energy balance equation that includes a storage term, using an Adams Moulton predictor-corrector numerical integrator with a Runge-Kutta starting algorithm. Intermediate derivatives are computed using a four point Lagrangian interpolation scheme (Porter and Mitchell 2006). Convective heat and mass transfer calculations from ground and
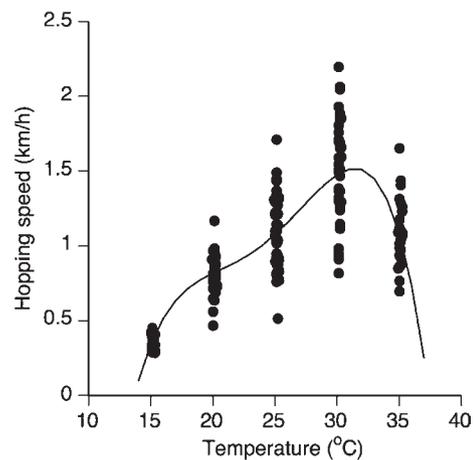

Figure 3. The relationship between locomotor performance (hopping speed across 2 m) and body temperature for *Bufo marinus*, pooling across four populations.

water surfaces were computed using a turbulent velocity profile approximately logarithmic in shape to calculate air temperatures, wind speeds and humidity between the 2 m reference height and the ground or water surface (Porter et al. 1973). A constant mass of water per unit volume in the air was assumed to correct for temperature-dependent relative humidity change between the 2 m input data and the surface over a 24 h period. The entire top surface of the vertically oriented short cylinder of the "pond" acted as a free water surface for evaporation. The mass of water evaporated each month (calculated as described above) was subtracted from the total volume and the depth re-calculated accordingly, prior to adding the rainfall for the subsequent month. We ran 10 iterations of each year to ensure a stable periodic annual cycle in pond depth.

Solution of the transient-state energy balance equation for the pond provides an estimate of the hourly "core temperature" of the pond throughout the year. We assumed the water temperature at the edge of the pond equaled the soil temperature in full sun at 2.5 cm depth, as estimated by the microclimate model. Eggs were assumed to develop at a fixed location where the temperature was the average of the edge and core temperature of the pond. Larvae were assumed to select a temperature within the edge-core gradient, choosing their preferred temperature (28.8°C, Floyd 1984) wherever possible. Eggs and larvae were modelled not to survive hourly exposures of below 8.8°C or of above 43.4°C (Floyd 1983a, b, 1984). Egg development was modelled to cease below 17.5°C and above 34.5°C, and eggs were modelled to die if they spent the entire day above or below these limits. The corresponding limits of development for larvae were 19.0°C and 38.0°C. Within these limits, the percentage of egg development completed per hour (E_h) as a function of egg temperature (T_{egg}) was determined as $E_h = 0.2310 \times T_{egg} - 3.6916$, as determined by Floyd (Floyd 1983a). The percentage of larval development per hour (L_h) as a function of larval temperature (T_{lar}) was determined as $L_h = (82.9370 - 10.6589 \times T_{lar} + 0.4414 \times T_{lar}^2 - 0.0057 \times Tl_{ar}^3)/24$ (Floyd 1983a).

Spatial datasets and climate change scenario

We based our analyses on monthly maximum and minimum values of air temperature, humidity and wind speed, as well as mean monthly rainfall and cloud cover, and the number of rainy days per month, averaged over 30 yr (Kearney and Porter 2004). Slope, aspect, and elevation were based on a 9″ DEM for Australia (Hutchinson et al. 2000). Temperature measures (initially 0.05° resolution) were corrected to the fine-resolution DEM using an adiabatic lapse rate of -5.5°C km^{-1} elevation increase. Coarse-scale analyses were based on queries to these layers for a grid of 1936 points 0.5° apart, while fine-scale analyses were based on a grid of 17417 points 0.18° apart.

We used the software package Ozclim (CSIRO, Australia) to derive predictions for changes in monthly maximum and minimum air temperature and relative humidity, as well as mean monthly rainfall by 2050 under a moderate scenario of climate change (SRES marker scenario B1 mid, CSIRO mk2, 0.8–1.5°C increase in mean annual temperature).

