The impact of invasive cane toads on native wildlife in southern Australia

Christopher J. Jolly, Richard Shine & Matthew J. Greenlees
School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia

Keywords
Bufo marinus, ecological impact, invasive species, predator–prey, surveys.

Correspondence
Christopher J. Jolly, School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia.
Tel: 0418 259 161;
E-mail: cjol6201@uni.sydney.edu.au

Funding Information
Sutherland Shire Council, the Foundation for National Parks and Wildlife and the Australian Research Council.

Received: 20 April 2015; Revised: 15 July 2015; Accepted: 25 July 2015

Ecology and Evolution 2015; 5(18): 3879–3894
doi: 10.1002/ece3.1657

Abstract
Commonly, invaders have different impacts in different places. The spread of cane toads (Rhinella marina: Bufonidae) has been devastating for native fauna in tropical Australia, but the toads’ impact remains unstudied in temperate-zone Australia. We surveyed habitat characteristics and fauna in campgrounds along the central eastern coast of Australia, in eight sites that have been colonized by cane toads and another eight that have not. The presence of cane toads was associated with lower faunal abundance and species richness, and a difference in species composition. Populations of three species of large lizards (land mullets Bellatorias major, eastern water dragons Intellagama lesueurii, and lace monitors Varanus varius) and a snake (red-bellied blacksnake Pseudechis porphyriacus) were lower (by 84 to 100%) in areas with toads. The scarcity of scavenging lace monitors in toad-invaded areas translated into a 52% decrease in rates of carrion removal (based on camera traps at bait stations) and an increase (by 61%) in numbers of brush turkeys (Alectura lathami). The invasion of cane toads through temperate-zone Australia appears to have reduced populations of at least four anurophagous predators, facilitated other taxa, and decreased rates of scavenging. Our data identify a paradox: The impacts of cane toads are at least as devastating in southern Australia as in the tropics, yet we know far more about toad invasion in the sparsely populated wilderness areas of tropical Australia than in the densely populated southeastern seaboard.

Introduction
Invasive species imperil native biodiversity (Mack et al. 2000; McGeoch et al. 2010), but invader impacts are highly heterogeneous (Melbourne et al. 2007). Some invaders have catastrophic impacts, whereas others may benefit native taxa; some native taxa are more vulnerable than others (Woinarski et al. 2001, 2004). To incorporate the influence of habitat and climate, studies of invader impacts on large, mobile vertebrates must employ multiple sites with a sampling design that captures a range of natural heterogeneity.

Since its introduction in 1935, the cane toad (Rhinella marina) has spread rapidly through Australia (Lever 2001; Kolbe, Kearney & Shine 2010). Extensive research in tropical Australia has demonstrated that the arrival of cane toads is consistently followed by population-level declines of some species of large predators that are fatally poisoned when they eat the toxic toads (Letnic et al. 2008; Brown et al. 2009). However, impacts on the (virtually unstudied) southern edge of the toads’ range expansion may be very different from those in the tropics. For effects, we must measure changes in abundance of native species coincident with the presence of an invader. This task may be simple in some cases (e.g., for sessile organisms), but is more challenging if the impact falls on vagile, rare predators (Caughley 1977; Woinarski et al. 2001, 2004). To incorporate the influence of habitat and climate, studies of invader impacts on large, mobile vertebrates must employ multiple sites with a sampling design that captures a range of natural heterogeneity.
example, the tropical invasion front is dominated by large adult toads; any predator that consumes a large toad will be fatally poisoned (Shine 2010). In contrast, the southern front contains small as well as large toads (McCann 2014). A small toad offers a nauseating but nonfatal meal that may allow aversion learning by predators, thereby ameliorating population-level impact (O’Donnell, Webb & Shine 2010).

The temperate-zone invasion front also facilitates spatial comparisons of affected versus unaffected sites. In the tropics, toads invade in a rapidly advancing, continuous front hundreds of kilometers wide, precluding comparisons between adjacent sites with versus without toads (Shine 2010). Thus, these studies yield before–after data on population-level impacts of toad invasion, a critical difficulty in the wet–dry tropics where even minor year-to-year variation in rainfall patterns can induce massive changes in faunal populations (Brown et al. 2002; Madsen et al. 2006; Shine and Brown 2008). Those temporal shifts make it difficult to attribute specific faunal shifts to cane toad invasion. For example, some declines in predator populations coincident with toad invasion in tropical Australia were caused by stochastic weather events, not toads (Brown et al. 2011).

The toad invasion into southern Australia is progressing slowly (McCann et al. 2014) and in a patchwork fashion (likely due to multiple translocations of toads by humans: White and Shine 2009). Adjacent areas with versus without cane toads create an opportunity for direct and concurrent comparisons. Such spatial comparisons do not overcome all of the problems associated with inferring toad impact—for example, invaded and unininvaded sites may differ in ways that affect faunal assemblages (Suarez et al. 1998; Bolger et al. 2000; Holway et al. 2002a,b). Nonetheless, confounding variables can be measured; and such a study is not weakened by the influence of annual variation.

Despite logistical advantages (a fragmented invasion front, a significantly higher human population, and infrastructure that facilitates research), the impact of cane toads in southern Australia has been largely ignored. We conducted surveys to quantify the characteristics of native faunal assemblages in adjacent sites that contained versus those that did not contain cane toads to test what impact toads have on fauna assemblages. We predicted that native fauna that prey on toads would be less abundant in toad-invaded areas than in areas that did not contain toads. We also surveyed habitat variables to test for potential confounding factors between invaded versus uninvaded sites, and measured rates of carrion removal to test the hypothesis that this critical ecological function would be affected by toad-induced declines of scavengers.

Materials and Methods

Study region

The Northern Rivers region encompasses the northeastern corner (50,266 km²) of New South Wales (NSW), Australia (DECCW 2010; Fig. 1). Although it occupies less than 10% of the state, this area supports more than 40% of the threatened species and 20% of the threatened communities of NSW (Goldingay et al. 1999; (DECCW 2010; Newell 2011). The region experiences a warm temperate to subtropical climate with warm humid summers (mean average maximum 26–30°C) and moderate winters (mean average minimum 6–10°C; Bureau of Meteorology 2014). Most rainfall occurs during summer and early autumn (Taylor and Goldingay 2003). Many native taxa (both ectotherms and endotherms) of this region are most active in the warmer, wetter months (September to February: Shine 1979; York et al. 1991; Christian and Weavers 1996; Kavanagh and Stanton 2005; Daly and Lemckert 2011), so we confined our surveys to the spring and summer months of 2013–2014.

Study species

Cane toads (Rhinella marina) are large (to 230-mm snout-urostyle length [SUL] and 500 g mass: Zug and Zug 1979; Brown et al. 2013a,b) toxic bufonid anurans (Tyler 1975; Pramuk 2006), native to Central and South America (Lever 2001). Introduced from Hawaii to northeastern QLD in 1935, this highly toxic anuran has since invaded more than 1.2 million km² of tropical and subtropical Australia (Lever 2001; Urban et al. 2007, 2008) and has also spread into southeastern QLD and northeastern NSW (Seabrook 1993; Lever 2003). Cane toads were introduced to NSW between 1964 and 1966, when a satellite population was established in Byron Bay (van Beurden and Grigg 1980). By 1989, this satellite population had merged to form a continuous population from the Northern Rivers region of NSW into QLD (Seabrook 1991, 1993). Presumably due to constraints of climatic conditions on toad breeding, feeding, and locomotion (Semeniuk et al. 2007; Kearney et al. 2008), cane toads are expanding their range far less rapidly in this region than at the tropical invasion front (1–3 km/year vs. 55 km/year: Seabrook 1993; Phillips et al. 2006, 2007; Urban et al. 2007). Although toads have been in NSW for almost 50 years (van Beurden and Grigg 1980), they remain patchily distributed (Seabrook 1993). That patchy distribution likely reflects anthropogenic habitat fragmentation, human-assisted dispersal, and heterogeneity of densely vegetated habitats (Seabrook 1993; Semeniuk et al. 2007). Hence, large tracts of suitable, but as yet
Figure 1. Study site locations within the Northern Rivers region, New South Wales, Australia, depicting toad-present (■) and toad-absent (□) campgrounds, which were surveyed between October 2013 and February 2014.
uncolonized, native bushland occur near long-term toad-colonized areas.

