

# Spatial and temporal variation in the morphology (and thus, predicted impact) of an invasive species in Australia

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The impact of an invasive species is unlikely to be uniform in space or time, due to variation in key traits of the invader (e.g. morphology, physiology, behaviour) as well as in resilience of the local ecosystem. The weak phylogeographic structure typical of an invasive population suggests that much of the variation in an invading taxon is likely to be generated by the environment and recent colonisation history. Here we describe effects of the environment and colonisation history on key morphological traits of an invader (the cane toad *Bufo marinus*). These “key traits” (body size and relative toxicity) mediate the impact of toads on Australian native predators, which often die as a consequence of ingesting a fatal dose of toad toxin. Measurements of museum specimens collected over >60 yr from a wide area show that seasonal variation in toad body size (due to seasonal recruitment) effectively swamps much of the spatial variance in this trait. However, relative toxicity of toads showed strong spatial variation and little seasonal variation. Thus, the risk to a native predator ingesting a toad will vary on both spatial and temporal scales. For native predators capable of eating a wide range of toad sizes (e.g. quolls, varanid lizards), seasonal variation in overall toad size will be the most significant predictor of risk. In contrast, gape-limited predators restricted to a specific range of toad sizes (such as snakes) will be most strongly affected by the relative toxicity of toads. Gape-limited predators will thus experience strong spatial variation in risk from toad consumption.

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Invasive species are generally considered to be a major threat to global biodiversity (Mack et al. 2000, Anon. 2001). Human-assisted transport and environmental change has broken down biogeographic barriers in many parts of the world leading to species invasions and irrevocable changes to native communities. Although some invaders have little impact on natural ecosystems, other taxa exert varying levels of impact, and this process can lead to local or global extinction (e.g. Williamson 1996, Ogutu-Ohwayo 1999).

Clearly, the magnitude of impact of an invasive species will be different not only for different native species, but also may vary among populations of any given species. Even if we restrict analysis to interactions

between a single predator-prey species-pair, for example, the magnitude of impact will be far from constant through space and time. For example, some populations of native taxa may be more or less vulnerable to the threat posed by the invader; and similarly, populations of the invader may differ in traits (such as body size or toxicity) that determine the intensity of their effect on the native system. Such spatial and temporal variance in traits of the invader may be generated either by plasticity or local adaptation; and if invading populations vary in such ways, this variation needs to be considered by ecologists and conservation biologists attempting to understand or manage the system (Parker et al. 2003).

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Because invasive populations typically exhibit minimal phylogeographic structure (associated with strong biogeographical non-independence following rapid population expansion), much of the variation within the total population of invaders is likely to be attributable to environmental effects, being expressed either through plasticity or rapid adaptation (Sakai et al. 2001, Allendorf and Lundquist 2003). Hence, much of the potential variance in impact from an invader is also likely to be generated by the local environment. Understanding how the environment affects an invader and how this flows on to affect impacted native species has the potential to clarify much of the spatial and temporal variation in the impact of invasive species.

For any invading taxon, the effect of the environment on key traits may depend not only on the environment itself, but also on how long the invader has been present in an area. A longer duration of time in a given area may allow the invading population to adapt (Lambrinos 2004), and also may allow time for the invader to modify the environment (e.g. by depressing resource levels). Thus, any analysis of the effect of the environment on an invasive species should incorporate information on the duration of time for which the invader has been present. Factors such as distributional range (Elton 1958), resource availability and coadaptation with native communities (Thompson 1998) may all be strongly influenced by recent history in invasive species.

The above ideas suggest the following approach to assessing the spatial and temporal variation in impact by an invading taxon: 1) First, we need to understand the mechanism of impact, in order to identify what traits of the invader (and possibly the native species) mediate that impact. These traits may be behavioural, morphological, and/or physiological. The important challenge is to identify traits for which changes are likely to modify the level of impact. 2) These traits need to be sampled at different locations and at different times. At each location, environmental variables that may influence the trait (including colonisation history) should also be sampled. 3) The effects of the environment and time on each trait should be modelled so that the resulting model can be mapped onto the area of interest.

