Invasive cane toads might initiate cascades of direct and indirect effects in a terrestrial ecosystem

Benjamin Feit · Christopher E. Gordon · Jonathan K. Webb · Tim S. Jessop · Shawn W. Laffan · Tim Dempster · Mike Letnic

Received: 9 April 2016 / Accepted: 12 January 2018 / Published online: 19 January 2018
© The Author(s) 2018. This article is an open access publication

Abstract Understanding the impacts that invasive vertebrates have on terrestrial ecosystems extends primarily to invaders' impacts on species with which they interact directly through mechanisms such as predation, competition and habitat modification. In addition to direct effects, invaders can also initiate ecological cascades via indirect population level effects on species with which they do not directly interact. However, evidence that invasive vertebrates initiate ecological cascades in terrestrial ecosystems

remains scarce. Here, we ask whether the invasion of the cane toad, a vertebrate invader that is toxic to many of Australia's vertebrate predators, has induced ecological cascades in a semi-arid rangeland. We compared activity of a large predatory lizard, the sand-goanna, and abundances of smaller lizards preyed upon by goannas in areas of high toad activity near toads' dry season refuges and areas of low toad activity distant from toads' dry season refuges. Consistent with the hypothesis that toad invasion has led to declines of native predators susceptible to poisoning, goanna activity was lower in areas of high toad activity. Consistent with the hypothesis that toad-induced goanna decline lead to increases in abundance

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10530-018-1665-8>) contains supplementary material, which is available to authorized users.

B. Feit (✉) · S. W. Laffan · M. Letnic
Centre for Ecosystem Science, University of New South Wales, Sydney, NSW 2052, Australia
e-mail: benjamin.feit@slu.se

B. Feit
Hawkesbury Institute for the Environment, Western Sydney University, Sydney, NSW 2751, Australia

B. Feit
Department of Ecology, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden

C. E. Gordon
Centre for Environmental Risk Management of Bushfires, University of Wollongong, Wollongong, NSW 2522, Australia

J. K. Webb
School of the Environment, University of Technology Sydney, Sydney, NSW 2007, Australia

T. S. Jessop
School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia

T. Dempster
Department of Zoology, University of Melbourne, Melbourne, VIC 3010, Australia

the prey of goannas, smaller lizards were more abundant in areas of high toad activity. Structural equation modelling showed a positive correlation between goanna activity and distance from dry season refuge habitats used by toads. The abundances of small lizards was correlated negatively with goanna activity and distance from dry season refuges of toads. Our findings provide support for the notion that invasions by terrestrial vertebrates can trigger ecological cascades.

Keywords Cane toad · Invasive species · *Rhinella marina* · Semi-arid · Trophic cascade · *Varanus gouldii*

Introduction

The invasion of ecosystems by non-indigenous plant and animal species is a major driver of global environmental change and recognized as a serious threat to biodiversity (Vitousek and D'Antonio 1997; Mack et al. 2000). Research on the ecological consequences of biological invasions has focused largely on direct population-level impacts on single or specific guilds of native species through mechanisms such as predation (Risbey et al. 2000; Roy et al. 2012), competition (Corbin and D'Antonio 2004; Miller and Gorchov 2004) and habitat modification (Rodriguez 2006). However, population-level effects that invaders have on species they do not directly interact with (i.e., indirect effects) are often overlooked, even though there is evidence that such effects can manifest in the reorganization of recipient ecosystems (White et al. 2006).

Invaders are likely to induce cascades of indirect effects if they influence the abundance of strongly interactive species such as predators, pollinators and ecosystem engineers or substantially alter primary productivity or vegetation structure (Anderson and Rosemond 2007; Gooden et al. 2009; Letnic et al. 2009). In such circumstances, invaders can propagate ecological cascades whereby shifts in the abundance of one species indirectly affect the abundance and biomass of others (Terborgh and Estes 2010). Such ecological cascades may become evident temporally or spatially as alternating patterns in the abundances of species are affected directly and indirectly by invaders

(Estes et al. 2011; Letnic et al. 2009). Ecological cascades initiated by invasive species is a relatively well documented phenomenon in aquatic systems (e.g. Simon and Townsend 2003; Baxter et al. 2004; Strayer 2010) with increasing evidence suggesting similar effects of invasive vertebrates on the terrestrial ecosystems of offshore islands (Roemer et al. 2002; Croll et al. 2005; Thoresen et al. 2017), but few studies have reported invasive species driving cascades in terrestrial ecosystems of mainland continents.