**Study sites**

We surveyed habitat characteristics and fauna at 16 camp-grounds and picnic areas surrounded by bushland (from 28°22'S, 153°14'E to 29°57'S, 153°15'E) between October 2013 and February 2014. We selected eight sites in areas where toads are currently present (from 2 to 25 years postinvasion) and eight sites where toads are predicted to invade (Urban et al. 2007; Kolbe et al. 2010) but have not yet done so. Due to the patchy distribution of cane toads at the southern edge of their invasion, we were able to select interspersed study sites to minimize the confounding effects of latitude, longitude, elevation, climate, or vegetation. All campgrounds and picnic areas were adjacent to or within state forests or national parks (Fig. 1, see Supplementary Information for Table S1). Each site consisted of a cleared campground or picnic area plus an adjacent 5-km section of access road through native bushland.

Human-supplied food and water subsidies attract both native and invasive fauna to disturbed patches such as campgrounds, picnic areas, and landfill dumps located within reserves (Warnken et al. 2004; Piper and Catterall 2006; Jessop et al. 2012). Compared to the surrounding bushland, campgrounds and access roads also offer reduced canopy cover (and hence, greater sun exposure) at ground level, potentially facilitating reptile thermoregulation (Sartorius et al. 1999; Heard et al. 2004; McDonald 2012). Additionally, access roads provide corridors for animals to move between vegetation remnants (Taylor and Goldingay 2003), rendering the animals more easily observable during surveys. Cane toads regularly use roadways as dispersal corridors (Seabrook and Dettmann 1996; Brown et al. 2006) and prefer the sparse vegetation associated with human-modified areas within this region (e.g., campgrounds, golf courses, paddocks, parkland: Seabrook 1993; Semeniuk et al. 2007).

**Fauna surveys**

We examined the abundance and diversity of native predators using standardized surveys for a five-month period spanning the spring and summer peak period of faunal activity in this region. We recorded all reptile, bird (predatory and scavenger species), and mammal taxa that were encountered in these surveys (see Supporting Information for Table S2). Because populations of large elapid snakes, varanid and scincid lizards, and dasyurid marsupials have suffered severe declines as a result of the toad’s tropical invasion, our surveys were designed to detect any toad-imposed differences in the abundance of these taxa.

We actively sampled each site to count reptiles, birds, and mammals. As sites differed in extent (see Supporting Information for Table S1), survey effort was standardized (1 h/survey). For the first 15 min, we actively searched for fauna in and around campground areas on foot. The remaining 45 min was conducted from a slow-moving car (20–40 km/h along 5-km road transect), from which we scanned the road for crossing animals, and roadside areas (e.g., trees, branches, fallen logs, termite mounds) for sequestered animals. Data for each campground and road transect within a site were combined to give total number of species and total number of individuals of each species for each site (standardized per 15 h of survey time). All animals observed were identified to species, using field guides and keys (taxonomy follows Pizzey and Knight 2012; Wilson and Swan 2013; Van Dyck et al. 2013).

During the five-month survey period, each site was sampled in 10-h-long diurnal surveys (on sunny days, >23°C), conducted at 0900–1200 h and 1300–1800 h, and in 5-h-long nocturnal surveys (on dry nights, >16°C), conducted at 1930–2330 h. To avoid bias, we rotated the time of day that each site was surveyed from day to day. For practical reasons, groups of three adjacent sites were surveyed for at least three concurrent days, in random order with respect to each group of sites and sites within each group. For statistical analysis, data for rarely encountered species (<8 individuals across all sites) were excluded.

**Habitat variables**

At each site, we recorded habitat variables to determine whether any spatial differences in fauna composition might be attributable to such factors rather than to the impacts of cane toads. Twenty-eight structural habitat variables (see Supporting Information for Table S3) were measured following a protocol similar to that of Brown et al. (2008). Beginning at the center of each campground or picnic area, we marked out two transects (north–south and east–west) into the surrounding bushland. From the origin point, we marked out four 10 × 10 m square plots centered at 20-m intervals along each transect line (within the cleared area of the site) and a further four plots at 10-m intervals in the surrounding bushland. The distances between adjacent plots were smaller in the bushland because our primary interest was the transitional zone and because of the greater apparent homogeneity of habitat conditions within the open areas. Within each plot, we estimated the proportions of the substrate covered by bare ground, lawn, leaf litter, rock, log, grass/herb, small shrub, tree trunk, and human debris (e.g., graveled roads, corrugated iron). To quantify structural aspects of the vegetation, we estimated percentage cover
of the understory, midstory, and canopy. Percentage of the ground within each plot that was exposed to direct sunlight at midday was also recorded. We noted the numbers of small (1–10 cm diameter at breast height [dbh]), medium (11–30 cm dbh), and large (>31 cm dbh) trees per plot, as well as mean tree height (Brown et al. 2008). In each plot, the following structural variables were also measured: leaf litter depth (cm); number of tree stumps (<5 m in height); number of fallen logs; number of hollows in tree trunks and limbs; and number of termite mounds in trees and on the ground. Additionally, we recorded the distance from the center of each plot to the closest building, tent, or car; water source; road, track, or trail; and tree.

Additional whole-campground variables measured at the commencement of surveys comprised: area cleared (m²); number of car spaces and campsites; number of campsites occupied; number of people and cars present during surveys; number of rubbish bins; number of barbeques; number of outside taps; number of access roads and walking trails; and distance (m) to nearest permanent freshwater. Landscape-scale parameters were assessed using satellite and aerial maps of the region (Google Earth). Connectivity, disturbance, and isolation were quantified by measuring cover of wooded vegetation (km²), area cleared for agricultural or residential purposes (km²), length of roadways (km), and average speed limit (km/h) of roadway, all within a 5 km radius of each site. Climatic variables were extracted from BIOCLIM climate layers to predict mean annual precipitation (mm) and mean annual maximum and minimum temperatures (°C) of each site as a function of latitude, longitude, and elevation (Busby 1991). Climatic variables were checked against long-term data sets of local weather stations (Bureau of Meteorology 2014).

**Rates of carrion removal**

To record rates of carrion removal in sites with and without cane toads, as well as the identity of the species responsible for carrion removal, we set up eight bait stations with remotely triggered cameras at each of 12 sites. Four bait stations were located in the bushland surrounding each campground and picnic area (in bushland vegetation plots; see above), and four bait stations were located 2 km away, along the ingress road (two on either side, and within 10 m of the road). All bait stations consisted of 10 chicken necks, lightly concealed with substrate, that were monitored by motion-sensitive infrared-triggered digital video cameras (Moultrie M-990i: EBSCO Industries, Birmingham, Alabama) for 48 h. Once this period had elapsed, we counted the remaining baits and reviewed the camera footage to determine the identity of the scavenging species. Only data from baits that were deployed during a 48-h period of suitable weather (clear, sunny days >23°C, and fine, warm nights >16°C) were used in comparisons between sites.