Below we describe a case study examining temporal and spatial variation in predicted impact from an invasive species as a consequence of environmental factors, including colonisation history.

### **Case study: Australian predators and the invasive cane toad**

Cane toads are large, toxic anurans native to Central and South America. Introduced into Australia in 1935, toads have spread throughout large areas of Queensland and have recently entered the Northern Territory and New

South Wales. This invasive taxon currently occupies a range of more than one million square kilometres within Australia (Lever 2001). Toads reach extremely high densities in suitable habitat (densities  $>2000 \text{ ha}^{-1}$  have been recorded; Freeland 1986). Toads have three types of potential impact on Australian native species (Freeland 1987): 1) predation on small animals; 2) competition for food and/or shelter resources; and 3) because they are extremely toxic and the toxin is novel to Australian predators, toads are likely to kill most native predators that attempt to eat them.

Despite these three possibilities, the ecological impact of toads on the native Australian fauna has been poorly elucidated, mainly due to logistical difficulties and a lack of baseline data for comparison (van Dam et al. 2002). Nevertheless, there is mounting evidence that the bufonid invasion has massively impacted populations of native predators that attempt to eat toads and die as a consequence of ingesting the toxin. Specifically, evidence is accumulating that toads have had a severe impact on native snakes (Covacevich and Archer 1975, Fearn 2003, Phillips et al. 2003, Phillips and Fitzgerald 2004, Webb et al. 2005), varanid lizards (Burnett 1997, Smith and Phillips 2005), and quolls (a medium sized marsupial carnivore; Burnett 1997, van Dam et al. 2002, Oakwood 2003) all of which die attempting to eat toads. This mode of impact is the focus of the current analysis.

For a predator consuming a toad, the dose of toxin will depend upon two factors: the body size of the toad (bigger toads carry more toxin; Phillips and Shine 2005a), and the relative toxicity of the toad (even at the same size, some toads will be more toxic than others). These factors will be of different importance to different kinds of predator taxa. Some species (e.g. quolls and large varanids) are capable of capturing and consuming toads of a very wide range of body sizes. This is because either they are not gape-limited (quolls) or they are partially gape-limited but so large that they are able to ingest even the biggest toad (large varanids). For these species, toad size will be the most important variable determining the probability of the predator's survival after it has ingested a toad. For smaller species of gape-limited predators, however, such as most snakes and small varanid lizards, the size range of toads that can be ingested is limited by the predator's ability to swallow large prey (Shine 1991, Arnold 1993). Thus, such predators will capture and consume only relatively small toads. For these predators, maximal toad body size within a population will be irrelevant to risk; instead, the vulnerability of such predators will depend upon the relative toxicity of the toad (i.e. its toxicity relative to body size). Thus we need to examine two traits of cane toads: variation in body size, and variation in relative toxicity. Body size can be measured directly, using snout-ischium length (SIL) as a measure. Relative toxicity is more difficult to assess but conveniently, most toxin in

the skin of toads is stored in the large parotoid glands located above the shoulders (Meyer and Linde 1971). Thus, we can use the size of the parotoids as an index of the amount of toxin carried by a toad.

## Methods

### Collection of morphological data

We measured the 140 cane toads present in the collection of the Queensland Museum. This specimen series represented animals collected since 1935 (the year of toad arrival). Each individual was measured for snout-ischium length (SIL), parotoid gland length (PL) and parotoid gland width (PW). Information on collection locality and date of collection was also taken from the museum database.