One reason for the scarcity of studies on the indirect impacts of vertebrate invaders in terrestrial ecosystems is that studies investigating biological invasions are difficult to plan. Hence, most studies reporting impacts of biological invasions are conducted post-invasion and typically evaluate the impacts of invasive vertebrates by manipulating their abundance or access to the species or ecosystem of interest. However, demonstrating that vertebrate invaders can have cascading effects in terrestrial ecosystems often requires conducting manipulative experiments at large spatial scales, which are logistically difficult (Parker et al. 1999). One way to advance knowledge of invasive vertebrates' indirect impacts on ecosystems is to utilize "natural experiments" whereby the abundance of invaders varies in time or space in otherwise similar landscapes. Such studies can provide valuable insights into ecological processes at spatial and temporal scales that cannot be achieved through experimentation (Sax et al. 2005). In the semi-arid rangelands of northern Australia, spatial structuring of cane toad populations, whereby their activity is concentrated around dry season refuge habitats (Letnic et al. 2014, 2015), provides the opportunity to conduct a "large-scale" natural experiment to examine the role that introduced species have in structuring ecosystems.

The cane toad (*Rhinella marina*) is an anuran native to South America, that is currently invading northern and semi-arid regions of Australia (Florance et al. 2011). Cane toads contain toxins that are absent from Australian anurans. Consequently, most native Australian vertebrate predator species lack an evolutionary history of exposure to these toxins and many die after attacking or consuming toads (Shine 2010). Due to poisoning of individuals, populations of marsupial quolls, monitor lizards (i.e., goannas), freshwater crocodiles and some snake species have undergone marked declines following the arrival of toads (Shine

2010; Feit and Letnic 2015). Because cane toads have driven declines in predator populations, it follows that diminished levels of predation could lead to increases in abundance or survivorship of prey species in areas where cane toads have suppressed the abundances of predators (Doody et al. 2013, 2015).

Cane toads are now spreading through Australia's vast semi-arid rangelands (Tingley et al. 2014). In semi-arid regions, cane toads require regular access to water to survive sustained periods of hot, dry weather without accessing water (Florance et al. 2011; Jessop et al. 2013b). As a result, during prolonged periods of dry conditions the distribution of cane toads in semi-arid landscapes is restricted to isolated populations at places where permanent water is available (Letnic et al. 2014). Because natural sources of water are normally scarce in Australia's semi-arid regions, their invasion has been facilitated by the presence of earthen dams at artificial water points (AWP) (Florance et al. 2011) (Fig. 1a). These dams function as reservoirs for water pumped from bores and normally provide drinking water to livestock via a gravity fed trough (Fig. 1d). Although toads cannot normally access the water held in livestock troughs, water stored in dams is readily accessible to them. Consequently, during dry periods, earthen dams function as refuges that support dense cane toad populations (Florance et al. 2011; Letnic et al. 2014) (Fig. 1b). Previous studies have demonstrated that cane toad population can be suppressed by restricting their access to water at AWP either by installing toad-proof fences at dams or by using tanks made of plastic or steel as reservoirs instead of earthen dams (Letnic et al. 2014; Feit et al. 2015) (Fig. 1c). In rangeland areas of the Tanami Desert in Australia's Northern Territory, the existence of AWP fitted with reservoirs that support high density (dams) and low density (tanks) cane toad populations provided us with the opportunity to conduct a large-scale natural experiment to examine the effects that toads have had on lizard assemblages.

Based on prior knowledge of cane toad biology, cane toads' suppressive effects on varanid lizard populations (Doody et al. 2009, 2014, 2015) and varanid lizards' predatory effects on populations of smaller lizard species (Olsson et al. 2005; Doody et al. 2012, 2015), we tested the following predictions: (1) toad activity should decrease with distance from AWP and be greater in the vicinity of dams where toads are abundant than tanks where toads are rare; (2) because

encounter rates between toads and varanid lizards should decrease with distance from AWP, varanid lizard foraging activity should increase with distance from AWP and should be greater in the vicinity of tanks where toads are rare than dams where toads are abundant when distance from water is set to the mean distance; and (3) because of reduced predation by varanid lizards, the abundance of small lizards (Scincidae and Agamidae) should be greater in the vicinity of dams where toads are abundant than tanks where toads are rare.

We tested our predictions by comparing the abundance of cane toads, the foraging activity of the sand goanna (*Varanus gouldii*) (Fig. 1e, f) and the abundance of skinks and dragons along 12 km road transects in the vicinity of dams and tanks, respectively. We used structural equation modelling (SEM) to investigate the hypothesized direct and indirect relationships among the response variables. We also tested alternative hypotheses in our SEM based on prior knowledge that the abundances of goannas and smaller lizards are influenced by predation from mammalian predators (Olsson et al. 2005) and disturbances to vegetation by livestock grazing (James et al. 1999) and fire (Letnic et al. 2004).

