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REVIEW PAPER

# Species level traits determine positive and negative population impacts of invasive cane toads on native squamates

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**Abstract** The novel interactions posed by invasive species can have complex effects on ecosystems owing to both their direct and indirect effects on other species. Consequently, the effects of invasive species can be hard to forecast owing to the diversity of interaction-pathways and number of species they can potentially affect. Ultimately, the strength and direction of an invader's inter-specific effects will be determined by both the traits of the invader and the species they interact with. The cane toad (*Rhinella marina*) is a highly successful invasive species that poses a serious threat to ecosystem integrity in tropical Australia. Reptilian predators have been particularly affected by the invasion of cane toads because toads possess toxins that are novel to native Australian predators. We used a meta-regression approach to explore how cane toads' impacts on Australian squamates are modulated by their phylogenetic, behavioural and morphological traits. Species primarily foraging in riparian and terrestrial habitats tended to decline in abundance while population sizes of arboreal squamates might have increased following toad arrival. The negative impact of cane toads on anurophagous squamates scaled with gape size and body mass. Squamate species with smaller heads or body mass tended to increase in abundance while species with larger heads or body mass tended to decline. Our study provides insight into the complexity of impacts that invasive species can have on native species assemblages and highlights how morphological and behavioural factors can mediate the impact of invasive on native species.

**Keywords** Behavioral traits · Invasive species · Meta-regression analysis · Morphological traits · *Rhinella marina*

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## Introduction

The novel inter-specific interactions posed by invasive plant and animal species are a major driver of global environmental change (Vitousek and D'Antonio 1997). While much of the research on invasive species' effects has focused on the negative population level effects they can have on native species, their impacts within communities can be highly variable and range from negative, neutral to positive (Parker et al. 1999; Strayer et al. 2006; Letnic et al. 2009).

Positive or facilitatory effects of invaders can arise in numerous ways. For example, invaders can benefit other species by providing an ample source of food or suitable habitat. Invaders can also benefit some species within ecosystems via cascades of indirect interactions that occur when invaders shift the balance of competitive and predatory interactions so that populations of species are no longer regulated by competition or predation (Parker et al. 1999; Mack et al. 2000; Bruno et al. 2003; Rodriguez 2006). Thus, even if an invader directly interacts with only a few species in its new environment it can potentially disrupt the structure and function of whole ecosystems (Mack et al. 2000).

While much research investigating the relative success and impact of invasive species has focused on the traits of the invader, the strength and direction of invasive species interactions can also be determined by the traits of species and individuals within the ecosystems that are invaded (Fisher and Owens 2004). For example, behavioural traits that influence encounter rates with an invader such as habitat selection or morphological traits such as the body size of the animals within invaded assemblages can be important determinants of invasive animals' impacts (Phillips and Shine 2004; Johnson and Isaac 2009; Letnic et al. 2009).

The cane toad (*Rhinella marina*) is one of the world's most successful invasive species (Shine 2010). Since their introduction to Australia in 1935, cane toads have spread across more than 1.2 million square kilometres of the continent (Urban et al. 2007). As members of the bufonids, cane toads possess potent chemical defences such as bufotoxins and bufogenins (Zug and Zug 1979) that are absent from Australia's native fauna (Daly et al. 1987). Consequently, most native Australian predators lack the evolutionary history of exposure to these chemicals and many of them die after consuming toads (Lever 2001; Ujvari et al. 2012).

Predictions of cane toads' impacts on Australian wildlife have focused largely on negative impacts, arising from lethal ingestion of toads by predators, competition with toads and predation by toads (e.g., Phillips et al. 2003; Smith and Phillips 2006; Greenlees et al. 2007). However, recent studies suggest that the impacts of cane toads on populations of native Australian species are more complex, with populations of some species negatively affected (Doody et al. 2006; Griffiths and McKay 2007; Letnic et al. 2008) and populations of other species being either unaffected or even benefitting from the arrival of cane toads (Doody et al. 2006, 2013; Brown et al. 2013a, b). Indeed, the complexity of cane toads' impacts on reptilian predator assemblages is highlighted by recent studies indicating that the impacts of toads vary dramatically between populations of the same species with some populations showing dramatic declines following cane toad arrival while other populations appear unaffected (Doody et al. 2013, 2014; Somaweera et al. 2013).