Results

Constraints on adult toads

Toad hopping speed ranged from 0.3 km h^{-1} at 15°C to as high as 2.2 km h^{-1} at 30°C, with speed declining precipitously between 30°C and 35°C (Fig. 3). There was no significant effect of population on sprint speed (repeated measures ANOVA $F_{3,23} = 2.15$, $p = 0.12$). A quartic function provided the best fit to the hopping speed vs temperature curve, and a minor extrapolation of this curve to zero hopping speed gave limits to locomotion of 13.7 and 37.4°C.

Using these hopping speed limits as thresholds for activity, our landscape-level simulations show a progressive decrease in potential hours of activity per year from 3591 h (virtually every hour of every night) in the far north of Australia to zero for the more southern regions (Fig. 4a). In our simulations, toad activity was never limited by the high temperature threshold, although we note that our predictions are based on monthly averages and the high temperature limit may be exceeded on extremely hot nights in some localities. The present southern border of the cane toad's range in Australia closely approaches the zero activity region, and toad presence locations are rarely found in regions of fewer than 500 h activity per year (Fig. 4a).

Implementation of the thermal performance curve for hopping speed, together with the field-measured estimate of movement tendency, predicts potential annual movement of 50–130 km in northern areas (Fig. 4b) and that activity could occur year-round from a thermal perspective (Supplementary material, Fig. S2a). These results are consistent with recent estimates of the current expansion rate near the north-western range-limit (30–78 km yr^{-1} observed (Phillips et al. 2007) vs our 60–65 km yr^{-1} prediction). Yet in the vicinity of the southern range border, movement potential is predicted to drop as low as 500 m yr^{-1} (Fig. 4b), with activity constrained to the months of December, January, February and March (Supplementary material, Fig. S3a). Again, this low movement potential reflects the low rate of advance (ca 1.1 km yr^{-1}) of this southern front (Seabrook 1991, Estoup et al. 2004).

Our model predicted discrepancies of up to 5–6°C between body temperature and local air temperature, due to evaporative cooling from the combined effects of wind speed and relative humidity (Fig. 5). Such discrepancies are in line with general analyses of heat exchange in amphibians (Tracy 1976), as well as field measures of toad body temperatures (Johnson 1972) (Fig. 6). Limiting toad activity to rainy days only, with high levels of humidity (90%), extended the southern zero-activity limit in all regions (Supplementary material, Fig. S9). The imposition of rain-limited activity also significantly curtailed the potential distance moved in northern parts of the range, with the maximum potential distance reducing to 52.6 km yr^{-1} (Supplementary material, Fig. S9). This reduction was driven by the limited number of "winter" rainy days across

much of northern Australia (Supplementary material, Fig. S10).

By assuming activity is limited only by temperature and not by rainfall, our combined estimates of thermally imposed metabolic demand and potential activity time predict required foraging rates generally $< 1\,g\,h^{-1}$ throughout the present range of the toad in Australia (Fig. 4c). Near the south-eastern border, this rate increases to up to 15 g h^{-1} just prior to the zero-activity limit. Monthly patterns of food requirements are shown in Supplementary material, Fig. S4. Assuming the maintenance level of food is consumed (69% water) and that activity is thermally dependent only, we predict toads would have to drink/ absorb $> 1\,L\,yr^{-1}$ of water to maintain positive water balance (Fig. 4d). This water requirement reaches a maximum of $10\,L\,yr^{-1}$ in the arid northern regions, driven particularly by high water demand in the months of November–January (Supplementary material, Fig. S4).