Materials and methods

Study area and time

We conducted our surveys on two neighboring cattle stations, Dungowan (16°42'S, 132°16'E) and Camfield (17°2'S, 131°17'E), located in the northern margin of the Tanami Desert in the Northern Territory, Australia. Bore-fed reservoirs at AWP on both stations consist of a mix of earthen dams and tanks made of plastic or steel (Fig. 2). At both reservoir types, livestock are supplied with water through troughs located within 50 m of the reservoir (Fig. 1d). The troughs are fed by gravity and fitted with a float-valve to prevent them from over-flowing. Permanent fences prevent livestock from accessing the water stored in dams.

The study area has a mean annual rainfall of 580 mm, of which 96% falls in the wet season (November to April) and 4% in the dry season (May–October; Australian Bureau of Meteorology). The vegetation of the study area consists of open semi-

Fig. 1 **a** Earthen dam (arrowed) used as reservoir at an AWP. **b** Dams support large numbers of cane toads (*Rhinella marina*) because they allow ready access to water for rehydration and reproduction. **c** Tank used as reservoir at an AWP. In comparison to dams, tanks support few toads because they allow only little access to water. **d** A trough from which livestock drink in our study area. Gravity supplies the trough with water from a dam or tank. Toads cannot normally access water in troughs. **e** Sand goanna (*Varanus gouldii*). **f** Ellipsoid foraging pit created by a sand goanna when digging for fossorial prey

Cane toad abundance at AWP and along road transects

We estimated the abundance of toads in the direct vicinity of AWP by conducting nocturnal 4 m × 150 m strip transects radiating away from the AWP (n = 4 per AWP) using handheld 12 V spotlights with 25 W halogen bulbs. Cane toad abundance was calculated as the sum of individuals encountered along the four transects. We conducted a total of 42

Fig. 2 Map of the study area showing the location of transects (solid lines) in the vicinity of AWP fitted with dams (black) and tanks (dark grey). The inset shows the location of study area (shaded) within Australia

arid savannah woodland with the dominant woody species of lancewood (*Acacia shirleyi*) and eucalypts (*Eucalyptus leucophloia*) and an understory dominated by grasses (*Eriachne* spp. and *Sorghum* spp.). We surveyed the foraging activity of sand goannas and the abundance of cane toads, skinks and dragons in April and November 2012, April and November 2013 and September 2014.

cane toad counts at 31 AWP (ten dams and 21 tanks) (Online Resource 1); four dams and seven tanks were sampled twice during the study period with a minimum of 12 months between surveys.

Cane toads frequently travel along roads during dispersal periods (Brown et al. 2006). To document the distribution of toads with respect to distance from AWP, we conducted nocturnal surveys along low-use single lane dirt roads in a 4WD vehicle during a period

when many toads had dispersed away from their dry season refuges at the end of the wet season in April 2012. Because of logistical constraints during field work, it was not possible to conduct road transects from all AWP. Hence, distance mediated effects were evaluated at a subset of dams ($n = 4$) and tanks ($n = 5$). We surveyed toad abundance over a total of 110 km at distances of up to 12 km from both reservoir types. The surveys were undertaken at a speed of 20 km/h and an observer noted with a GPS the location of all toads sighted. Toad activity was documented as number of toads per 500 m transect section.

Goanna activity indices

Sand goannas are difficult to survey using mark-recapture methods because they rarely enter traps (Letnic et al. 2004) and, in habitats with dense understory vegetation such as our study area, are difficult to sight and approach for the purposes of noosing, hand capture or visual surveys. Previous studies have used the occurrence of fresh goanna tracks and pits that goannas create whilst foraging to index goanna abundance (Paltridge 2002; Bird et al. 2014; Read and Scoleri 2014). Both indices have been validated against known abundances in other varanid species (Anson et al. 2014). Following these previous studies, we used two methods to index goanna activity, the occurrence of tracks (i.e. footprints and tail drag marks) crossing single-lane dirt roads and the occurrence of recent goanna foraging pits. Our track count index provided a measurement of goanna activity over a 24 h period, while the foraging pit index provided a cumulative measure of goanna activity for a period of approximately 1 month prior to our surveys. We conducted all monitoring under environmental conditions that favored lizard activity and ensured equal and high detection probabilities among track plots and surveys (Jessop et al. 2013a).

The track-based index of goanna activity was derived by scoring the occurrence (presence/absence) of tracks crossing 50 m track plots located along road transects radiating from dams and tanks. The transects were situated on low-use single lane dirt roads (Paltridge 2002; Read and Scoleri 2014). We surveyed 403 track plots over a total of 201.5 km (Online Resource 2). Each track plot consisted of a 50 m road section that was cleared of tracks on the day before the

survey. Track plots were spaced 500 m apart and located between 0 and 12 km from the nearest AWP. We walked along each track plot and recorded the presence or absence of fresh goanna tracks (i.e., distinctive tail drags and claw imprints). As daily activity areas of sand goannas are unlikely to exceed an area of 200 m by 200 m (Green and King 1978), we are confident that each recorded track originated from a different individual.