In the case of Australia's reptilian predators, the variation in toad impact between species does not appear to just be a function of resistance to toad toxins, as most species are highly susceptible to toad toxins (Phillips et al. 2003; Smith and Phillips 2006; Shine 2010). Plausible explanations for the variation in cane toad impacts on reptilian predators are that the strength of cane toads' inter-specific interactions are modulated by environmental factors (Somaweera et al. 2013), complex networks of direct and indirect interactions within ecosystems (Montoya et al. 2006; Doody et al. 2013) and species-level traits that determine the frequency and outcomes of encounters with toads such as the occurrence of anurans in the natural diet and the morphological ability to prey on especially large anurans such as the cane toad (Phillips and Shine 2004).

In this article we used a meta-regression approach to conduct the first quantitative review on the impact of cane toads on native Australian wildlife. We synthesised the results of published studies on the population-level impacts of cane toads on Australian squamates to explore how the magnitude and direction of these impacts are modulated by phylogenetic and behavioural traits. In addition, we tested the hypothesis introduced by Phillips et al. which predicts that cane toad impact could be a function of morphological traits, across multiple species.

## Materials and methods

### Literature survey

To assemble a collection of studies for our analyses, we searched within the online databases of ScienceDirect, JSTOR, Zoological Record and Google Scholar using combinations of the keywords *Bufo marinus*, *Rhinella marina* and cane toad with the keywords impact, effect, invasive species and survey. Additionally, we screened articles already retrieved and the reference list of a qualitative review on the impact of cane toads (Shine 2010). We restricted the studies included in our meta-regression analyses to those published in peer-reviewed journals that reported quantitative results of fauna surveys (abundances, trapping or survey success rates) conducted before and after the arrival of cane toads in the habitat.

### Data collection and analysis

We calculated effect sizes to quantify the statistical relationship between the presence of cane toads and changes in abundance for each species in each study (Table 1). When studies presented data from several survey areas we treated them as independent datasets and calculated effect sizes for each area separately. Multiple effect sizes for a single species from different studies or survey areas were treated as individual data points. To compensate for potential non-independence of response variables, study and species were included as random effects in our linear mixed effects models (see below).

As a metric of effect size, we calculated Pearson's correlation coefficient $r$ for each study survey from the combined mean results of surveys conducted before the invasion of toads and the combined mean results of surveys conducted after toad invasion. Data were retrieved by extracting means, sample sizes and standard deviations for each survey before and after the arrival of toads from text, tables or figures of the studies. The values of data extracted from figures were determined by using electronic callipers. In studies where values for the standard deviations were missing we deduced them from standard errors or confidence intervals and sample sizes. For one publication (Price-Rees et al. 2010) we used the given $F$- value and probability to calculate the effect size.

We used Fisher's $Z_r$ transformation on our metric of effect size in combination with the respective sample size to transform the not normally distributed $r$-variable into the normally distributed $Z_r$-variable. Negative $Z_r$-values indicated a decrease in abundance of the

Table 1 List of species and body measurements used for the meta-regression analyses