Constraints on egg and larval stages, and full life-cycle predictions

In contrast to the adult stage of the life cycle, our analysis indicates that the egg and larval stages of the cane toad could survive and complete development
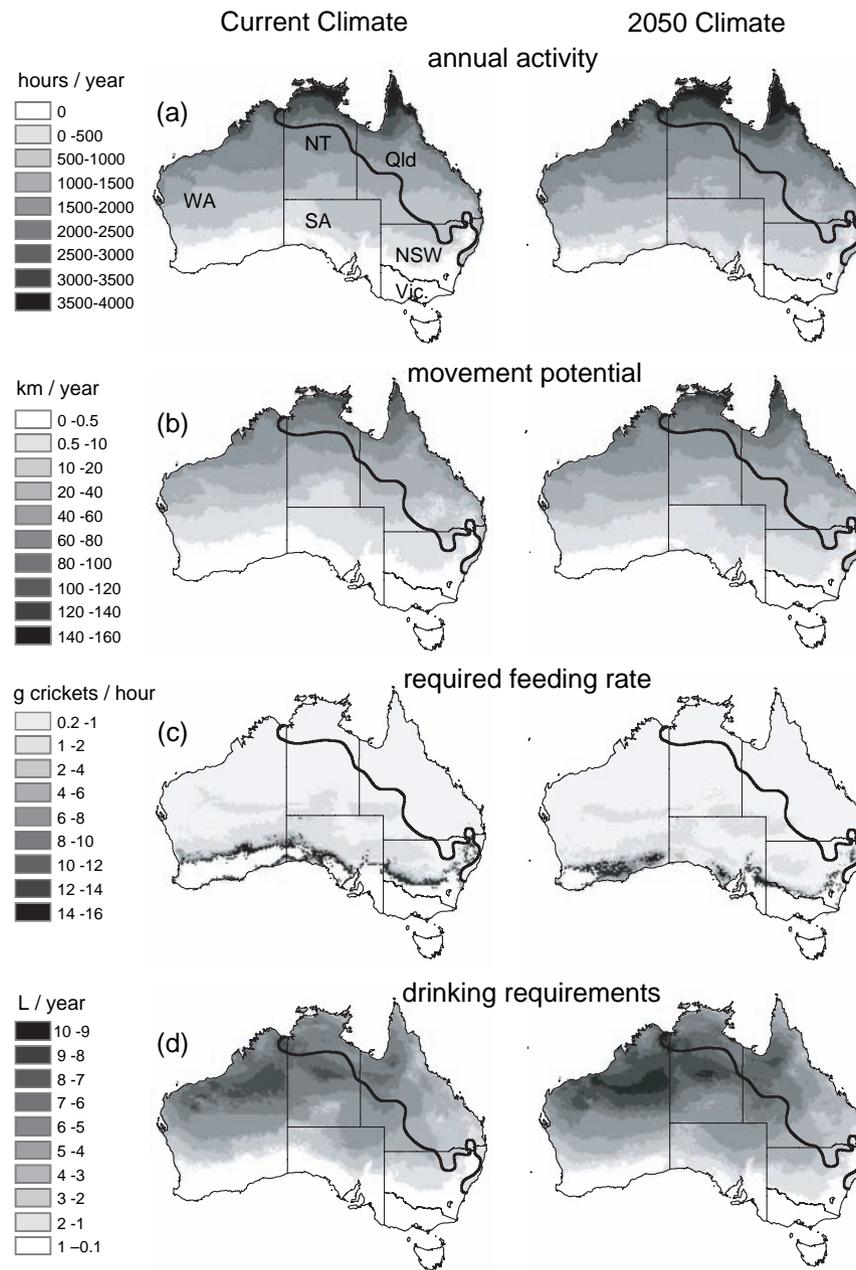