The foraging-pit based index of goanna activity was derived by scoring the presence or absence of recent goanna foraging signs during 2 min active searches in the vicinity of each track plot (Jessop et al. 2013a). Whilst digging for fossorial prey, sand goannas leave characteristic ellipsoid foraging pits that often show deep scratch marks left by their strong forelimbs during excavation of the soil (Read and Scoleri 2014). We estimated the approximate age of foraging pits based on two criteria: the amount of leaf litter and other debris in the excavation and the coloration and texture of the excavated soil (initially darker and softer than the topsoil, gradually fading and hardening over the course of several weeks). To provide an indication of the age of foraging pits that we encountered, we excavated pits similar to goanna foraging pits and monitored them over a 2 month period. This allowed us to classify foraging pits into the two age classes of recent (i.e. younger than approximately 1 month) and old (i.e. older than 1 month). Only the presence of foraging pits younger than approximately 1 month was used for further analyses.

Small lizard abundance

To monitor the abundance of small lizards, we conducted 198 active diurnal searches (total search duration of 1980 min) following the methods of Lunney and Barker (1986) (Online Resource 3). During each of the surveys in April and November 2012 and 2013, we conducted 40 active diurnal searches (20 sites located near dams, 20 near tanks), during the survey in September 2014 we conducted 38 searches (20 sites located near dams, 18 near tanks). Active search sites comprised 1 ha (100 m $\times$ 100 m) plots and were spaced a minimum of 2 km apart and located along the same transects used to survey goanna activity. At each site, active searches were conducted simultaneously by two observers who portioned their search effort so that each observer restricted their

search to a 50 × 100 m quadrat within each site. We recorded reptiles encountered on the ground, under logs, in litter, in grass and on stems and branches of trees. An observers' experience bias was avoided by using random observer combinations for each survey. Each site was actively searched for 10 min (5 min per observer) and was conducted between 9:00 and 10:30 am. To prevent double counting, observers avoided walking the same paths twice. Sighted reptiles were identified to family level by their pattern and size and the microhabitat they were encountered in. All encountered skink species belonged to four genera (*Carlia*, *Ctenotus*, *Lialis* and *Menetia*), all encountered dragon species belonged to two genera (*Amphibolurus* and *Diporiphora*). The total number of individuals recorded during 10 min of active search was used as an index of the abundance of skinks and dragons at each active search site.

Mammal activity

To investigate the alternative hypotheses that habitat disturbance by cattle or predation by dingoes or feral cats were factors influencing the abundance of goannas and/or smaller lizards, we recorded the presence of tracks of cattle, dingoes, and feral cats at each tracking plot. An index of cattle activity for each track plot and each active search site was expressed as the percentage of track plots with fresh tracks within a 1.5 km radius. To account for the wide-ranging habitat of dingoes, dingo activity was expressed as mean values obtained for each sub-site. Cat activity was omitted from the analyses owing to the low activity of cats (only 3.8% of the track plots contained cat tracks).

Fire history

The reduction of vegetation coverage by fire is known to influence the abundance of sand goannas and smaller lizard species (Letnic et al. 2004; Bird et al. 2014). To investigate whether differences in the fire history could explain differences in the abundance of goannas, skinks and dragons we obtained data on the fire history of each active search site from the North Australian Fire Information.

Statistical analyses

Cane toad abundance at AWP and along road transects

We analyzed differences in cane toad density in the direct vicinity of AWP using a generalized linear mixed model (GLMM) with a Poisson distribution and a log link function. To account for multiple sampling between years, AWP identity was included as random factor. We analyzed differences in cane toad density along 12 km road transects radiating from the two different reservoir types using a generalized additive model (GAM) with a Poisson distribution and a log link function. To account for the nested structure of the data, we included the identity of each transect and the year in which the survey was conducted in as random factors. All GLMM and GAM analyses were performed in R Version 3.0.3 using the 'glmm' and 'mgcv' libraries.

Goanna activity and small lizard abundance along transects

We combined the track and foraging pit indices of goanna activity in our analysis and defined a plot as indicating recent goanna activity if goanna tracks and/or recent foraging pits were present. Because our road surveys revealed a decline of cane toad abundance at distances of up to 3 km from dams, followed by a steady count to distances up to 12 km (see "[Results](#)" section), we divided our 12 km transects into two sections (i.e. < 3 and > 3 km). For the initial analysis of goanna activity and small lizard abundance along transects we compared the averaged goanna activity and lizard abundance of each transect section between individual transects using GLMM with a normal distribution and log link function. Type of nearest AWP, distance to AWP and the interaction of type and distance were included as fixed factors in the models. To account for the nested structure of the data, we included the identity of each transect and the year in which the survey was conducted in as random factors.