### Collection of climatic data

We derived several climatic layers for Australia using the program ANUCLIM (Hutchinson et al. 1999) and a digital elevation model of Australia with 0.05° grid cells. Toad locality data were laid over the resultant climate grids in ARCVIEW. We extracted climatic data for each locality using the ARCVIEW extension BIOCLIMav (Moussalli 2003). We used several climatic variables that plausibly might influence toad morphology: annual mean temperature (AMT), minimum temperature of the coldest period (MinTempCP), annual precipitation (APrecip), precipitation seasonality (PrecipSeas), moisture index seasonality (MoisIndSeas), and annual mean humidity at 1500 h (AMHumid). While other variables were available, they were either highly correlated with our chosen variables (e.g. mean temperature of the warmest month is closely correlated with AMT) or unlikely to be of importance to toads (e.g. incident radiation – toads are nocturnal).

### Collection of data on time since colonisation

More than 2000 records of toad locality and date were available from the Queensland Museum and from the dataset collected by Floyd et al. (1981). These records were used to interpolate a map surface describing the arrival date of toads throughout Queensland (see Phillips and Shine 2004 for more details). Following the derivation of this surface, the Queensland Museum toad locality records were plotted and the year of toad arrival at each site was extracted. For each measured toad we subtracted the collection year (from the Queensland Museum database) from the year of toad arrival (from the GIS layer) to yield time since colonisation (TSC) – that is, the number of years a population of

toads had been present in an area at the time a toad was collected.

## Data analysis

Our primary aim was to derive a model that would capture as much of the effect of the environment on toad morphology as possible. For this purpose, we adopted a model selection approach. By testing the relative information content of all possible models, we selected the most parsimonious model (i.e. the model that explained the most variance with the least number of factors) describing environmental variation in toad morphology. This is easily done using Aikake's Information Criterion (AIC) which scores each model relative to others in a candidate set, penalising models with higher numbers of parameters and thus reducing the likelihood of over-fitting models.

Once we selected the best model we used it to map predicted body size and relative parotoid size within the toad's distribution. We predicted that collection month (the month in which a toad was collected), latitude, annual mean temperature, annual precipitation, minimum temperature of the coldest period, precipitation seasonality, moisture index seasonality and annual mean humidity may all influence toad morphology. Because many of the climatic variables were correlated to varying degrees, and to reduce the number of factors, we calculated the first three principal components of climatic and latitude variables. These principal components were used, along with TSC and collection month (CM) as independent variables in a multiple regression. We predicted that parotoid size and body size may vary throughout the year, hence the inclusion of CM. However if morphology does vary with CM, it is likely to be a quadratic relationship, therefore we also included a CM<sup>2</sup> term. Two analyses were run for each species. The first used toad snout-ischium length (SIL) as the dependent variable and the second used toad parotoid size. Parotoid size (PS) was calculated as the first principal component of the two parotoid size variables we measured (PL and PW). The first principal component of several linear measures is likely to be a more reliable indicator of structural size than either a single measure or than calculations based on assumptions about shape (e.g. Green 2001, Magnusson et al. 2003).

The multiple regression for toad parotoid size also included toad body size (SIL) as a fixed independent variable as we were only interested in changes in relative parotoid size. We log-transformed all variables prior to the calculation of principal components. Those variables not involved in principal components (TSC and CM) were mean-centered ( $y' = y - \bar{y}$ ) prior to analysis. Mean-centering (such that the new mean is zero) ensures

that estimated coefficients are informative even in the presence of interactions; this method also reduces colinearity between variables and their interaction terms (Jaccard and Turrisi 2003).

With six independent, non-fixed variables we had 62 combinations of primary variables that could produce a multiple regression model (ignoring interaction terms). To make model exploration and interpretation tractable we only examined first order interactions between factors. Each of these 62 combinations was run as a full model and we deleted interaction terms if p-values indicated they were not significant (i.e.  $p > 0.05$ ). For each combination of primary variables we thus derived the most parsimonious reduced model and we calculated the AIC value for this model. We collected the best set of multiple regression models for each species and each independent variable based upon these AIC values, with models  $< 2$  units from the best model (i.e.  $\Delta_i < 2$ ) retained within the best set (Burnham and Anderson 2001). All statistical analyses were performed with the JMP (v. 5.0) package (Anon. 2002).