Figure 4. Biophysical model predictions for adult *Bufo marinus* of the potential for (a) activity and (b) movement, as well as (c) minimum foraging requirements and (d) water requirements under current climatic conditions and under a predicted climate change scenario for Australia in they year 2050. The heavy, black line defines the approximate spatial limit of all toad locality records.
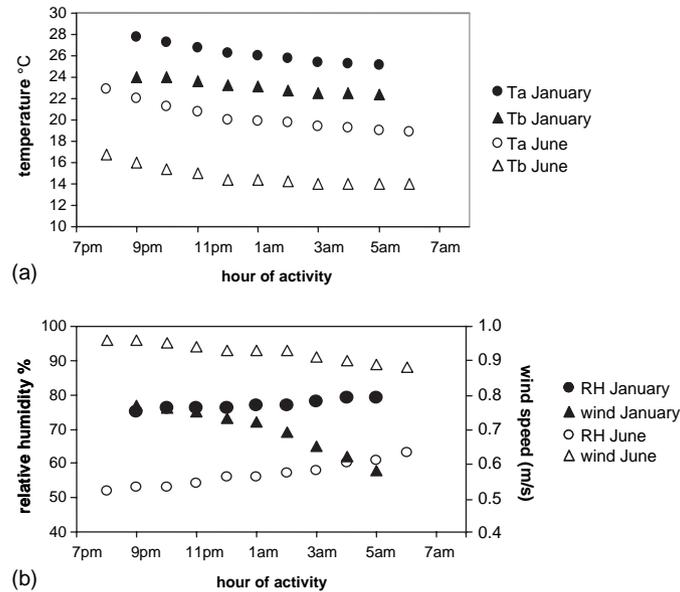
Figure 5. Model predictions of (a) the discrepancy between hourly core body temperature (T_b) and air temperature (T_a) for *Bufo marinus* during January and June in the northern Australian city of Darwin, and (b) the corresponding relative humidity and wind speed at the height of the toad (3 cm). The abscissa shows hours of activity, assuming nocturnality. Day length effects result in a longer activity period for June (8 pm to 6 am) than for January (9 pm to 5 am).

throughout most of southern Australia except for very high altitude areas and the southern island of Tasmania (Fig. 7b, c). Egg development at the southern extent of the range was predicted to be prohibited thermally between the months of May and September, and larval development was similarly prohibited between June and August (Supplementary material, Fig. S6–7). Inland areas were predicted to have insufficient water in rain-fed ponds for development, whereas some water was predicted to be present in ponds through the year in all regions presently within the toad's range (Fig. 7a–c, Supplementary material, Fig. S5).

We derived a composite surface of the constraints on egg, larval and adult stages of the life cycle that depicts dimensions of the fundamental niche of the toad. For each location, and for each month, we asked: a) were conditions suitable for adult activity; b) was there >1 cm of water in the pond; c) could the eggs survive and complete development, and d) could the larvae survive and develop within a three month window? If all of these conditions were true for a given location in a given month, it was given a value of one. Summing these across all months of the year provided a map of the total length of the breeding season (Fig. 7d). For these calculations we used a minimum potential movement per night of 5 m, to approximate required movement from a retreat-site to a breeding/feeding site, which is likely to be conservative since toads have been shown to
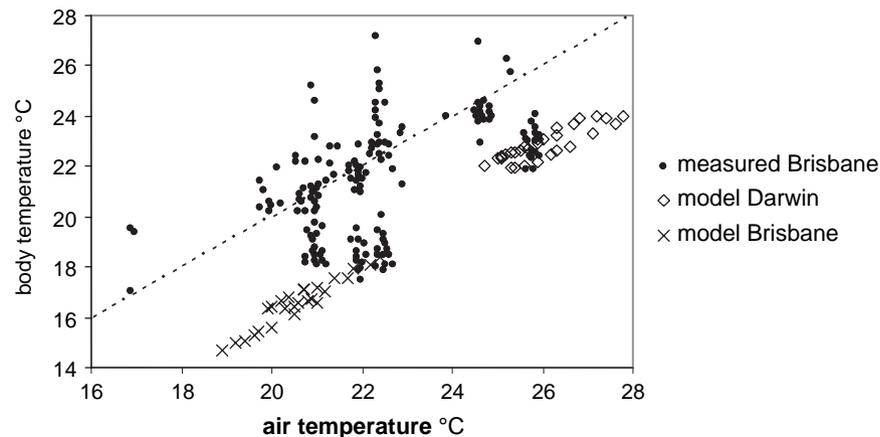

Figure 6. Model predictions of the relationship between core body temperature and air temperature of field-active *Bufo marinus* under average summer climatic conditions in the northern Australian cities of Brisbane and Darwin, compared with recorded body temperatures and air temperatures of field-active toads during summer in the Brisbane area (Johnson 1972). On rainy nights body temperature is likely to be very close to air temperature due to higher local humidity. See Supplementary material, Fig. S9 for the impact of this ''rainy night'' effect on our conclusions.

move average distances of 30 m or more per night (Seebacher and Alford 1999).