Because our expectation in this study system was that even though the biomass of lizards (i.e., as small ectotherms) would be relatively high, the distribution of individuals is expected to be very patchy. This reflects well known observations, that semi-arid lizards, as consequences of sensitivity to heterogeneity

in structural habitat resources (e.g. ground vegetation cover, coarse woody debris) and relatively small home ranges, can be extremely variable in spatial occurrence (Letnic et al. 2004). Our survey design thus considered that an increased number of plots sampled once, rather than fewer plots sampled repeatedly, would permit better encounter rates and less variation in lizard detection in an otherwise very large study area. We however acknowledge, that as a potential trade-off of this approach, our measurements of naive count data could not account for imperfect detection (Guillera-Arroita et al. 2014). Ideally, if time had permitted, we would have performed repeated count surveys on a large number of sites to allow use of potentially more robust count estimation methods (Royle and Nichols 2003).

Structural equation modelling

Because our initial analysis indicated significant differences in cane toad abundance, recent goanna activity and small lizard abundance between transects in the vicinity of tanks and dams (see “Results” section), we used piecewise SEM to further test hypotheses based on a priori knowledge of interactions hypothesized to occur between cane toads, goannas and smaller lizard species (Grace 2006). We constructed our a priori SEM model based on trophic cascade theory and prior knowledge of factors impacting the abundance of small terrestrial lizards. As opposed to classical SEM, where covariance matrices are used, piecewise SEM uses localized estimates to deduce direct and indirect effect pathways (Grace 2006; Colman et al. 2014). This approach allows the modelling of data that do not meet the assumptions of classic SEM and the incorporation of exogenous factors such as spatial dependence (Pasanen-Mortensen et al. 2013; Colman et al. 2014). Localized estimates within the SEM were fitted using a GLMM (Poisson log-link function; skink and dragon models) or LMM (goanna model). To account for the nested structure of the data we included the identity of each transect as a random factor. For the GLMM, an observation level random effect was included to account for overdispersion (Harrison 2014).

Our initial models were parameterized with values obtained for each active search site for the variables goanna activity (percentage of plots with recent goanna tracks and/or foraging pits within 1.5 km of

the active search site), cattle activity (percentage of plots with cattle tracks within 1.5 km of the active search site) and the number of months since the last fire as well as with mean values obtained for each sub-site for dingo activity (percentage of plots with dingo tracks) to account for the wide-ranging habitat of dingoes. Because the impact of cane toads on goannas was negatively correlated with increasing distance from dams whereas increasing distance from tanks was not correlated with goanna abundance (see “Results” section), we used the distance from the nearest dam to each of the active search sites as a proxy for the impact of cane toads on goannas. We used a backwards step-wise elimination process for model simplification whereby the most non-significant predictor variables were sequentially deleted until all interaction were significant. The most parsimonious model was then selected using Akaike’s Information Criterion for small sample sizes (AICc) as that with the lowest AICc value (Burnham and Anderson 2002). Standardized path coefficients were calculated by normalizing data to fall within one standard deviation of a mean centered on zero and the amount of variance explained by each ‘piece’ of the SEM (i.e., the goanna, skink and dragon models) was assessed using marginal R^2 values. The overall fit of the SEM was assessed using a Fisher C test and associated p value. The model is a good representation of the data if the Fisher C p -value is > 0.05 . All SEM analyses were performed in R Version 3.0.3 using the ‘piecewiseSEM’ library.

Model justification

Interaction pathways between variables were determined by applying a priori knowledge, which resulted in the following set of hypothesized pathways (Fig. 5a): (1) Cane toad activity should negatively affect goannas owing to lethal ingestion; (2) the foraging activity of goannas should negatively affect the abundance of skinks and dragons (Olsson et al. 2005); (3) because of selective predation pressure, goanna activity should have a stronger impact on skinks than dragons (Sutherland 2011); (4) we used distance to the nearest dam as a proxy for the impact of cane toads because the impact of cane toads on goannas was negatively correlated with distance from dams (see “Results” section); (5) dingo activity should negatively affect goanna activity owing to predation (Paltridge 2002); (6) habitat modification

resulting from grazing by livestock can have detrimental effects on both the abundance of goannas and of smaller lizard species such as skinks and dragons (James 2003); (7) time since fire was hypothesized to positively affect populations of goannas (Bird et al. 2014) and to negatively affect skinks and dragons (Letnic et al. 2004).

Results

Cane toad abundance at AWP and along road transects

Cane toads were 5.2 times more abundant in the direct vicinity of dams (mean $\pm$ 1SE = 15.0 ± 2.9) than tanks (2.4 ± 0.6 ; $F_{1,39} = 32.68$, $p < 0.001$). For both reservoir types, the number of cane toads encountered along road transects during the wet season was correlated negatively with distance from AWP (Fig. 3). In the vicinity of dams we encountered relatively high numbers of cane toads within the first 3 km of transects in comparison to distances > 3 km (Fig. 3). We did not encounter cane toads at distances > 3 km from tanks (Fig. 3). We found no spatial autocorrelation among the Pearson residuals generated by the model (Mantel test, $r = 0.04$, $p = 0.2$).