Following the derivation of the best model, we reconstructed this model in Arcview, using the component factors to map environmental variation in toad morphology within the toad's Queensland range. Because collection month was an important factor in both models (see Results) we calculated each model at each month (1–12). We then averaged the results across the 12 months (to describe spatial variation in morphology) and also calculated the coefficient of variation (to describe the relative amount of seasonal variation). Because the relative parotoid size model also included toad body size (SIL) as a factor we calculated all maps for the relative parotoid size of a 60 mm toad.

## Results

### Calculation of multivariate model components

The first three principal components of climatic and latitude variables accounted for almost 95% of the variation in these seven factors (Phillips and Shine 2005b). Eigenvectors indicate that PCClimLat1 is principally a latitude/temperature axis and captures most of the latitudinal variation in the environmental factors. PCClimLat2 appears to be principally a precipitation axis, capturing the resultant variation in humidity and moisture index seasonality. PCClimLat3 is more difficult to interpret but may capture altitudinal variation in the environmental variables.

For toad parotoid size (PS), the first principal component of PW and PL captured  $> 99\%$  of the variation in both these variables (reflecting their strong correlation) with equal loadings on both.

### Toad snout-ischium length

The best model describing spatial and temporal variation in toad body size included all six independent variables and accounted for  $> 38\%$  of the variation in toad SIL. However we were unable to exclude the possibility of a second model in which PCClimLat3 was absent (Table 1).

### Toad parotoid size

The single best model describing variation in relative parotoid size was also complex, involving six independent variables (Table 1). All the climatic variables and both TSC and CM were present, although  $CM^2$  was absent. The single best model accounted for 98.7% of the variation in absolute parotoid size. However, almost all of this variance (98%) was explained simply by the size variable, SIL (i.e. bigger toads have bigger parotoid glands). Thus, our model explained 0.7% of the remaining 2% of variance. Hence, factors other than SIL (i.e. climatic and spatial factors) accounted for 35% of the residual variation in parotoid size (i.e. relative parotoid size).

### Mapping spatial variation in toad size and relative parotoid size

In both cases, our models explained ca 35% of the variation of our variable of interest (toad size or relative parotoid size). However, in both cases the model is complex, with several interaction terms making

Table 1. Parameter estimates for the best models describing toad body size (SIL) and relative parotoid size as a function of climate (PCClimLat1, 2 and 3), time since colonisation (TSC) and collection month (CM). Coefficients significantly different from zero are shown in bold. For brevity, PCClimLat has been further abbreviated to PC for interaction terms.  $\Delta_i$  represents the difference in AIC value from the best model.

Factors	Snout-ischium length		Parotoid size
	Model 1	Model 2	Model 3
Intercept	-0.183	-0.146	-0.009
SIL	-	-	<b>2.529</b>
PCClimLat1	<b>-0.050</b>	<b>-0.052</b>	<b>0.039</b>
PCClimLat2	<b>0.161</b>	<b>-0.125</b>	<b>0.049</b>
PCClimLat3	-0.195	-	-0.131
TSC	<b>-1.290</b>	<b>-1.547</b>	<b>-0.370</b>
CM	<b>-0.001</b>	<b>0.005</b>	<b>0.009</b>
$CM^2$	<b>0.013</b>	<b>0.011</b>	-
PC1 $\times$ PC2	<b>-0.064</b>	-	<b>-0.044</b>
PC1 $\times$ CM	<b>0.015</b>	<b>0.018</b>	-
PC1 $\times$ TSC	-	-	<b>0.176</b>
PC2 $\times$ TSC	<b>1.013</b>	<b>0.735</b>	<b>0.279</b>
PC2 $\times$ CM	<b>-0.031</b>	<b>-0.029</b>	-
PC3 $\times$ CM	-	-	<b>0.024</b>
$\Delta_i$	0	1.926	0
$r^2$	0.387	0.355	0.987

interpretation difficult. To examine the spatial pattern of body size and relative parotoid size variation, we translated our best models into GIS layers derived from the appropriate independent variables.