**Statistical analysis**

**Habitat variables**

Using the software package SPSS (SAS Institute, Cary, NC), we carried out a principal components analysis (PCA) to reduce the number of intercorrelated variables. Variances were homogeneous (Levene’s test; P > 0.05). Bartlett’s test of sphericity rejected the null hypothesis that variables were not correlated with habitats (P < 0.05), and identified 12 principal components (PCs; eigenvalue >1) in the rotated component matrix (using varimax with Kaiser normalization, accounting for >95% of variance in the habitat data). However, only five of these PCs were deemed to be biologically relevant. We used a multivariate analysis of variance (MANOVA) with toad exposure as the factor (two levels; cane toad present vs. absent), to explore determinants of variation in each PC axis (dependent variables). To test the roles of toads versus preexisting habitat conditions as determinants of wildlife assemblages, we constructed a series of multivariate regression models to explain (1) species richness and (2) faunal abundance at the 16 study sites. In these models, the predictor variables were toad invasion status (coded as either presence/absence or number of years since invasion [uninvaded sites were scored as 0]), the five PC habitat axis scores, and all interactions between these factors. We assessed model fit using the corrected Akaike’s information criterion (AIC). We ran separate models with toad status treated as either a nominal variable (present/absent) or a continuous variable (years since toad arrival) because plausibly, the impact of toads might be immediate; or might change through time (either increasing or decreasing) if native fauna are affected through indirect processes (which might thus take significant time to eventuate), or are vulnerable only under specific environmental conditions.

**Fauna surveys**

Univariate analyses were conducted using general linear models in the statistical software JMP Pro 9.0 (SAS Institute). Data were visually assessed for normality, and variances were homogeneous (Levene’s test, P > 0.05). One-factor (toad exposure) analyses of variance (ANOVA) were used to test for effects of the independent variable (two levels; cane toad present vs. absent) on total abundance and species richness of native vertebrates.
We used the program PRIMER v5 (PRIMER-E, Plymouth, UK) to assess differences in diversity and composition of native vertebrate species between sites with and without cane toads. Using the Bray–Curtis similarity coefficient (Bray and Curtis 1957), we calculated a similarity matrix with data from fauna surveys (abundance of each native vertebrate species at each site). Abundance data were fourth-root-transformed to reduce the influence of common species relative to rarer species (e.g., Clarke 1993; Quinn and Keough 2002; Lassau and Hochuli 2005). Standardization of the data was unnecessary due to prior standardization of sampling design. We employed nonmetric multidimensional scaling (nMDS: Clarke and Warwick 2001), using Bray–Curtis similarity measures, to plot a two-dimensional ordination and determine whether native vertebrate assemblages differed between sites with versus without cane toads. To compare between toad-present versus toad-absent sites in a multivariate similarity matrix, we performed analysis of similarities (ANOSIM) with 999 permutations (Sokal and Rohlf 1995; Anderson 2001; Bond and Lake 2003). As the presence of cane toads contributed to differences in species composition (see Results), we used a similarity percentage analysis (SIMPER: Clarke 1993) to identify individual species that contributed most to those differences (Clarke and Warwick 2001).

Based on those analyses, we then proceeded to compare the abundances of three species of lizard (land mullets Bellatorias major, eastern water dragons Intellagama lesueurii, lace monitors Varanus varius) and one species of snake (red-bellied black snake Pseudechis porphyriacus) between sites where toads were present versus absent. Data on the three lizard taxa were assessed independently because they were identified as having declined by SIMPER. The abundance of P. porphyriacus was assessed because this species has been anecdotally reported to experience severe toad-imposed population declines (Rayward 1974; Covacevich and Archer 1975; Fearn 2003; Phillips et al. 2003; Phillips & Fitzgerald 2004). Using JMP Pro 9.0, we compared the abundance of each species between sites where toads were present versus absent (independent variable). Because the abundance data of these individual species could not be normalized via transformation, data were analyzed using nonparametric Kruskal–Wallis analysis of variance tests (Crossland 1998; Ujvari et al. 2011; Crossland and Shine 2012).

Rates of carrion removal

Data conformed to the assumptions of normality and variance homogeneity. Using JMP Pro 9.0, we compared the number of chicken necks removed from bait stations (both in campgrounds and in surrounding bushland) in both toad-present and toad-absent sites. The number of baits removed per bait station was the dependent variable, and toad exposure (two levels; toad present vs. absent) and location (two levels; campground vs. bushland) were the independent variables in a two-way analysis of variance (ANOVA). Site was included as a random factor. Differences in numbers of goanna vs. nongoanna scavengers between toad-present and toad-absent sites were compared using Fisher’s exact test.

Results

Surveys of native taxa

We recorded 554 individual reptiles (of 14 species), 643 birds (of 10 species), and 250 mammals (of 10 species; see Supporting Information for Table S2). Combining counts for all native species, toad-occupied areas contained 40% fewer animals (one-way ANOVA: \( F_{1,14} = 6.20, \ P = 0.03 \); Fig. 2A) and 31% fewer species (\( F_{1,14} = 11.82, \ P = 0.004 \); Fig. 2B) than did areas without toads. The composition of faunal assemblages differed strongly between toad-present and toad-absent sites (ANOSIM: global \( R = 0.36, \ P = 0.005 \); 58% average dissimilarity; Fig. 3). Toad presence correlated with decreased abundances of three lizard species (lace monitors Varanus varius, \( Z = 3.35, \ P = 0.001 \); water dragons Intellagama lesueurii, \( Z = 3.03, \ P = 0.003 \); land mullets Bellatorias major, Kruskal–Wallis one-way ANOVA: \( Z = 3.07, \ P = 0.002 \); Fig. 4A–C) and increased abundance of brush turkeys (Alectura lathami, \( Z = 2.28, \ P = 0.03 \); Fig. 4E). There was no overall difference in snake abundance between toad-present and toad-absent sites (MANOVA: Wilks’ Lambda = 0.013, \( P = 0.67 \)), but one species showed a significant effect: No red-bellied black-snakes Pseudechis porphyriacus were encountered in sites with toads, whereas they were found in most toad-absent sites (Kruskal–Wallis one-way ANOVA: \( Z = -2.14, \ P = 0.03 \); Fig. 4D).

Habitat variables

From the 49 input habitat and climatic variables, we retained five PC axes (eigenvalue >4.3; each accounting for >8.9% of variance). The first axis (PC1, 19.9% of variance) loaded on campground size. PC2 (15.2% of variance) was linked to forested sites with high human resource subsidies. PC3 (11.9% of variance) was linked to leaf litter and dense vegetation. PC4 (9.2% of variance) was associated with naturally sparse vegetation, and PC5 (8.9% of variance) was associated with warm, woody sites. A MANOVA with toad presence/absence as the factor, and scores on these PC axes as dependent variables,
showed no overall habitat differences between the two groups of sites (MANOVA: Wilks’ Lambda = 1.63, P > 0.05).

Of the models we constructed to explain species richness and faunal abundance at the 16 study sites, the best-fitting models all included the impact of cane toads rather than (or as well as) habitat variation. If we included toad presence/absence as a factor, the best-fitting model for species richness included toad presence/absence and PC axis 4; the second-best (not significantly different) model included only toad presence/absence (Table 1). The results for faunal abundance were the same, except that PC1 took the role of PC4 (Table 2). If we included the impact of toads as a continuous variable (years since arrival) rather than a dichotomy, faunal species richness was best explained by a model that included only time since toad arrival and PC3 (Table 3). For faunal abundance, the top three models were equally well supported (AICc < 2), and all included time since toad arrival (one also contained PC1, one contained PC2, and one contained both PC1 and PC2; see Table 4). Thus, all of the models to explain variation among sites in faunal richness and abundance included the effect of cane toads, even after the effects of habitat variation were taken into account.