Our composite prediction of the spatial extent of the fundamental niche of the cane toad in Australia encompasses the entire known range of the toad, and the southeastern interior border is tightly aligned with the contour for a breeding season of three months duration. For regions with a breeding season less than three months, cane toads were predicted to travel no more than 65 m on the average night during the active season (Supplementary material, Fig. S2a) and would require average rates of prey capture of at least 0.8

g h^{-1} (assuming an insect diet) to meet annual metabolic requirements (Supplementary material, Fig. S3).

Discussion

The fundamental niche of the cane toad

The methods of biophysical ecology provide a powerful tool for predicting species' potential ranges by defining regions where survival is physiologically impossible. The approach
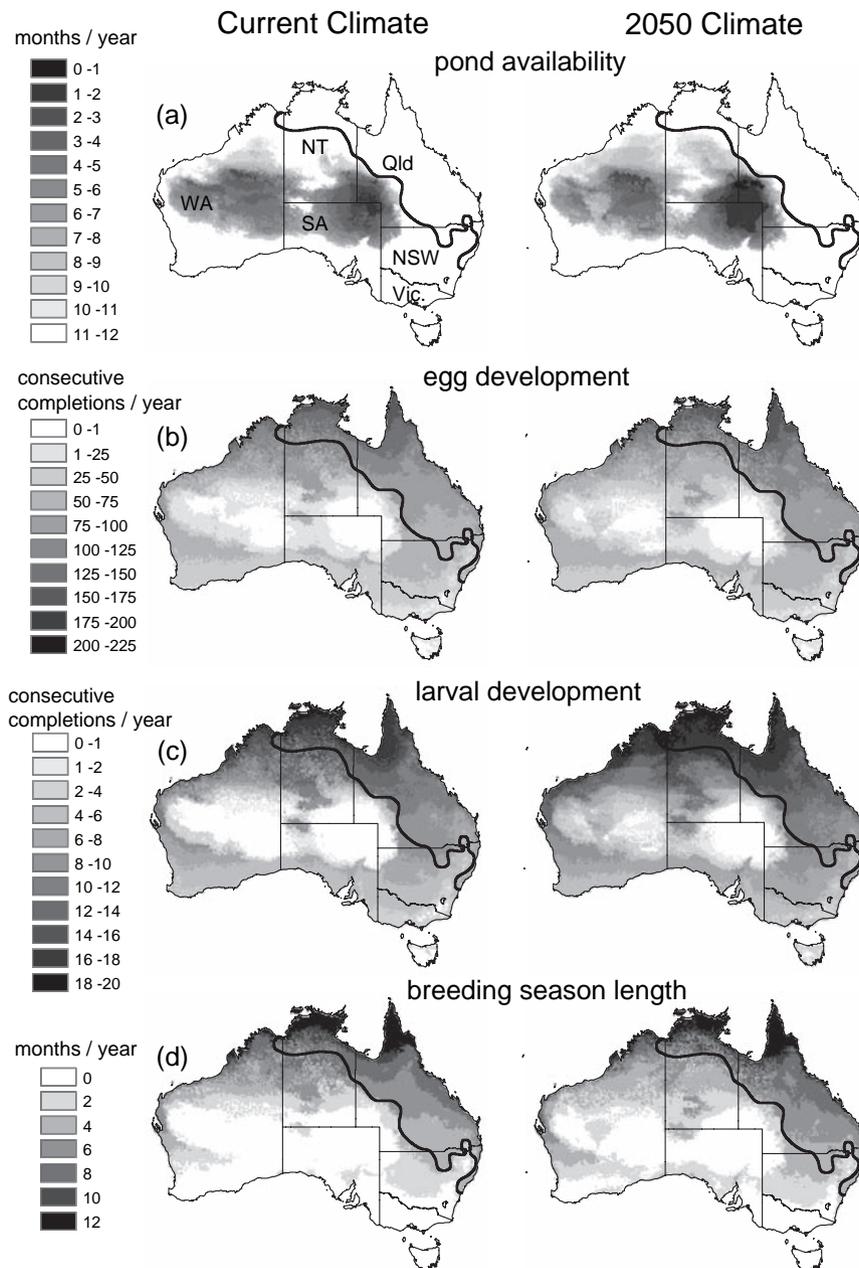