Fig. 3 Average number of cane toads (*Rhinella marina*) encountered on 500 m road sections along transects radiating from AWP fitted with two reservoir types, dams where toads were abundant ($n = 4$) and tanks where toads were rare ($n = 5$), during a period of rainy conditions. Lines are regressions and 95% confidence limits fitted by a generalized additive model with a Poisson distribution and log link function. Error bars indicate ± 1 SE

Goanna activity along transects

Overall, the probability of detecting recent goanna activity was 3.3 times greater at plots in the vicinity of tanks where toads were rare (0.50 ± 0.08) than dams where toads were abundant (0.15 ± 0.03 , $F_{1,399} = 18.88$, $p < 0.01$). In the vicinity of dams, recent goanna activity was 2.0 times greater within the > 3 km transect sections (0.10 ± 0.04) than < 3 km transect sections (0.20 ± 0.03 , $F_{1,399} = 4.43$, $p < 0.05$; Fig. 4a).

Small lizard abundance along transects

We encountered 6.0 times more skinks during 10-min active searches along transects in the vicinity of dams where toads were abundant (0.13 ± 0.02) than tanks where toads were rare (0.02 ± 0.01 , $F_{1,198} = 31.48$, $p < 0.001$). In both the vicinity of dams and tanks, skink abundance was greater within the < 3 km transect sections (dams: 0.19 ± 0.03 , tanks: 0.07 ± 0.02) than the > 3 km transect sections (dams: 0.10 ± 0.01 , tanks: 0.01 ± 0.004 , $F_{1,198} = 17.61$, $p < 0.01$, Fig. 4b).

We encountered 2.0 times more dragons during 10-min active searches along transects in the vicinity of dams where toads were abundant (0.06 ± 0.01) than tanks where toads were rare (0.03 ± 0.001 , $F_{1,198} = 6.18$, $p < 0.05$). Dragon abundance did not differ between the < 3 and > 3 km transect sections within transects from dams or tanks, respectively ($F_{1,198} = 1.71$, $p = 0.19$, Fig. 4c).

Structural equation modelling

Our proxy for cane toad abundance and impact, that is distance from dams, had a strong positive correlation with goanna activity and a strong negative correlation with skink and dragon activity (Fig. 5b). Goanna activity was correlated negatively with skink activity (Fig. 5b). Thus, increasing distance from dams, because it had a positive correlation with goanna activity (path co-efficient = 0.70), had a negative, indirect correlation with the abundance of skinks (indirect path co-efficient = -0.62 ; 0.70; Fig. 5b). Dingo activity was correlated negatively with goanna activity (Fig. 5b) and cow abundance was correlated positively with dragon activity (Fig. 5b). Marginal R^2 values were relatively high for the skink and goanna

Fig. 4 a Average probability of encountering recent signs of sand goanna (*Varanus gouldii*) foraging activity within 50 m road sections ($n = 403$) and average number of skinks (b) and dragons (c) encountered during 10 min searches ($n = 198$) at distances of under 3 km and over 3 km from AWP fitted with two reservoir types, dams where toads were abundant and tanks where toads were rare. Error bars indicate ± 1 SE

components of the SEM (0.48 and 0.35, respectively) but relatively low for the dragon component (0.04). The Fisher C p -value was > 0.05 (Fisher C value = 17.32, $p = 0.07$), suggesting that our most parsimonious SEM was a good representation of the data.

Discussion

In accord with our a priori predictions, the results of this study demonstrate that: (1) cane toad abundance in the late wet season decreased with distance from AWP and their numbers were greater in the vicinity of dams than tanks when distance from AWP was held constant; (2) goanna activity increased with distance from dams and, when distance to water was set to mean distance, goanna activity was greater in the vicinity of tanks where toads were rare than dams where toads were abundant; (3) the abundance of skinks and dragons was greater in the vicinity of dams where toads were abundant than tanks where toads were rare and skink abundance was negatively correlated with distance from AWP. In comparison to distance to dams (our proxy for the abundance and impact of cane toads), cattle activity, time since last fire and mammalian predator activity were weak predictors of goanna activity and skink abundance. However, cattle activity was the best predictor of dragon abundance. Taken together, these findings provide support for the idea that the invasion of cane toads has propagated an ecological cascade whereby cane toad induced declines of goanna populations near toads' dry season refuges have facilitated increased abundances of small lizards. More generally, our results provide support for the notion that terrestrial invaders may trigger ecological cascades that become evident as alternating spatial patterns in the abundances of species negatively and positively affected by invaders.