| Species | Habitat | Anurophagy | Head width (mm) | Body mass (g) | $Z_r$ | Study |
|---|---|---|---|---|---|---|
| Agamidae | | | | | | |
| *Amphibolurus gilberti* | Arboreal | No | $15.0^{a}$ | $30^{a}$ | 0.51 | Doody et al. (2009) |
| *Amphibolurus gilberti* | Arboreal | No | $15.0^{a}$ | $30^{a}$ | 0.40 | Doody et al. (2009) |
| *Chlamydosaurus kingii* | Arboreal | No | $48.3^{b}$ | $395^{b}$ | 0.70 | Ujvari et al. (2011) |
| *Chlamydosaurus kingii* | Arboreal | No | $48.3^{b}$ | $395^{b}$ | −0.68 | Ujvari et al. (2011) |
| *Chlamydosaurus kingii* | Arboreal | No | $48.3^{b}$ | $395^{b}$ | 0.08 | Ujvari et al. (2011) |
| Boidae | | | | | | |
| *Antaresia childreni* | Terrestrial | Yes | $15.5^{c}$ | $228^{c}$ | 0.13 | Brown et al. (2011) |
| *Liasis fuscus* | Riparian | No | $17.7^{b}$ | $541^{b}$ | −0.18 | Brown et al. (2011) |
| *Morelia spilota* | Terrestrial | No | $55.1^{d}$ | $2{,}139^{d}$ | −0.22 | Brown et al. (2011) |
| Colubridae | | | | | | |
| *Boiga irregularis* | Arboreal | No | $21.9^{c}$ | $300^{c}$ | 0.39 | Brown et al. (2011) |
| *Dendrelaphis punctulatus* | Arboreal | Yes | $19.7^{c}$ | $218^{c}$ | 0.43 | Doody et al. (2013) |
| *Dendrelaphis punctulatus* | Arboreal | Yes | $19.7^{c}$ | $218^{c}$ | 0.49 | Doody et al. (2013) |
| *Stegonotus cucullatus* | Terrestrial | Yes | $18.6^{c}$ | $303^{c}$ | 0.11 | Brown et al. (2011) |
| *Stegonotus cucullatus* | Terrestrial | Yes | $18.6^{c}$ | $303^{c}$ | 0.61 | Brown et al. (2013b) |
| *Tropidonophis mairii* | Terrestrial | Yes | $12.5^{c}$ | $84^{c}$ | 0.21 | Brown et al. (2011) |
| *Tropidonophis mairii* | Terrestrial | Yes | $12.5^{c}$ | $84^{c}$ | −0.61 | Brown et al. (2013b) |
| Elapidae | | | | | | |
| *Acanthophis praelongus* | Terrestrial | Yes | $20.1^{c}$ | $118^{c}$ | −0.45 | Brown et al. (2011) |
| *Acanthophis praelongus* | Terrestrial | Yes | $20.1^{c}$ | $118^{c}$ | −0.58 | Phillips et al. (2010) |
| *Cryptophis pallidiceps* | Terrestrial | Yes | - | - | 0.27 | Brown et al. (2011) |
| *Furina ornata* | Terrestrial | No | - | - | 0.26 | Brown et al. (2011) |
| *Pseudechis australis* | Terrestrial | Yes | $55.0^{e}$ | $3{,}000^{f}$ | −0.19 | Brown et al. (2011) |
| *Pseudonaja nuchalis* | Terrestrial | Yes | $37.4^{g}$ | $3{,}000^{f}$ | −0.01 | Brown et al. (2011) |

**Table 1** continued

| Species | Habitat | Anurophagy | Head width (mm) | Body mass (g) | $Z_r$ | Study |
|---|---|---|---|---|---|---|
| Pygopodidae | | | | | | |
| *Lialis burtonis* | Terrestrial | No | $10.0^{a}$ | $15^{a}$ | −0.20 | Brown et al. (2011) |
| Scincidae | | | | | | |
| *Tiliqua scincoides* | Terrestrial | Yes | $36.7^{h}$ | $510^{h}$ | −0.94 | Brown et al. (2011) |
| *Tiliqua scincoides* | Terrestrial | Yes | $36.7^{h}$ | $510^{h}$ | −0.70 | Price-Rees et al. (2010) |
| Varanidae | | | | | | |
| *Varanus mertensi* | Riparian | Yes | $34.2^{b}$ | $1,689^{b}$ | −0.71 | Doody et al. (2009) |
| *Varanus mertensi* | Riparian | Yes | $34.2^{b}$ | $1,689^{b}$ | −1.12 | Doody et al. (2009) |
| *Varanus mertensi* | Riparian | Yes | $34.2^{b}$ | $1,689^{b}$ | −0.52 | Griffiths and McKay (2007) |
| *Varanus mertensi* | Riparian | Yes | $34.2^{b}$ | $1,689^{b}$ | −1.42 | Doody et al. (2014) |
| *Varanus mitchelli* | Terrestrial | Yes | $22.8^{b}$ | $214^{b}$ | −0.77 | Doody et al. (2009) |
| *Varanus mitchelli* | Terrestrial | Yes | $22.8^{b}$ | $214^{b}$ | −1.55 | Doody et al. (2009) |
| *Varanus panoptes* | Terrestrial | Yes | $38.8^{b}$ | $2,849^{b}$ | −1.81 | Doody et al. (2006) |
| *Varanus panoptes* | Terrestrial | Yes | $38.8^{b}$ | $2,849^{b}$ | −1.46 | Doody et al. (2006) |
| *Varanus panoptes* | Terrestrial | Yes | $38.8^{b}$ | $2,849^{b}$ | −1.36 | Doody et al. (2009) |
| *Varanus panoptes* | Terrestrial | Yes | $38.8^{b}$ | $2,849^{b}$ | −1.34 | Doody et al. (2009) |
| *Varanus panoptes* | Terrestrial | Yes | $38.8^{b}$ | $2,849^{b}$ | −2.24 | Brown et al. (2013b) |