**Carrion removal trials**

The numbers of baits removed did not differ significantly between campground and bushland bait stations (two-way ANOVA, location: F_{1,20} = 1.94, P = 0.18; interaction location * toad exposure F_{1,20} = 0.04, P = 0.84). Despite variation among sites (F_{20,72} = 2.20, P = 0.008), fewer baits were removed from bait stations in areas where toads were present (F_{1,20} = 24.29, P < 0.001; Fig. 5). Lace monitors comprised 35 of 47 (74%) of the scavengers that removed carrion from toad-absent sites, but only 6 of 14 (43%) of the scavengers at toad-present sites (Fisher’s exact test, χ² = 4.9, P = 0.03).

**Discussion**

Invasive cane toads have massively affected the abundance and species richness of native fauna in temperate-zone Australia. In sites where toads were present, we recorded 40% fewer species and 31% fewer individuals. A causal role for toad invasion in faunal decline was supported by (1) the similarity in habitat structure and climate between toad-present versus toad-absent areas; and (2) the nature of faunal differences: The species that were less common in toad-invaded areas were reptile taxa that eat anurans. In contrast, the ground-dwelling brush turkey increased in abundance, consistent with reduced predation by goannas (Jones 1988; Goth and Vogel 2002). Our data thus suggest both direct and indirect impacts of cane toad invasion. Below, we consider native species that (1) were not affected; (2) decreased coincident with toads; and (3) increased in toad-invaded areas.

Most species were equally common in sites with and without cane toads with no negative effect on any surveyed native mammal or bird taxa. Studies on toad impact in tropical Australia have reported the same general result. Most Australian birds that prey on anurans can detect and tolerate the toad’s toxin (Beckmann and Shine 2009, 2011; Beckmann et al. 2011). Although one of the bird species we counted can be killed by ingesting toads (laughing kookaburra *Dacelo novaeguineae*: Covacevich and Archer 1975; but see Ringma 2013), this vulnerability has not translated to population-level impacts. Broadly, then, direct impacts...
of cane toads on predatory birds appear to be minimal, as in tropical Australia.

Similarly, we found no significant changes in mammal abundance associated with toad presence. Only three of the ten species we surveyed are likely to consume toads (fawn-footed melomys *Melomys cervinipes*; bush rat *Rattus fuscipes*; feral cat *Felis catus*). Rodents can kill and consume cane toads without ill effects (Cassels 1966; Cabrera-Guzmán et al. 2015), reflecting ancestral exposure to Asian bufonids (Fitzgerald 1990; Shine 2010). The remaining seven mammal species we surveyed (see Supporting Information for Table S2) do not eat anurans; thus, any impact to these species would have been indirect (e.g., through a reduction in goanna predation). Small sample sizes (number of individuals encountered) weakened our ability to detect any changes, and further research would be valuable.

Our surveys failed to include some rare mammal species that might be affected by toads. In tropical Australia, the northern quoll (*Dasyurus hallucatus*) has experienced severe declines from toad invasion (Burnett 1997; O’Donnell et al. 2010; Shine 2010). Two related dasyurid species (spotted-tailed quoll *Dasyurus maculatus* and brush-tailed phascogale *Phascogale tapoatafa*) are found in northeastern (NSW) (Van Dyck et al. 2013). However, both are rare and neither was encountered during our surveys. We saw a single *P. tapoatafa* at one toad-free site, but not during standardized surveys.

Our data do not reveal any overall declines in snake abundance. Phillips et al. (2003) predicted that cane toads

---

**Figure 3.** A nonmetric multidimensional scaling (nMDS) ordination plot showing the composition of faunal assemblages sampled from toad-present (solid circles) and toad-absent (open circles) campground sites in northeastern New South Wales, Australia (stress = 0.13).
would cause population declines in 30% of Australia’s snake species (including eight of nine species recorded in the present study), but our results suggest a more encouraging scenario. Most snake taxa, even frog specialist species (e.g., *Dendrelaphis punctulata*, *Tropidechis carinatus*) predicted to suffer toad-imposed impacts (Phillips et al. 2003), were unaffected. That lack of effect may be due to small sample sizes, to morphological or behavioral traits that render the snakes invulnerable to toads (Llewelyn et al. 2012), or to indirect positive effects (e.g., of goanna mortality) that outweigh any direct negative effects (Brown et al. 2011, 2013b; Doody et al. 2013).

Although most taxa were unaffected, toads appear to have caused catastrophic declines in populations of four reptile taxa in temperate Australia. The three lizard species affected have not been studied previously in this respect, but toad-induced declines in red-bellied blacksnakes have been reported (Pockley 1965; Rayward 1974), based on anecdotal evidence (but see Seabrook 1993). This species was absent from our toad-invaded sites. Both lace monitors and water dragons are widely sympatric with cane toads in Australia (Lever 2001; Wilson and Swan 2013), so the lack of prior reports of toad impact on these taxa is surprising.

Although these reptile species span four phylogenetically diverse families (*Varanidae*, *Agamidae*, *Scincidae*, and *Elapidae*), they share three attributes common to predators that are vulnerable to toads (Shine 2010):

1. **Low resistance to toad toxins.** Lace monitors, land mullets, and red-bellied blacksnakes can be fatally poisoned by ingesting toads (Covacevich and Archer 1975; Fearn 2003; Phillips and Shine 2006a,b; Ujvari et al. 2013). Toxin resistance is unknown for water dragons, but is low in related species (e.g., *Chlamydosaurus kingii*: Pearson et al. 2014).

2. **Anurophagy.** All of these species eat anurans (Shine 1977; Phillips and Shine 2006a,b) or are generalists with broad diets (Shea 1999; Wilson 2012). A close relative of the land mullet, the blue-tongued lizard (*Tiliqua scincoides intermedia*), has shown dramatic population declines due to toad invasion in tropical Australia (Price-Rees et al. 2010).

3. **Large size.** All four taxa are among the largest members of their respective families in Australia (Cogger 2014). Because toxin volume increases rapidly with toad...
size (Phillips and Shine 2006a,b), larger predators (which attack larger toads) are most at risk (Shine 2010).

In tropical Australia, the decline of large predatory lizards (e.g., *Varanus panoptes*) means that some native species indirectly benefit from the toad’s arrival (Brown 2010).