*a) Toad body size*

Despite significant spatial variation in average toad size, seasonal variation was even greater (Fig. 1). A high coefficient of variation across most of Queensland points to strong seasonal fluctuations in average body size, particularly in the north. This most likely reflects a massive seasonal influx of young toads each year, due to seasonal recruitment. The model predicts that average body size of toads will be highest in the Wet Tropics and

south-east Queensland, with low to moderate levels of seasonal variation in those areas.

*b) Relative parotoid size*

The spatial pattern in predicted relative parotoid size was complex but did not exhibit the massive seasonality apparent in the SIL model (Fig. 2). High seasonal variation was restricted to the Wet Tropics and small areas of south-east Queensland. Toads with relatively large parotoids were predicted to be present towards the north of the state with pockets of large-glanded individuals present in the Wet Tropics, mid-east and south-eastern Queensland. The model suggests that large-glanded individuals are present in some of the

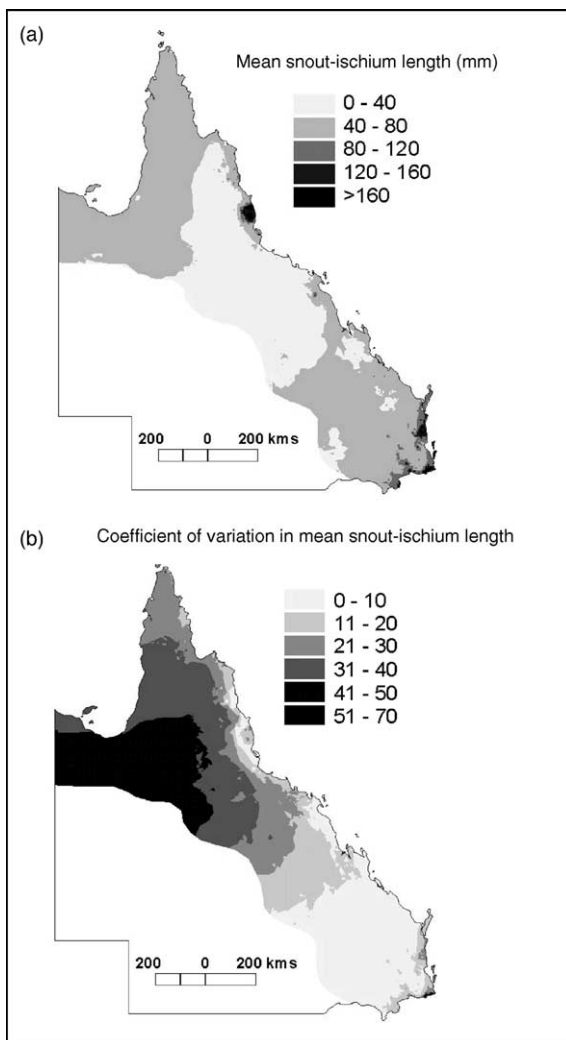


Fig. 1. Spatial and temporal variation in toad body size as predicted by climatic and temporal data. a) Mean snout-ischium length (SIL) across months, and b) the coefficient of variation for mean SIL across months.