$Z_r$ is the effect size calculated from Pearson's correlation coefficient $r$ using Fisher's $Z_r$ transformation

[a] Own measurements

[b] Smith and Phillips (2006)

[c] Phillips et al. (2003)

[d] Pearson et al. (2002)

[e] Thomson (1933)

[f] Kuch et al. (2005)

[g] Skinner (2009)

[h] Herrel et al. (1997)

respective species after toad invasion while positive values indicated an increase in abundance. We considered $Z_r$-values ranging from 0 to ±0.1 as unaffected, ±0.1 to ±0.3 as a weak, ±0.3 to ±0.5 as a moderate and values exceeding ±0.5 as a strong effect. In cases where the 95 % confidence intervals crossed zero, results were regarded as no general effect.

### Predictor variables

We selected a set of variables as predictors of expected differences in the risk of population level effects due to the presence of cane toads. The environmental predictors included the categorical variables diet and foraging habitat. We expected anurophages to have experienced a higher risk of lethal ingestion and thus a stronger negative impact than non-anurophages. As cane toads are restricted to terrestrial and in particular aquatic environments (Zug and Zug 1979), we predicted that squamates foraging in these habitats should have experienced a higher impact than arboreal species. To test whether the impact of cane toads differs between different squamate lineages, we used family as an additional categorical predictor variable.

In addition to the categorical variables, we expected the morphological traits of head width and body mass to be important determinants of the impact of cane toads on species foraging on anurans. As the effect of toxin on an individual squamate is dose-dependent (Phillips et al. 2003) species with a wider head and therefore a larger mouth gape size are able to ingest bigger toads that might deliver a potentially fatal dose of toxin. Hence, it has been hypothesized that species with wider heads could experience a stronger negative impact than squamate species with more narrow heads (Phillips and Shine 2006a). Accordingly, we expected a negative relationship between body mass and effect size in anurophage squamates. In contrast, squamate species with higher body mass might be more likely to survive attacking or consuming a cane toad. Hence, we expected a positive relationship between body mass and effect size in anurophage squamates. Average body measurements for head width and body mass of adult squamates have been acquired from the literature. To normalize variability in body mass and head width, $\log_{10}$ values were used for the analysis.

### Statistical analyses

We used linear mixed models (LMMs) fitted by the relative maximum likelihood to conduct meta-regression analyses following the method of Nakagawa et al. (2007). This approach allowed us to use grouping random factors even though one or more groups included only a single effect size (i.e., only one effect size per species) without the necessity of merging groups with multiple effect sizes to one overall effect size (i.e., for different populations of the same species; Nakagawa et al. 2007). In each model we used effect sizes as dependent variables and study and species as random factors.

To test whether variation in effect sizes within the dataset could be partitioned among the subgroups of family, diet and habitat we generated LMM using each of the subgroups as fixed predictors.

To test whether variation in effect sizes within the dataset could be explained by physiological traits we generated LMM with body mass and head width as covariates for the subgroups of anurophages and non-anurophages.

We located 10 studies reporting impacts of cane toads on a total of 19 tropical squamate species published in peer-reviewed scientific journals between 2006 and 2014 (Table 1).

Based on results reported from multiple survey areas within these studies, we could calculate 35 independent effect sizes. Because research on the ecological impacts of cane toads has only been published within the last 10 years, the dataset used in this paper is relatively small when compared to those in some meta-analyses. However, as an estimator of publication bias we calculated the fail-safe number, which indicates the number of studies that would have to be added to change the results of our analyses from significant to non-significant as 288 (Rosenthal 1979). As this value is larger than $5N + 10 = 185$ with $N$ number of effect sizes in our dataset, we are confident that, despite the small sample size, the observed results can be regarded as reliable estimates of the true impacts. Furthermore, an additional visual inspection funnel plot of effect size versus sample size did not indicate publication biases that could be expected if non-significant results with low replication were less likely to be published (Møller and Jennions 2001).

## Results

We found no overall significant effect of cane toads for all the data combined (Fig. 1). To explore factors that might explain variability in effect sizes we generated LMM with the factors diet, habitat and family and the covariates body mass and head width.