Fig. 5 **a** A priori piecewise structural equation model (SEM) describing the response of populations of sand goannas (*Varanus gouldii*), skinks (Scincidae) and dragons (Agamidae) to the cane toad invasion of semi-arid rangelands in northern Australia. **b** Most parsimonious SEM explaining the activity of

goannas, skinks and dragons. R^2 = marginal R^2 values; path coefficients (± 1 SE) are shown adjacent to arrows; dashed arrows show negative interaction and solid arrows show positive interaction; + = p value of 0.05–0.1, * = p value of 0.05–0.01, ** = p value of 0.01–0.001, *** = p value of < 0.001

A short-coming of our study is that we did not experimentally manipulate cane toad abundance but instead relied upon natural differences in cane toad activity resulting from the type of reservoir utilized at AWP and distance from AWP (Letnic et al. 2014). Because natural systems are intrinsically variable, it remains possible that confounding factors such as differences in grazing pressure, vegetation type, geomorphology, fire history and the activity of mammalian predators may have contributed to the differences we observed (Underwood 1990). During the design of our study, we attempted to control for variation in these variables in two ways. First, we selected study sites with little variation in underlying geology, vegetation type, land use and fire history. Second, at each of our study sites we measured indices of cattle grazing activity, mammalian predator activity and time since last fire, and included these variables as alternative hypotheses to explain goanna activity and lizard abundances in our SEM. None of these variables explained as much variation in goanna activity or skink abundance as the direct or indirect effects of our proxy for cane toad abundance and impact, distance from dam.

Our results are consistent with the hypothesis that higher encounter rates between toads and goannas in the direct vicinity of dams was the driver of the reduction in goanna activity near dams. In turn, lower

rates of predation by goannas near dams has allowed for increased abundances of small lizards. This hypothesis is supported by earlier studies showing that cane toads are more abundant at dams than tanks (Feit et al. 2015), that goanna populations have declined following the invasion of cane toads (Griffiths and McKay 2007, Doody et al. 2009) and that suppression of goanna populations can drive increases in the abundances of skinks and dragons (Olsson et al. 2005; Doody et al. 2013; Read and Scoleri 2014). Moreover, the stronger negative correlation between goanna and skink activity as opposed to that between goannas and dragons is consistent with previous studies showing that sand goannas consume skinks more frequently than dragons (Losos and Greene 1988; Sutherland 2011). Nevertheless, our results indicate that, in addition to goanna activity, factors not measured in this study could influence skink abundance along road transects in our study system. The strength of the indirect path coefficient of the effect of distance to dams on skink abundance mediated by goanna activity is -0.62 (i.e. 0.70×-0.88), approximately half the strength of the direct pathway between dams on skinks (1.33), suggesting that goannas explain about half of the response of skinks to increasing distance to dams. This could reflect an underestimation of goanna foraging by the activity indices used in this study or factors affecting skink

activity not measured during our surveys. We therefore caution that controlled experiments are required to confirm or refute our cane toad induced ecological cascade hypothesis.

Central to our hypothesis that cane toads' impacts on lizard assemblages decrease with distance from dams is the idea that cane toads are largely restricted to refuge sites with water during the dry season and disperse away from refuges during the wet season (Letnic et al. 2014). Thus, during the wet season, encounters between cane toads and goannas could occur anywhere in the landscape, while in the dry season goannas would most likely encounter toads within 500 m of permanent water (Florance et al. 2011). However, during the wet season, the density of cane toads and hence likelihood of a goanna encountering a cane toad should decrease with distance from refuges because as they disperse they are in effect diffusing away from a point source (Florance et al. 2011; Tingley et al. 2013). We contend then that the patterns in goanna and small lizard abundance we report are legacy effects that reflect higher encounter rates between goannas near (< 3 km) sources of permanent water during both the wet season and dry season.

Our SEM analysis suggests that distance to the nearest dam, and thus the population density and impact of cane toads, was not the only factor influencing the foraging activity of goannas and the abundance of small lizards in our study. Goanna activity was also negatively correlated with the activity of dingoes and, contrary to our expectations, positively correlated with cattle activity. In contrast to increasing distance to dams, however, the activity of cattle and dingoes had only weak effects on the foraging activity of goannas in our SEM. Similarly, habitat disturbance by cattle and the reduction of vegetation coverage by fire had weak effects on lizard abundance in our SEM. Nevertheless, the correlation between the abundance of skinks and goanna activity was stronger than the correlation between their abundance and cattle activity or the time since last fire.