Table 1. Model selection table showing results of Akaike’s information criterion tests for determinants of faunal species richness, using toad presence or absence as a dichotomous variable. The top ten highest ranked models are shown. “Prin” refers to axes of variation from principal components analysis of habitat features.

| Model                           | Number of parameters | $R^2$  | AIC score | Δ AICc | AIC weight |
|---------------------------------|----------------------|--------|-----------|--------|------------|
| TOAD VS NO-TOAD {1-0}, Prin4    | 2                    | 0.572  | 89.0531   | 0      | 0.2509     |
| TOAD VS NO-TOAD {1-0}           | 1                    | 0.4578 | 89.2014   | 0.1483 | 0.2330     |
| TOAD VS NO-TOAD {1-0}, Prin3    | 2                    | 0.4997 | 91.5532   | 2.5001 | 0.0719     |
| TOAD VS NO-TOAD {1-0}, Prin3, Prin4 | 3                  | 0.6149 | 91.7272   | 2.6741 | 0.0659     |
| TOAD VS NO-TOAD {1-0}, Prin5    | 2                    | 0.4854 | 92.003    | 2.9499 | 0.0574     |
| TOAD VS NO-TOAD {1-0}, Prin4, Prin5 | 3               | 0.5981 | 92.4111   | 3.358  | 0.0468     |
| TOAD VS NO-TOAD {1-0}, Prin1    | 2                    | 0.4603 | 92.7661   | 3.713  | 0.0392     |
| TOAD VS NO-TOAD {1-0}, Prin2    | 2                    | 0.459  | 92.8026   | 3.7495 | 0.0385     |
| TOAD VS NO-TOAD {1-0}, Prin1, Prin4 | 3             | 0.5749 | 93.0875   | 4.2556 | 0.0299     |

Table 2. Model selection table showing results of Akaike’s information criterion tests for determinants of faunal abundance, using toad presence or absence as a dichotomous variable. The top ten highest ranked models are shown. “Prin” refers to axes of variation from principal components analysis of habitat features.

| Model                           | Number of parameters | $R^2$  | AIC score | Δ AICc | AIC weight |
|---------------------------------|----------------------|--------|-----------|--------|------------|
| TOAD VS NO-TOAD {1-0}, Prin1    | 2                    | 0.5063 | 164.7220  | 0      | 0.2498     |
| TOAD VS NO-TOAD {1-0}           | 1                    | 0.3069 | 166.5150  | 1.7930 | 0.1019     |
| TOAD VS NO-TOAD {1-0}, Prin1, Prin2 | 3               | 0.5729 | 166.7671  | 2.0451 | 0.0898     |
| TOAD VS NO-TOAD {1-0}, Prin2    | 2                    | 0.4370 | 166.8256  | 2.1036 | 0.0873     |
| Prin2                           | 1                    | 0.2908 | 166.8832  | 2.1612 | 0.0848     |
| TOAD VS NO-TOAD {1-0}, Prin1, Prin5 | 3             | 0.5340 | 168.1624  | 3.4404 | 0.0447     |
| TOAD VS NO-TOAD {1-0}, Prin1, Prin3 | 3               | 0.5165 | 168.7523  | 4.0303 | 0.0333     |
| TOAD VS NO-TOAD {1-0}, Prin1, Prin4 | 3             | 0.5085 | 169.0163  | 4.2943 | 0.0292     |
| Prin2, Prin5                    | 2                    | 0.3504 | 169.1145  | 4.3925 | 0.0278     |
| TOAD VS NO-TOAD {1-0}, Prin5    | 2                    | 0.3440 | 169.2708  | 4.5488 | 0.0257     |

Table 3. Model selection table showing results of Akaike’s information criterion tests for determinants of faunal species richness, using years since toad arrival as a continuous variable. The top ten highest ranked models are shown. “Prin” refers to axes of variation from principal components analysis of habitat features.

| Model                           | Number of parameters | $R^2$  | AIC score | Δ AICc | AIC weight |
|---------------------------------|----------------------|--------|-----------|--------|------------|
| Prin3, years since toad invasion | 2                    | 0.7013 | 83.3006   | 0      | 0.4589     |
| Years since toad invasion      | 1                    | 0.5476 | 86.3062   | 3.0056 | 0.1021     |
| Prin2, Prin3, years since toad invasion | 3             | 0.7197 | 86.6440   | 3.3434 | 0.0862     |
| Prin3, Prin5, years since toad invasion | 3           | 0.7192 | 86.6752   | 3.3746 | 0.08491    |
| Prin3, Prin4, years since toad invasion | 3           | 0.7077 | 87.3178   | 4.0172 | 0.0615     |
| Prin1, Prin3, years since toad invasion | 3           | 0.7014 | 87.6589   | 4.3583 | 0.0519     |
| Prin2, years since toad invasion | 2                    | 0.5701 | 89.1258   | 5.8252 | 0.0249     |
| Prin5, years since toad invasion | 2                    | 0.5647 | 89.3266   | 6.026  | 0.0225     |
| Prin4, years since toad invasion | 2                    | 0.5614 | 89.4456   | 6.145  | 0.0213     |
| Prin1, years since toad invasion | 2                    | 0.5488 | 89.8988   | 6.5982 | 0.0169     |
et al. 2011, 2013a; Doody et al. 2013). Similarly, a reduction in the abundance of varanid lizards may explain the increase in the number of brush turkeys (Alectura lathami) in our toad-present sites. The ground-nesting habits of brush turkeys may render them (and their eggs) highly vulnerable to predation by monitors (Jones 1988; Goth and Vogel 2002). In addition to increasing brush turkey abundance, the toad-induced decline in lace monitors results in an indirect reduction to scavenging rates by 74% in toad-invaded sites. That situation also may allow increases in other scavengers (such as insects) and might create health problems for human users of the campgrounds if discarded food is left to rot. Scavengers can strongly influence the structure and function of faunal assemblages (Wilson and Wolkovich 2011).

What can be concluded, overall, about the impacts of the invasive cane toad (Rhinella marina) on the abundance, diversity, and composition of Australian wildlife? Although brief, our study incorporated more spatial replication and “control” sites than have been possible in the wet–dry tropics (Doody et al. 2006, 2009, 2013; Letnic et al. 2008; Phillips et al. 2010; Brown et al. 2011, 2013b; Ujvari et al. 2011). The ability to compare faunal assemblages between areas that differ mostly in exposure to toads (rather than in environmental factors) provides convincing evidence of population-level declines in native taxa due to toad arrival. Our results support the conclusion that toad impacts on native taxa are complex and proceed via both direct and indirect pathways (Shine 2010; Brown et al. 2013a). Additionally, our study provides evidence of invader impact in a region that heretofore has been largely ignored.

Cane toads are publicly vilified Australia-wide, and the public views this invasive anuran with abhorrence (Clarke et al. 2009; Shine 2010). That passion has encouraged extensive research, as well as community-based “toad busting” (Shine and Doody 2011). Given this high public profile and substantial governmental investment into cane toad issues (Shine et al. 2006), the lack of previous research on toad impacts in southern Australia is remarkable. Our study paints a bleak cautionary tale; even in an intensively studied invasive species system, major impacts on iconic native species have been overlooked. Remarkably, even anecdotal reports of cane toad impacts are rare in southern Australia, despite the dense human population. Nonchalance among the general public appears to have had flow-on effects for political and research priorities.

The scientific neglect of the toad’s impacts at the southern invasion front stands in contrast to the situation in tropical Australia. Many topics related to toad biology

Table 4. Model selection table showing results of Akaike’s information criterion tests for determinants of faunal abundance, using years since toad arrival as a continuous variable. The top ten highest ranked models are shown. “Prin” refers to axes of variation from principal components analysis of habitat features.

| Model                                               | Number of parameters | $R^2$  | AIC score | $\Delta$ AICc | AIC weight |
|------------------------------------------------------|----------------------|--------|-----------|---------------|------------|
| Prin1, Prin2, years since toad invasion              | 3                    | 0.645  | 163.812   | 0             | 0.1944     |
| Prin2, years since toad invasion                     | 2                    | 0.5062 | 164.7279  | 0.9158        | 0.1230     |
| Prin1, years since toad invasion                     | 2                    | 0.4812 | 165.516   | 1.7039        | 0.0829     |
| Years since invasion                                | 1                    | 0.3067 | 166.5204  | 2.7083        | 0.0502     |
| Prin1, Prin2, Prin5, years since toad invasion      | 4                    | 0.692  | 166.8725  | 3.0604        | 0.0421     |
| Prin2                                               | 1                    | 0.2908 | 166.8832  | 3.0711        | 0.0419     |
| Prin2, Prin5, years since toad invasion              | 3                    | 0.5571 | 167.3503  | 3.5382        | 0.0331     |
| Prin1, Prin2, Prin4, years since toad invasion      | 4                    | 0.6724 | 167.8578  | 4.0457        | 0.0257     |
| Prin1, Prin4, years since toad invasion              | 3                    | 0.5274 | 168.3864  | 4.5743        | 0.0197     |
| Prin1, Prin5, years since toad invasion              | 3                    | 0.5265 | 168.4171  | 4.605         | 0.0194     |

Figure 5. Impacts of cane toad presence and habitat type on mean number (± SE) of chicken necks removed from camera-monitored bait stations in campgrounds and surrounding bushland areas in toad-present and toad-absent areas of northeastern New South Wales, Australia.