The regression analysis with diet as sole predictor revealed that anurophages responded with moderate population level declines to the presence of cane toads whereas populations of non-anurophages remained more stable (Fig. 1). The regression analysis with habitat as sole predictor revealed that predators in terrestrial and riparian habitats on average responded with strong declines in abundance following the arrival of cane toads contrasting the response of arboreal species which showed a general trend to moderately increasing abundances (Fig. 1).

The regression analysis with head width as covariate showed, in line with our expectations, a negative correlation between head width and effect size in anurophages ($-0.42 \pm 0.19$, $t = -2.24$, $p < 0.05$) but no correlation in non-anurophages ($-0.25 \pm 0.22$, $t = -1.15$, $p = 0.248$; Fig. 2).

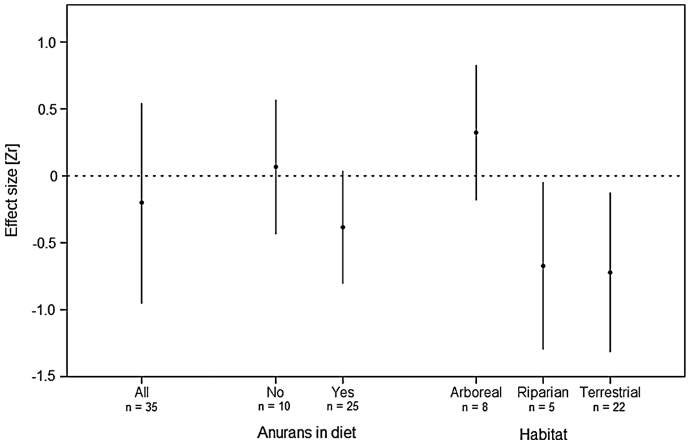
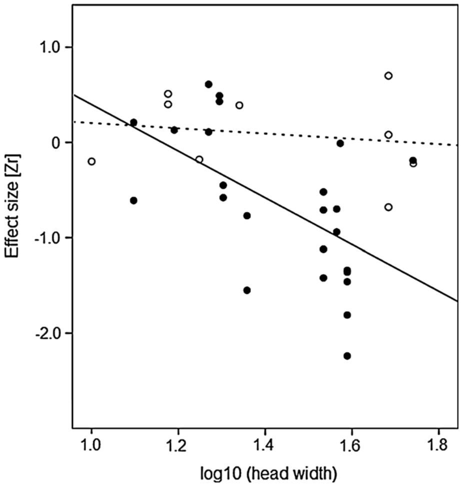


**Fig. 1** The impact of cane toads on Australian squamates categorized by diet and habitat. Mean effect sizes and 95 % confidence intervals were generated by linear mixed-effect models fitted with restricted maximum likelihood. All models include the random effect terms study and species

**Fig. 2** Correlation between the impact of cane toads (*Rhinella marina*) and head width of Australian squamates. *Lines* indicate linear regressions calculated for the two subgroups of anuran consuming squamates (*filled circles*) and squamates that do not consume anurans as regular part of their diet (*open circles*)



The regression analysis with body mass as covariate showed, contrary to our expectations, a negative correlation between body mass and effect size in anurophages ($-1.25 \pm 0.56$, $t = -2.20$, $p < 0.05$). We found no correlation between body mass and effect size in non-anurophages ($-0.87 \pm 0.55$, $t = -1.51$, $p = 0.132$; Fig. 3).

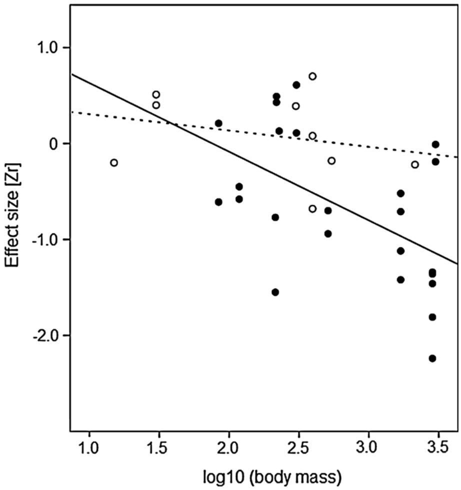
The regression analysis with family as sole predictor revealed that populations of Agamidae and Colubridae on average increased following toad arrival (Fig. 4). In contrast, monitor lizards and bluetongues [only one species, northern bluetongue skinks (*Tiliqua scincoides intermedia*), included in the analysis] experienced strong population declines (Fig. 4). Populations of snakes belonging to the families of Boidae and Elapidae showed no general trend after the arrival of cane toads (Fig. 4).