Figure 7. Biophysical model predictions of (a) pond availability, (b) egg development, (c) larval development and (d) length of the breeding season for *Bufo marinus* under current climatic conditions and under a predicted climate change scenario for Australia in the year 2050. The units for egg and larval development are the predicted number of consecutive completions of development (from egg to hatching, and from hatching to metamorphosis, respectively) for the entire year. The heavy, black line defines the approximate spatial limit of all toad locality records. The predictions for the length of the breeding season is based on both the potential for adult toads to be active, and on the potential for eggs and larvae to complete development in the simulated pond.

can be described as first mechanistically determining aspects of a species' fundamental niche, and then mapping that niche to the landscape (Kearney and Porter 2004, Kearney 2006). However, because we can never capture all factors constraining the fundamental niche, our strongest inference is on the identification of areas outside the fundamental niche; areas within which it is impossible for the organism in question to survive. Thus, the actual geographical range is likely to be more restricted than what we predict, either because of additional unconsidered aspects of the fundamental niche, or because of biotic interactions which constrict the fundamental niche to a narrower realized niche (but see Pulliam 2000).

The current range of the cane toad in Australia largely fills areas we have predicted to be within dimensions of its fundamental niche (Fig. 7d). This fact is perhaps not surprising since the species has relatively few natural competitors in Australia (Lever 2001). The major constraints driving our predictions are the climatically imposed limitations on movement potential in adult toads at the southern range borders, and the availability of water for breeding in natural ponds at the interior limit. Obviously, cane toads cannot exist in regions where activity potential is zero, and this activity constraint eliminates as potential habitat most of the southern state of Victoria, as well as the southwest of Western Australia and southern South Australia (Fig. 4a, b; Supplementary material, Fig. S8). Yet the fundamental niche of the cane toad, as it pertains to adult activity potential, will be defined by a certain (non-zero) minimum foraging potential that allows sufficient resources to be acquired for reproduction, as well as sufficient movement for courtship and breeding. Locality records of cane toads never occur in areas we predict would allow <500 h of potential activity per year (Fig. 4a), <500 m of activity per year (Fig. 4b), or that require >1 g of food per hour (Fig. 4c). Our analysis coupled with locality records thus implies that cane toads cannot maintain stable populations if activity constraints or feeding rate requirements extend beyond these limits.

Another potential constraint on adult cane toads is desiccation (Schwarzkopf and Alford 1996, Seebacher and Alford 2002). We have made a crude estimate of desiccation risk by calculating water balance as a function of metabolically required food (and thus water) input, evaporative and respiratory water loss, and excretion. Our predictions are conservative in assuming water loss only occurs during activity, since many retreat-sites used by toads in nature can impose significant rates of desiccation (Seebacher and Alford 1999). Opposing this, however, is our assumption that toads will emerge to forage independent of the desiccating power of their environment; presumably only a certain rate of water loss would be tolerated by toads before activity ceases. Unfortunately we have no information on the rate of desiccation at which a toad will stop activity and so cannot use this layer to constrain our range prediction. Our results, however, qualitatively show the desiccation risk to toads across the Australian landscape (Fig. 4d, Supplementary material, Fig. S4). Presumably, much of the arid interior of Australia would be unsuitable for adult activity due to the high desiccation risk and low water availability.