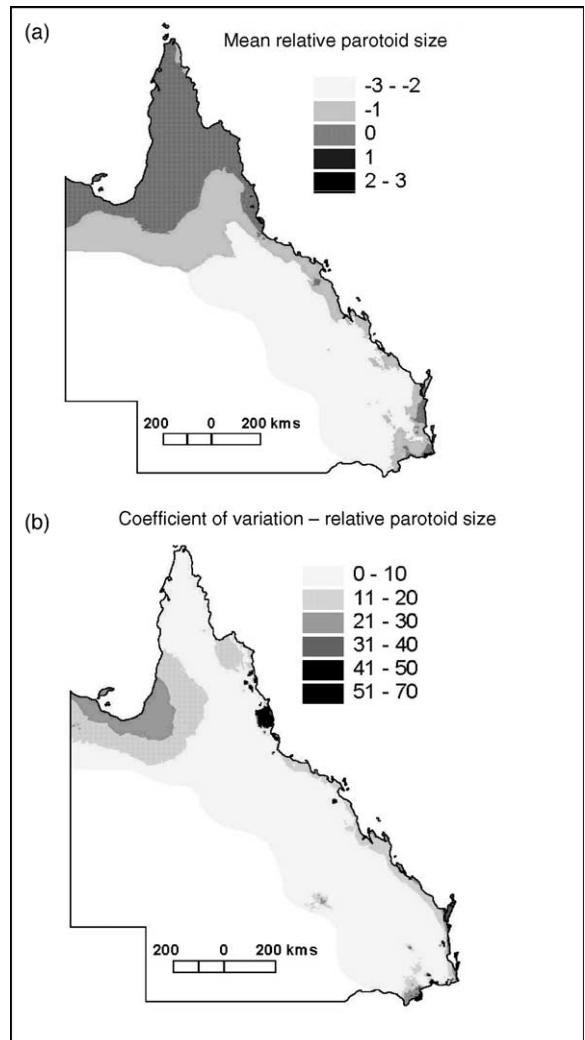


Fig. 2. Spatial and temporal variation in toad relative parotoid size (PS) as predicted by climatic and temporal data. a) Mean relative parotoid size across months, and b) the coefficient of variation for relative parotoid size across months.

areas that have been occupied by toads for long periods (mid and north Queensland), despite an overall trend for relative parotoid size to decrease with time since colonisation.

## Discussion

Our results suggest that climate, collection month, and time since colonisation all influence toad morphology. Because the resultant models are complex, mapping them across collection months enabled a better understanding of the results than simply examining coefficients. Additionally, mapping the models also provided a description of the spatial and temporal variation in our traits of interest. Mapping revealed that while spatial variation in toad body size (SIL) appears to be influenced by climate and time since colonisation, collection month has an overwhelming effect on predicted average SIL. Seasonal variation in SIL thus is likely to swamp the spatial effect of climate, particularly in north and north-west Queensland. In these areas, seasonal rather than spatial variation in toad size is likely to be the most important factor for a predator whose vulnerability to death by poisoning depends upon toad SIL (i.e. quolls and large varanids).

Conversely, relative parotoid size, although influenced by collection month, showed greater spatial variation and was affected by both time since colonisation and climatic variables. For predators constrained by prey size (and thus for which relative parotoid size determines predator vulnerability, e.g. snakes and small varanids), there appears to be meaningful spatial variation in the potential impact imposed by toads. Some of this variation can be explained by climatic variables and some of it can be explained by time since colonisation.

It is, however, important to note two caveats to these observations. First, our study used parotoid size as an index of toxicity, and we were not able to assess variation in the composition of the toxin. Presumably, these toxins may also display spatial and temporal heterogeneity. Thus two toads with the same parotoid size may differ in their toxicity to predators. Second, in any study utilising museum collections there is the potential for collection bias to influence results. Some of the patterns we observed (e.g. consistently large and invariable body size in southern Queensland) may reflect collection bias rather than reality. In these two regards, our conclusions are tentative and require further investigation.

Interestingly though, our models reiterate an earlier result from a simpler analysis (Phillips and Shine 2005b), in that time since colonisation (TSC) had had a significant effect on toad morphology, in terms of both SIL and relative parotoid size. In areas where toads have

been present for a long period, the animals tend to be small and to have relatively small parotoid glands. Our maps of toad morphology represent an extrapolation from our original dataset in that TSC is currently greater than 66 yr in many areas although it rarely exceeded 55 yr in our dataset. The extrapolation of the negative trend in relative parotoid size with TSC is reflected in predicted values of relative parotoid size that are rarely positive in our map. The strong effect of recent colonisation history on toad morphology is a powerful reminder of the importance of history in landscape-level patterns, and thus of the need to incorporate recent history into models such as ours.