© 2015 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.
and ecological impacts have been investigated in remote tropical regions (review by Shine 2010). Between 1963 and 2014, 102 scientific publications assessed the ecological impacts of cane toads on the native fauna of northern Australia (i.e., north of Brisbane) compared to 14 articles on cane toad impacts in southern Australian (Shine 2010, 2014). Of those 14 articles, the most recent was completed more than 20 years ago (Seabrook 1993). This disparity in research effort is perplexing in light of the logistical difficulties that have compromised experimental designs in these tropical studies.

In summary, we found that toad invasion has caused population declines in some large anuraphagous predators in temperate Australia similar to those documented in the more intensively studied tropics (Shine 2010). Ultimately, the neglect of toad impact in temperate-zone Australia reflects the fact that debates about invasive species occur within a sociopolitical framework. Geographic differences in the priority given to competing issues can influence funding incentives and research effort. The forests of northern NSW have been the focus of vigorous “environmental” battles over many years relating to forestry practices (Lemckert 1999; Kavanagh and Stanton 2005). That focus may have drawn public attention away from feral species impacts, but it is difficult to understand why scientific efforts were equally scarce. Whatever the reasons behind the disproportionate allocation of research effort toward the cane toad problem in tropical versus southern Australia, the result is clear. We have failed to recognize a major ecological problem unfolding in a place close to major cities where logistics are straightforward, and robust experimental designs are possible. If that can happen with cane toad impact, it may well happen in other ecological issues as well.

Acknowledgments

We thank the staff from NSW National Parks and Wildlife Services for access to study sites and R. Jago, M. Elphick, B. Kals, and M. Crowther for assistance. We thank Sutherland Shire Council, the Foundation for National Parks and Wildlife, and the Australian Research Council for funding.

Data accessibility

Upon acceptance of the article, data will be deposited in Dryad.

Conflict of Interest

None declared.

References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26:32–46.
Beckmann, C., and R. Shine. 2009. Impact of invasive cane toads on Australian birds. Conserv. Biol. 23:1544–1549.
Beckmann, C., and R. Shine. 2011. Toad’s tongue for breakfast: exploitation of a novel prey type, the invasive cane toad, by scavenging raptors in tropical Australia. Biol. Invasions 13:1447–1455.
Beckmann, C., M. R. Crossland, and R. Shine. 2011. Responses of Australian wading birds to a novel toxic prey type, the invasive cane toad Rhinella marina. Biol. Invasions 13:2925–2934.
van Beurden, E. K., and G. C. Grigg. 1980. An isolated and expanding population of the introduced toad Bufo marinus in New South Wales. Wildl. Res. 7:305–310.
Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecol. Appl. 10:1230–1248.
Bond, N. R., and P. S. Lake. 2003. Characterizing fish-habitat associations in streams as the first step in ecological restoration. Austral Ecol. 28:611–621.
Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.
Brown, G. P., R. Shine, and T. Madsen. 2002. Responses of three sympatric snake species to tropical seasonality in northern Australia. J. Trop. Ecol. 18:549–568.
Brown, G. P., B. L. Phillips, J. K. Webb, and R. Shine. 2006. Toad on the road: use of roads as dispersal corridors by cane toads (Bufo marinus) at an invasion front in tropical Australia. Biol. Conserv. 133:88–94.
Brown, G. P., B. L. Phillips, and R. Shine. 2011. The ecological impact of invasive cane toads on tropical snakes: field data do not support laboratory-based predictions. Ecology 92:422–431.
Brown, G. P., B. Ujvari, T. Madsen, and R. Shine. 2013a. Invader impact clarifies the roles of top-down and bottom-up effects on tropical snake populations. Funct. Ecol. 27:351–361.
Brown, G. P., M. J. Greenlees, B. L. Phillips, and R. Shine. 2013b. Road transect surveys do not reveal any consistent effects of a toxic invasive species on tropical reptiles. Biol. Invasions 15:1005–1015.
Brown, G. W., A. F. Bennett, and J. M. Potts. 2008. Regional faunal decline – reptile occurrence in fragmented rural landscapes of south-eastern Australia. Wildl. Res. 35:8–18.
Bureau of Meteorology. (2014) Climate data online. Available from http://www.bom.gov.au/climate/data/ (accessed March 2014).
Burnett, S. 1997. Colonising cane toads cause population declines in native predators: reliable anecdotal information and management implications. Pac. Conserv. Biol. 3:65–72.
Busby, J. 1991. BIOCLIM – A bioclimate analysis and prediction system. Pp. 64–68 in C. R. Margules and M. P. Austin, eds. Nature conservation: cost effective biological surveys and data analysis. CSIRO, Collingwood, Vic., Australia.

Cabrera-Guzmán, E., M. R. Crossland, D. Pearson, J. K. Webb, and R. Shine. 2015. Predation on invasive cane toads (Rhinella marina) by native Australian amphibians. J. Pest Sci. 88:143–153.

Cassels, A. J. 1966. Disembowelled toads near water. North Qld. Nat. 34:6.

Cassels, A. J. 1966. Disembowelled toads near water. North Qld. Nat. 34:6.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18:117–143.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed. PRIMER-E, Plymouth, UK.

Clarke, R., A. Carr, S. White, B. Raphael, and J. Baker. 2009. Cane toads in communities: talking toads in Northern Australia. Executive Report to the Australian Government. Bureau of Rural Sciences, Canberra, ACT, Australia.

Cogger, H. G. 2014. Reptiles and amphibians of Australia, 7th ed. CSIRO Publishing, Collingwood, Vic., Australia.

Covacevich, J., and M. Archer. 1975. The distribution of the cane toad, Bufo marinus, in Australia and its effects on indigenous vertebrates. Mem. Queensl. Mus. 17:305–310.

Crossland, M. R. 1998. A comparison of cane toad and native tadpoles as predators of native anuran eggs, hatchlings and larvae. Wildl. Res. 25:373–381.

Crossland, M. R., and R. Shine. 2012. Embryonic exposure to conspecific chemicals suppresses cane toad growth and survival. Biol. Lett. 8:226–229.

Daly, G., and F. Lemckert. 2011. Survey of the reptiles and amphibians of the montane forests near Tenterfield on the north coast of New South Wales. Aust. Zool. 35:957–972.

Department of Environment, Climate Change and Water NSW (DECCW). 2010. Northern rivers regional biodiversity management plan. National recovery plan for the Northern Rivers Region. Department of Environment, Climate Change and Water NSW, Sydney, NSW, Australia.

Doody, J. S., B. Green, R. Sims, D. Rhind, P. West, and D. Steer. 2006. Indirect impacts of invasive cane toads (Bufo marinus) on nest predation in pig-nosed turtles (Carettochelys insculpta). Wildl. Res. 33:349–354.