Our analysis indicates that the interior range-edge of cane toads in Australia is constrained by the availability of water in rain-filled ponds for breeding (Fig. 7). The exact locality of this range edge is very sensitive to the pond size and catchment area we modeled (Supplementary material, Appendix 1, Table S1, Fig. S8), and unfortunately there is little information available on these characteristics and how they vary spatially. Additionally, since our estimates are based on mean monthly rainfall, they also do not incorporate the extremely high variability of annual rainfall in arid Australia. While these aspects of our calculations are perhaps the least certain, they nonetheless show that breeding site availability is a key constraint limiting the penetration of the toads inland. In comparison, our predictions of the potential for egg and larval development show that thermal constraints on these stages of the cane toad's life cycle are relatively unimportant in limiting the southern extent of the toad's range (Fig. 7).

The potential range of the cane toad under current and future climate

For species in the processes of spreading, such as the cane toad in Australia, predictions based on correlative analyses between species occurrence data and spatial data often require extrapolation of complex statistical models into unsampled environmental space (Davis et al. 1998, Peterson 2003, Phillips et al. 2008b). A clear advantage, then, of the mechanistic approach to range prediction is that it requires no extrapolation. This permits more confident inferences on a species' potential range irrespective of the stage of invasion or degree of expected climate change. One difficulty with the mechanistic approach, however, is that the fundamental niche is many-dimensional and we may not expect to explore all the abiotic factors constraining a species' range. Similarly, it is not always clear at what point in a gradient a species can no longer persist. For example, it is difficult to know in advance the yearly desiccation rate below which toad populations cannot persist. Thus, without additional data, our analysis will tend to over-predict the potential range.

The potential distribution of the cane toad derived from our simulations covers a large area of northern Australia, and agrees broadly in this regard with predictions of the toads' range made previously using correlative approaches (Fig. 1). However, our results differ from previous analyses in the predictions of habitat suitability in southern Australia. In this region, our results clearly indicate that cane toads cannot survive, primarily because adult toads are severely constrained in their ability to move (and therefore, to forage and spawn). Why do some correlative approaches predict that toads can occupy southern Australia when our results indicate that toads cannot survive in these areas? The likely reason is that the contentious areas represent combinations of environmental conditions outside those currently experienced by cane toads in Australia. Because of this, the correlative models must extrapolate to give a prediction and such extrapolation is error prone. One way to reduce such extrapolation would be to use a mechanistic approach to define areas in which the species cannot persist (as we have done here). Once these areas are defined, pseudo-absence points could be generated within them and these pseudo-absence points could then inform a correlative model. In addition, output layers of mechanistic models

could be used as input layers for correlative models. Such mechanistically-derived layers are composites of multiple environmental conditions transformed through the traits of the organism into one composite variable that directly reflects fitness impacts, providing highly proximal variables for modelling (sensu Austin 2002). Thus, mechanistic approaches can be used in synergy with correlative approaches. Such synergies would potentially extract distribution information from both the basic physiology of the organism as well as its current known range, and would be a valuable avenue for further research.

Under a moderate anticipated climate change scenario for Australia in 2050, our analysis predicts both expansions and contractions in the potential range of the cane toad and in the length of its breeding season (Fig. 7d). The southern border is predicted to move further south by ca 100 km, but the extent of this expansion is limited by the opposing influences of increasing air temperature and decreasing humidity on core body temperature. The only major city at further risk of colonization by toads under climate change is Perth. There is also a predicted reduction in the length of the breeding season of up to four months across much of northern Australia (Fig. 7d), which is the result of high evaporation and low rainfall reducing the availability of suitable temporary water bodies for breeding throughout the year (Fig. 7c; Supplementary material, Fig. S5). This effect may work in favor of any attempts to control toad populations in the future, but may also have major negative impacts on native species that depend on temporary ponds.

We acknowledge the significant variability and uncertainty in climate change forecasts, especially with respect to variables other than temperature. Our prediction of the southern potential range limit will be especially sensitive to projected changes in temperature, rainfall, humidity and wind speed, and their covariance, since these variables interactively affect the body temperatures of active toads. Most climate change scenarios are similar in predicting a drier summer period in southern Australia <http://www.climatechangeinaustralia.gov.au/>. Our prediction of climate change impacts on the southern range limit should thus hold in a qualitative sense under scenarios other than the one we considered, unless there is a dramatic shift to wet summers in this region.