## Discussion

Most of the studies on the impact of cane toads on native squamates have reported negative population level changes as a result of direct interactions with cane toads (i.e., poisoning). Our meta-analysis showed that these negative consequences can be found primarily in populations of squamates foraging in riparian and terrestrial environments. A likely explanation why negative impacts are frequent in these habitats is that species are at higher risk of population level declines because of the restriction of cane toads to terrestrial and in particular freshwater habitats (Zug and Zug 1979) that puts squamates in these environments at greater risk of a fatal encounter in comparison to species foraging in arboreal habitats.

In contrast, a differentiation between causality and coincidence between cane toad invasion and population level increases in arboreal species is more difficult. In particular, as it is unlikely that these positive impacts resulted from direct interactions due to cane toads acting as a food source, because squamates that experienced consistent population level increases are either highly susceptible to toad toxin [common tree snakes (*Dendrelaphis punctulatus*) and brown tree snakes (*Boiga irregularis*) Phillips et al. 2003] or do not feed on anurans [Gilbert's dragons (*Amphibolurus gilberti*)]. Observations on frill-necked lizards (*Chlamydosaurus kingii*), illustrate the difficulty in determining a causality

**Fig. 3** Correlation between the impact of cane toads (*Rhinella marina*) and body mass of Australian squamates. *Lines* indicate linear regressions calculated for the two subgroups of anuran consuming squamates (*filled circles*) and squamates that do not consume anurans as regular part of their diet (*open circles*)



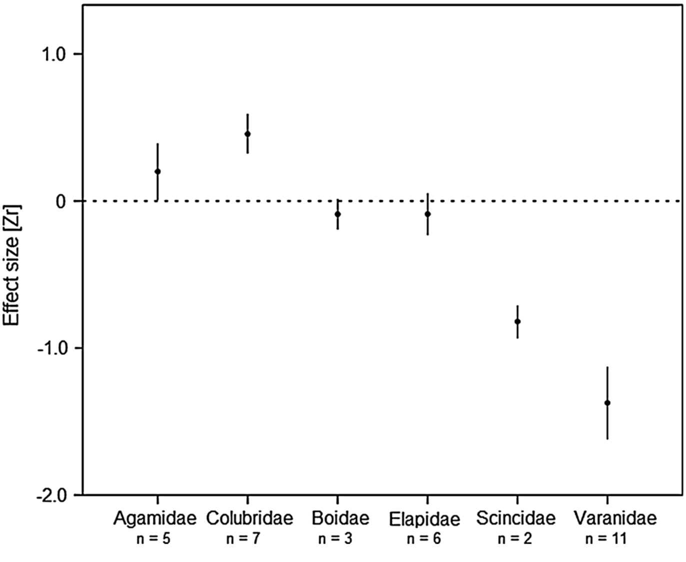


**Fig. 4** The impact of cane toads on Australian squamates categorized by family. Mean effect sizes and 95 % confidence intervals were generated by linear mixed-effect models fitted with restricted maximum likelihood. All models include the random effect terms study and species. Both studies included in the Scincidae family were of the same species, *Tiliqua scincoides intermedia*

for such changes from observations in singular studies (Ujvari et al. 2011). Here, one population increased, whereas another decreased and a third did not show changes in abundance after toad invasion. Studies on single populations could thus indicate a causality between cane toad invasion and changes in abundance whereas the three observations taken together suggest that cane toads had only little or no effect on the abundance of frill-necked lizards (Ujvari et al. 2011). Increases in abundance of common tree snakes and Gilbert's dragons, however, were consistent between populations and could thus illustrate indirect consequences of invasion by cane toads as a result from a release from predation by monitor lizards and snake species whose populations have been suppressed by toads (Doody et al. 2009, 2013).