Doody, J. S., B. Green, D. Rhind, C. M. Castellano, R. Sims, and T. Robinson. 2009. Population-level declines in Australian predators caused by an invasive species. Anim. Conserv. 12:46–53.

Doody, J. S., C. M. Castellano, D. Rhind, and D. Green. 2013. Indirect facilitation of a native mesopredator by an invasive species: are cane toads re-shaping tropical riparian communities? Biol. Invasions 15:559–568.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, et al. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Fearn, S. 2003. Pseudechis porphyriacus (red-bellied black snake). Diet. Herpetol. Rev. 34:253–254.

Fitzgerald, M. 1990. Rattus rattus: the introduced black rat, a successful predator on the introduced cane toad Bufo marinus in northern New South Wales. Herpetofauna 20:9–13.

Goldingay, R., D. Newell, and M. Graham. 1999. The status of rainforest stream frogs in north-eastern New South Wales: decline or recovery? Pp. 64–71 in A. Campbell, ed. Declines and disappearances of Australian frogs. Environment Australia, Canberra, ACT, Australia.

Goth, A., and U. Vogel. 2002. Chick survival in the megapode Alectura lathami (Australian brush-turkey). Wildl. Res. 29:503–511.

Heard, G. W., D. Black, and P. Robertson. 2004. Habitat use by the inland carpet python (Morelia spilota mertesii: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. Austral Ecol. 29:446–460.

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002a. The causes and consequences of ant invasions. Annu. Rev. Ecol. Syst. 33:181–233.

Holway, D. A., A. V. Suarez, and T. J. Case. 2002b. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. Ecology 83:1610–1619.

Jessop, T. S., P. Smissen, F. Scheelings, and T. Dempster. 2012. Demographic and phenotypic effects of human mediated trophic subsidy on a large Australian lizard (Varanus varius): meal ticket or last supper? PLoS ONE 7:e34069.

Jones, D. N. 1988. Hatching success of the Australian brush-turkey Alectura lathami in south-east Queensland. Emu 88:260–262.

Kavanagh, R. P., and M. A. Stanton. 2005. Vertebrate species assemblages and species sensitivity to logging in the forests of north-eastern New South Wales. For. Ecol. Manage. 209:309–341.

Kearney, M., B. L. Phillips, C. R. Tracy, K. A. Christian, G. Betts, and W. P. Porter. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. Ecography 31:423–434.

King, R. B., J. M. Ray, and K. M. Stanford. 2006. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. Can. J. Zool. 84:108–115.

Kolbe, J. J., M. Kearney, and R. Shine. 2010. Modeling the consequences of thermal trait variation for the cane toad invasion of Australia. Ecol. Appl. 20:2273–2285.

Lassau, S. A., and D. F. Hochuli. 2005. Wasp community responses to habitat complexity in Sydney sandstone forests. Austral Ecol. 30:179–187.
Toad Impacts in Southern Australia

C. J. Jolly et al.

Lemckert, F. 1999. Impacts of selective logging on frogs in a forested area of northern New South Wales. Biol. Conserv. 89:321–328.

Letnic, M., J. K. Webb, and R. Shine. 2008. Invasive cane toads (Bufo marinus) cause mass mortality of freshwater crocodiles (Crocodylus johnstoni) in tropical Australia. Biol. Conserv. 141:1773–1782.

Lever, C. 2001. The cane toad. The history and ecology of a successful colonist. Westbury Academic and Scientific Publishing, Otley, West Yorkshire, UK.

Lever, C. 2003. Naturalized Reptiles and Amphibians of the World. Oxford University Press, New York, United States of America.

Llewelyn, J., K. Bell, L. Schwarzkopf, R. A. Alford, and R. Shine. 2012. Ontogenetic shifts in a prey’s chemical defenses influence feeding responses of a snake predator. Oecologia 169:965–975.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10:689–710.

Madsen, T., B. Ujvari, R. Shine, and M. Olsson. 2006. Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. Austral Ecol. 31:30–37.

McCann, S. (2014) To boldly go where no toad has gone before; the spread of invasive cane toads into cool-climate montane habitats in north-eastern New South Wales. Honours thesis, University of Sydney, Sydney, NSW, Australia.

McCann, S., M. J. Greenlees, D. Newell, and R. Shine. 2014. Rapid acclimation to cold allows the cane toad (Rhinella marina) to invade montane areas within its Australian range. Funct. Ecol. 28:1166–1174.

McDonald, P. J. 2012. Snakes on roads: an arid Australian perspective. J. Arid Environ. 79:116–119.

McGeoch, M. A., S. H. M. Butchart, D. Spear, E. Marais, E. J. Kleynhans, A. Symes, et al. 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Divers. Distrib. 16:95–108.

Melbourne, B. A., H. V. Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, and A. L. Freestone. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecol. Lett. 10:77–94.

Newell, D. 2011. Recent invasions of World Heritage rainforests in north-east New South Wales by the cane toad Bufo marinus. Aust. Zool. 35:876–883.

O’Donnell, S., J. K. Webb, and R. Shine. 2010. Conditioned taste aversion enhances the survival of an endangered predator imperiled by a toxic invader. J. Appl. Ecol. 47:558–565.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol. Invasions 1:3–19.

Pearson, D. J., M. J. Greenlees, B. L. Phillips, G. S. Bedford, G. P. Brown, J. Thomas, et al. 2014. Behavioural responses of reptile predators to invasive cane toads in tropical Australia. Austral Ecol. 39:448–454.

Phillips, B. L., and R. Shine. 2006a. An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. Proc. R. Soc. B 273:1545–1550.

Phillips, B. L., and R. Shine. 2006b. Allometry and selection in a novel predator-prey system: Australian snakes and the invading cane toad. Oikos 112:122–130.

Phillips, B. L., G. P. Brown, and R. Shine. 2003. Assessing the potential impact of cane toads on Australian snakes. Conserv. Biol. 17:1738–1747.

Phillips, B., and M. Fitzgerald. 2004. Encounters between eastern brown snakes (Pseudonaja textilis) and cane toads (Bufo marinus) in northern New South Wales. Herpetofauna. 34:23–25.

Phillips, B. L., G. P. Brown, J. K. Webb, and R. Shine. 2006. Invasion and the evolution of speed in toads. Nature 439:803.

Phillips, B. L., G. P. Brown, M. Greenlees, J. K. Webb, and R. Shine. 2007. Rapid expansion of the cane toad (Bufo marinus) invasion front in tropical Australia. Austral Ecol. 32:169–176.

Phillips, B. L., M. J. Greenlees, G. P. Brown, and R. Shine. 2010. Predator behaviour and morphology mediates the impact of an invasive species: cane toads and death adders in Australia. Anim. Conserv. 13:53–59.

Piper, S. D., and C. P. Catterall. 2006. Impacts of picnic areas on bird assemblages and nest predation activity within Australian eucalypt forests. Landsc. Urban Plan. 78:251–262.

Pizzey, G., and F. Knight. 2012. Field guide to the birds of Australia. HarperCollins, Pymble, NSW, Australia.

Pockley, D. 1965. The free and the caged. Blackwoods Mag. 1965:439–466.

Pramuk, J. 2006. Phylogeny of South American Bufo (Anura: Bufonidae) inferred from combined evidence. Zool. J. Linn. Soc. 146:407–452.

Price-Rees, S. J., G. P. Brown, and R. Shine. 2010. Are bluetongue lizards (Tiliqua scincoides intermedia, Scincidae) threatened by the invasion of toxic cane toads (Bufo marinus) through tropical Australia? Wildl. Res. 37:166–173.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and analysis for biologists. Cambridge Univ. Press, Cambridge, U.K.