Evolution, phenotypic plasticity, and other extensions

In addition to delineating and mapping dimensions of the fundamental niche of an organism, our approach gives information on the key traits and environmental gradients behind range-constraints. Such information provides greater insight into the population-level limits to range spread (i.e. areas where population growth rate drops below one, or where dispersal drops to zero) as well as the potential for plastic (behaviour/acclimation) and evolutionary changes to alter these limits.

In this study we focused on traits that are clearly related to dispersal (e.g. movement potential) and population growth (e.g. opportunity for breeding). These are the two factors that determine the spread rate, and thus the ultimate extent of a species' range (Hengeveld 1989, Shigesada and Kawasaki 1997, Phillips et al. 2008b). Process-based models

of population spread usually must assume that the way a population grows and disperses is constant across that species' range (Hastings et al. 2005). While such an assumption is clearly incorrect, the difficulty of estimating the spatial variation in these factors has been a major impediment to long-range forecasting of the rates and routes of population spread. The approach we take here offers a solution to this difficulty; if we use physiological constraints to estimate dispersal and breeding opportunities we can express relative values in these key traits across space. Such data can be used as base-layers against which process-based models of population spread can be run (Hooten et al. 2007).

Additionally, our approach may provide information on the potential for species to evolve around current constraints because the capacity for adaptation along an environmental gradient will depend upon the steepness of that gradient (Hoffmann and Blows 1994). Thus, in northern Australia, the range of the cane toad is constrained by the limited availability of suitable natural water bodies, as well as by limitations on the tolerance of eggs and larvae to high temperature. Because this steep boundary mostly reflects the water-dependence of the larval stage, there may be little potential for evolutionary change to alter this range constraint in the cane toad. In southern Australia, however, the range limit is constrained by a gradual temperature and humidity boundary, which reduces the capacity for adult cane toads to forage. The gentle slope and stability of this gradient may present cane toads with an opportunity to evolve changes in their thermal sensitivity, and thus, to increase their range beyond that predicted by our models. Contrary to recent suggestions (Urban et al. 2007), however, our analysis requires no expansion of the niche of the cane toad since the species' arrival in Australia to explain its current range. Moreover there is no evidence that the thermal performance curve for locomotion has shifted at the southern border (Kolbe et al. unpubl.). Our sensitivity analyses did show that the posture of a foraging toad can have a significant impact on body temperature and thus activity potential (Supplementary material, Appendix 1), and geographical variation in this trait would be worthy of future study.

Generality of the approach and future directions

In summary, our analysis demonstrates the possibilities of combining the principles of biophysical ecology with high-resolution spatial data-sets to make inferences on a species' geographic constraints. Biophysical analyses can accommodate any kind of organism, life cycle, or habitat, including plants or animals, ectotherms or endotherms, and terrestrial or aquatic environments (Gates 1980, Porter et al. 2000, Porter and Mitchell 2006, Gilman et al. 2006). The Niche Mapper™ software we used is not due to be publicly available until late 2008. However it is available for collaborative work upon request (contact W.P.P). There is sufficient information in the literature (Porter et al. 1973, Gates 1980, Campbell and Norman 1998, Porter and Mitchell 2006) from which to construct customized biophysical models for any purpose (Gilman et al. 2006, Buckley 2008). While organism-specific data are necessary

to paramaterise the model, these data can be readily obtained with a relatively small, focused effort. The approach is based on an organism's traits and is completely independent of a species' current distribution. It thus circumvents the inherent uncertainty associated with the extrapolation of complex statistical models fitted to an organism's current range and thus allows more confident inferences on the potential range of range-shifting species. In addition, biophysical approaches provide insight into environmentally-driven spatial variation in population characteristics (such as dispersal and reproductive potential). Ultimately, such estimates can be used to drive models of population dynamics. Certainly, much can be inferred about the potential range of a species and the traits and environmental variables that constrain it, through identifying regions that are outside the fundamental niche.

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