Less difficult to examine than indirect positive effects is how potential direct negative impacts scaled with morphological traits of the affected species. The amount and composition of toxin in an individual toad depends on its body size with smaller adult and juvenile toads containing less and a different composition of chemical defences than larger toads (Phillips and Shine 2006b; Hayes et al. 2009). Because the size of prey that squamates can ingest is limited by their gape, ontogenetic variation in toad toxicity puts predators with wider heads that are capable of capturing and consuming large toads at greater risk of lethal ingestion (Phillips and Shine 2006a; Phillips et al. 2010). Conversely, species with smaller heads may not be capable of ingesting toads big enough to deliver enough poison to be fatal and thus remain unaffected by the invasion of cane toads. In line with this argument, we found that the magnitude of toads' population level effects on squamates that consume anurans as a regular part of their diet scaled with head width. Anurophagous squamates with smaller heads were less or not negatively affected by toad invasion while species with especially big gape sizes [monitor lizards (*Varanus spec.*), northern bluetongue skinks and death adders (*Acanthophis praelongus*)] experienced strong population declines following the arrival of toads. In contrast, effect size was not correlated with head width in squamate species that are not known to consume anurans as a regular part of their diet. Here, even species with large gape sizes did experience no (frill-necked lizards) or only weak population level declines [carpet pythons (*Morelia spilota*)] after toad arrival.

In contrast to our expectations, the impact of cane toads on anuran-consuming squamates was correlated negatively with body mass. The strong correlation between body weight and head width (Spearman's $\rho = 0.799$, $p < 0.001$) of species included in our analysis could be a factor contributing to this finding as species with higher body mass also had gape sizes that likely enabled them to prey on cane toads big enough to deliver a fatal dose of toxin. Indeed, some larger squamates need less than their maximum gape size to ingest a toad of a size sufficient to provide an $LD_{50}$ of bufotoxins [e.g., yellow-spotted monitors (*V. panoptes*) 55.3 % and frill-necked lizards 33.2 % Phillips et al. 2003]. However, in species of smaller body mass the gape size is more likely to limit toxin intake to a non-fatal level (e.g., keelback snakes (*Tropidonophis mairii*) 185.5 % Smith and Phillips 2006].

At family level, populations of monitor lizards (Varanidae) and northern bluetongue lizards (Scincidae) experienced the strongest and also the only consistent negative impact. In addition to their high vulnerability to toad poison (Smith and Phillips 2006; Price-Rees et al. 2010; Ujvari et al. 2012) these strong effects of toads on monitors and blue-tongue lizards may be due to their foraging in terrestrial and freshwater habitats which enhances the chance of potential fatal encounters with cane toads (Doody et al. 2009).

Colubrid snakes, in contrast, experienced population increases after toad arrival. In addition to the possibility of predatory release of common tree snakes following toad induced declines (Doody et al. 2013), the positive effect on the abundances of the two other Colubrids in our analysis, keelback snakes and slatey-grey snakes (*Stegonotus cucullatus*), could also be the result of these species benefiting from increased availability of prey following the invasion of cane toads, because these species have high levels of tolerance to toad toxin and are known to prey on toads with little ill effect (Phillips et al. 2003; Llewelyn et al. 2009). However, studies confirming such a cause and effect relationship are missing and these findings could be coincidental rather than a consequence of cane toad invasions.

We found no general impact of cane toads on populations of the two other snake families in our analysis, Boids and Elapids. The finding for Boids is consistent with pre-toad invasion predictions of toad impacts which placed Boids at low risk of toxic ingestion due to their preference for feeding on mammals and reptiles (Phillips et al. 2003). The absence of an overall effect of toads on Elapids despite their generally low resistance to toad toxins (Phillips et al. 2003) may be due to the wide range of life-history and morphological traits present in this group. While many species of Elapid such as death adders and king brown snakes (*Pseudechis australis*) are thought to be at risk of toad poisoning because of their preference for feeding on anurans and their large gape size (Phillips et al. 2003; Shine 2010), smaller species within this family which do not feed on toads, such as the orange-naped snake (*Furina ornata*) and the northern small-eyed snake (*Cryptophis pallidiceps*), have experienced population increases following the arrival of cane toads. These population increases may be due to predatory release, owing to cane toads suppressive effects on predators of small snakes such as the larger Elapid snakes and monitor lizards (Doody et al. 2009, 2013).

## Conclusion

Our study provides insight into the complexity of impacts that invasive species can have on native species assemblages and highlights how morphological and behavioural factors can mediate the impact of invasive on native species. In the case of cane toads in Australia, the variation in the direction and magnitude of their impact on native squamates can be linked to a combination of behavioural and morphological traits of these species. Terrestrial predators and predators capable of ingesting large prey are more likely to be negatively affected by the presence of cane toads. Conversely, some arboreal squamates and smaller species appear to have benefited from the arrival of cane toads owing possibly to the loss of top-down control from large terrestrial squamates that have experienced toad induced population declines.

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