Although spatiotemporal projection of our SIL model predicted high seasonal variation in toad body size, some areas are expected to maintain large average body sizes throughout the year (the Wet Tropics and south-east Queensland). These large body size areas included parts of the state where toads were first introduced (Fig. 2). Superficially, the prediction of large body sizes in some areas long after initial colonisation appears inconsistent with the overall negative effect (i.e. partial coefficient) of TSC. Mapping also revealed that some of the areas with the largest relative parotoid size are areas where toads were first introduced (the same anomalous areas as for variation in SIL; Fig. 2). This is another apparent contradiction of our overall prediction of a reduction in parotoid size with increasing time since colonisation (based simply on the partial coefficient for TSC).

These apparent anomalies can be explained by two facts. First, our model predicts shifts in the effect of TSC with precipitation and latitude (i.e. interactions). For SIL, the effect of TSC will be negative except in areas of high precipitation; for relative parotoid size both high precipitation and low latitude/high temperature will change the effect of TSC in a positive direction. These complexities reduce and sometimes reverse overall trends of toad body size relative to time since colonisation. Second, toads were not introduced to climatically random areas of Queensland. They were first introduced into major sugar cane growing districts i.e. areas with high precipitation and warm temperatures. Thus, the areas where toads were first introduced are the same areas where our model suggests that time since colonisation should cause little or no decrease in either body size or relative parotoid size. This effect could explain why a previous study based on comparison of “old” and “new” populations (Alford et al. 1995) found no effect of time since colonisation on toad body size.

Our best model describing toad size accounted for 38% of the variation in toad body size. Toad age presumably accounts for a large portion of the additional variation in toad size and was not explicit in our model. For relative parotoid size, our best model

accounted for 35% of the variation (both amounts indistinguishable from the mean value for  $r^2$  observed in observational ecological studies; Peek et al. 2003). Other factors such as water pH or the presence or absence of predators and competitors are known to affect amphibian morphology (Relyea 2001, van Buskirk 2002) and data on such topics were unobtainable in the current study. Additional investigation into the factors affecting the relative toxicity of toads would be of great interest, to further tease apart the processes generating spatial and temporal variation in morphological traits of this invading species.

Nevertheless, our models do indicate significant variation in relative parotoid size due to climate and colonisation history, and thus allow us to outline spatial variation in the likely intensity of selection that toads impose on native predators. This is especially true for gape-limited predators that are restricted to a specific size range of toads. Because of the spatial variation in relative toxicity of toads, two identical predators in different areas feeding on same-sized toads will have different chances of ingesting a fatal dose of toxin. Our model suggests that at least some of this difference in predator vulnerability can be related to differences in climate and time since colonisation. Further work is necessary to elucidate other environmental factors affecting toad parotoid size. An improved understanding of the factors influencing parotoid size will allow the identification of areas where selection from toads is weakest and it is in these areas that impacted native populations have the highest chance of survival and eventual adaptation. Certainly, evidence is mounting that impacted native predators do survive in some areas with toads and that these populations exhibit adaptive change in response to toad presence (Phillips and Shine 2004, Phillips 2005). The results here show that all areas are not equal in terms of toad impact. While the areas most suitable for a native predator to mount an adaptive response will be specific to each native species (due to their habitat preferences and the nature of their interaction with toads), there are obvious advantages in areas where toads are less toxic.

The approach that we have adopted in this analysis is potentially applicable to many invasive species systems. Identifying traits mediating the impact on natives and then quantifying spatial and temporal variation in those traits provides a tool for predicting the level of impact and how it varies in time and space. Such information can be used by both conservation biologists and managers in their attempts to mitigate impacts of invasion. Such analyses may also prove useful to ecologists and evolutionary biologists utilising invasive species systems to answer theoretical questions.

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