Rayward, A. 1974. Giant toads: a threat to Australian wildlife. Wildlife 17:507–507.

Ringma, J. 2013. Survival of a Laughing Kookaburra (Dacelo novaeguineae) after the predation of a Cane Toad (Rhinella marina). Mem. Queensl. Mus. 56:588–591.
Sartorius, S. S., L. J. Vitt, and G. R. Colli. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. Biol. Conserv. 90:91–101.

Seabrook, W. 1991. Range expansion of the introduced cane toad *Bufo marinus* in New South Wales. Aust. Zool. 27: 58–62.

Seabrook, W. A. (1993) Habitat use of the cane toad *Bufo marinus* implications for assessment of impact and control strategies. PhD thesis, University of Sydney, Sydney, NSW, Australia.

Seabrook, W. A., and E. B. Dettmann. 1996. Roads as activity corridors for cane toads in Australia. J. Wildl. Manage. 60:363–368.

Semeniuk, M., F. Lemckert, and R. Shine. 2007. Breeding-site selection by cane toads (*Bufo marinus*) and native frogs in northern New South Wales, Australia. Wildl. Res. 34: 59–66.

Shea, G. M. 1999. Morphology and natural history of the land mullet *Egernia major* (Squamata: Scincidae). Aust. Zool. 31:351–364.

Shine, R. 1977. Habitats, diets, and sympathy in snakes: a

®© 2015 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.

Shine, R., G. P. Brown, B. L. Phillips, J. K. Webb, and M. Hagman (2006) The biology, impact and control of cane toads: an overview of the University of Sydney’s research program. Pp. 18–32 in K. L. Molloy, W. R. Henderson, eds. Science of cane toad invasion and control. *Proceedings of the Invasive Animals CRC/CSIRO/Qld NRM6-W Cane Toad Workshop, June 2006*. Invasive Animals Cooperative Research Centre, Canberra, ACT, Australia.

Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? Biol. Invasions 13:1255–1268.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd ed. W. H Freeman, New York, NY.

Shine, R., and J. S. Doody. 2011. Invasive species control: understanding conflicts between researchers and the general community. Front. Ecol. Environ. 9:400–406.

Shine, R., G. P. Brown, B. L. Phillips, J. K. Webb, and M. Hagman (2006) The biology, impact and control of cane toads: an overview of the University of Sydney’s research program. Pp. 18–32 in K. L. Molloy, W. R. Henderson, eds. Science of cane toad invasion and control. *Proceedings of the Invasive Animals CRC/CSIRO/Qld NRM6-W Cane Toad Workshop, June 2006*. Invasive Animals Cooperative Research Centre, Canberra, ACT, Australia.

Shine, R. 2010. The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. Q. Rev. Biol. 85:253–291.

Shine, R. 2012. Invasive species as drivers of evolutionary change: cane toads in tropical Australia. Evol. Appl. 5: 107–116.

Shine, R. 2014. A review of ecological interactions between native frogs and invasive cane toads in Australia. Austral Ecol. 39:1–16.

Shine, R., and G. P. Brown. 2008. Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry tropics. Invited review. Philos. Trans. R. Soc. B 363:363–373.

Shine, R., and J. S. Doody. 2011. Invasive species control: understanding conflicts between researchers and the general community. Front. Ecol. Environ. 9:400–406.

Shine, R., G. P. Brown, B. L. Phillips, J. K. Webb, and M. Hagman (2006) The biology, impact and control of cane toads: an overview of the University of Sydney’s research program. Pp. 18–32 in K. L. Molloy, W. R. Henderson, eds. Science of cane toad invasion and control. *Proceedings of the Invasive Animals CRC/CSIRO/Qld NRM6-W Cane Toad Workshop, June 2006*. Invasive Animals Cooperative Research Centre, Canberra, ACT, Australia.

Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? Biol. Invasions 13:1255–1268.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd ed. W. H Freeman, New York, NY.

Somaweera, R., and R. Shine. 2012. The (non) impact of invasive cane toads on freshwater crocodiles at Lake Argyle in tropical Australia. Anim. Conserv. 15:152–163.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041–2056.

Taylor, B. D., and R. L. Goldingay. 2003. Cutting the carnage: wildlife usage of road culverts in north-eastern New South Wales. Wildl. Res. 30:529–537.

Tyler, M. J. (1975) *The Cane Toad Bufo marinus: An Historical Account and Modern Assessment*. Report to the Vermin and Noxious Weeds Destruction Board of Victoria and the Agriculture Protection Board, Western Australia, June 1975.

Ujvari, B., R. Shine, and T. Madsen. 2011. Detecting the impact of invasive species on native fauna: cane toads (*Bufo marinus*), frillneck lizards (*Chlamydosaurus kingii*) and the importance of spatial replication. Austral Ecol. 36: 126–130.

Ujvari, B., H. Mun, A. D. Conigrave, A. Bray, J. Osterkamp, P. Halling, et al. 2013. Isolation breeds naivety: island living robs Australian varanid lizards of toad-toxin immunity via four-base-pair mutation. Evolution 67:289–294.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2007. The cane toad’s (*Chaunus marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proc. R. Soc. B 274:1413–1419.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2008. A toad more traveled: the heterogeneous invasion dynamics of cane toads in Australia. Am. Nat. 171:134–148.

Van Dyck, S., I. Gynther, and A. Baker. 2013. Field companion to the mammals of Australia. New Holland Publishers, Sydney, NSW, Australia.

Warnken, J., S. Hodgkison, C. Wild, and D. Jones. 2004. The localized environmental degradation of protected areas adjacent to bird feeding stations: a case study of the Australian brush-turkey *Alectura lathami*. J. Environ. Manage. 70:109–118.

White, A. W., and R. Shine. 2009. The extra-limital spread of an invasive species via ‘stowaway’ dispersal: toad to nowhere? Anim. Conserv. 12:38–45.

Wilson, S. K. 2012. Australian lizards: a natural history. CSIRO Publishing, Collingwood, Vic, Australia.

Wilson, S., and G. Swan. 2013. A complete guide to reptiles of Australia, 4th ed. New Holland Publishers, Sydney, NSW, Australia.

Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carrion structure communities. Trends Ecol. Evol. 26:129–135.

Woinarski, J. C. Z., D. J. Milne, and G. Wanganneen. 2001. Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. Austral Ecol. 26:360–370.
fauna of Litchfield National Park, Northern Territory: monitoring over a 6-year period and response to fire history. Wildl. Res. 31:587–596.
Wonham, M. J., M. O’Connor, and C. D. G. Harley. 2005. Positive effects of a dominant invader on introduced and native mudflat species. Mar. Ecol. Prog. Ser. 289:109–116.
York, A., D. Binns, and J. Shields (1991) Flora and fauna assessment in NSW State Forests. Survey guidelines: procedures for sampling flora and fauna for Environmental impact statements, version 1.1. Unpublished report.
Forestry Commission of NSW, Sydney, NSW, Australia.
Zug, G. R., and P. B. Zug. 1979. The marine toad, Bufo marinus: a natural history resume of native populations. Smithson. Contrib. Zool. 284:1–54.

Supporting Information

Additional Supporting Information may be found in the online version of this article:
Table S1. Study sites located in the Northern Rivers region, New South Wales, Australia.
Table S2. Vertebrate taxa recorded during surveys of campgrounds in northeastern New South Wales, Australia.
Table S3. Habitat attributes of campgrounds and bushland in toad-present versus toad-absent sites.