We acknowledge that because our count estimates of lizard abundances did not consider imperfect detection, the large difference reported for lizard abundances between tanks and dams may be overestimated. Such a consequence could arise if goanna predation also induced increased lizard anti-predator behavior that could affect their detection probability

and our capacity to observe accurately lizards during count surveys. For example, if small lizards in high-goanna density areas are exposed to greater predation risk and respond through adjustments in daily activity patterns or microhabitat use, or variation in cryptic or flight initiation behavior this could affect our capacity to accurately count them (Vanhooydonck and Van Damme 2003; Cooper and Wilson 2007; Cooper and Frederick 2009). Whilst this is an important methodological consideration, reduced lizard abundance due to the respective contributions of direct mortality or increased anti-predator behavior, nevertheless represents the two key processes through which predators limit prey populations (Preisser et al. 2005). Further study is needed to better understand how goanna predation influences small lizard abundance. Such studies could include those that use a survey design that considers repeated lizard plot counts to enable abundance estimation analyses that consider imperfect detection (e.g. Royal–Nichols abundance type occupancy models; Royal and Nichols 2003), or explicitly set out to detect non-consumptive predation influences (e.g. predator induced spatial avoidance using 2-species occupancy models; Robinson et al. 2014). These studies alongside others that also directly quantify variation in small lizard anti-predator behavior across spatial gradients of goanna predation risk would greatly aid understanding of toad induced trophic consequences in this system.

Direct population level impacts of cane toads have not been restricted to a single goanna species but a multitude of native predators in terrestrial and aquatic ecosystems including other monitor lizards, crocodiles, snakes and quolls (Shine 2010; Feit and Letnic 2015). Doody et al. (2006, 2009, 2013, 2015) demonstrated that cane toad-induced decline of goannas can have cascading effects on species not predicted to be directly affected by cane toads such as small lizards, tree snakes, freshwater turtles and grain-eating birds in riparian systems in northern Australia. Cane toads have also been reported to have direct suppressive effects on their invertebrate prey, and to compete with nesting birds for burrows (Boland 2004; Greenlees et al. 2007; Feit et al. 2015). Given the extent of their reported direct impacts, we contend that it is likely that cane toads have also had indirect impacts on species which have strong interactions with species that have declined following the toad invasion. Indeed, given the multitude of possible indirect interaction pathways

they could potentially disrupt (Doody et al. 2009, 2013, 2015; Feit et al. 2015), we suspect that the invasion of cane toads has affected a much greater range of taxa than has thus far been reported.

Acknowledgements Funding was provided by the Hermon Slade Foundation and Mazda Foundation. We thank Frogwatch, Parks & Wildlife NT and the managers of Dungowan and Camfield for their support. A. Feit provided valuable comments on earlier drafts of the manuscript. Animal census procedures were conducted under the Northern Territory Parks and Wildlife Commission permit 44073, approved by the Animal Care and Ethics Committees of the University of New South Wales (12/103A) and Western Sydney University (A9776).

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* 154:141–153. <https://doi.org/10.1007/s00442-007-0757-4>
- Anson JR, Dickman CR, Handasyde K, Jessop TS (2014) Effects of multiple disturbance processes on arboreal vertebrates in eastern Australia: implications for management. *Ecography* 37:357–366. <https://doi.org/10.1111/j.1600-0587.2013.00340.x>
- Baxter CV, Fausch KD, Murakami M, Chapman PL (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663. <https://doi.org/10.1890/04-138>
- Bird RB, Taylor N, Coddling BF, Bird D (2014) Niche construction and dreaming logic: aboriginal patch mosaic burning and varanid lizards (*Varanus gouldii*) in Australia. *Proc R Soc B* 280:20132297
- Boland CR (2004) Introduced cane toads *Bufo marinus* are active nest predators and competitors of rainbow bee-eaters *Merops ornatus*: observational and experimental evidence. *Biol Conserv* 120:53–62. <https://doi.org/10.1016/j.biocon.2004.01.025>
- Brown GP, Phillips BL, Webb JK, Shine R (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. <https://doi.org/10.1016/j.biocon.2006.05.020>
- Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York
- Colman NJ, Gordon CE, Crowther MS, Letnic M (2014) Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proc R Soc B* 281:20133094. <https://doi.org/10.1098/rspb.2013.3094>
- Cooper WE, Frederick WG (2009) Predator lethality, optimal escape behavior, and autotomy. *Behav Ecol* 21:91–96
- Cooper WE, Wilson DS (2007) Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the phrynosomatid lizard *Sceloporus virgatus*. *Behaviour* 144:1235–1254
- Corbin JD, D'Antonio CM (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85:1273–1283. <https://doi.org/10.1890/02-0744>
- Croll DA, Maron JL, Estes JA, Danner EM, Byrd GV (2005) Introduced predators transform subarctic islands from grassland to tundra. *Science* 307:1959–1961
- Doody JS, Green B, Sims R, Rhind D, West P, Steer D (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, Green B, Rhind D et al (2009) Population-level declines in Australian predators caused by an invasive species. *Anim Conserv* 12:46–53. <https://doi.org/10.1111/j.1469-1795.2008.00219.x>
- Doody J, Hall M, Rhind D, Green B, Dryden G (2012) *Varanus panoptes* (yellow-spotted monitor) diet. *Herpetol Rev* 43:491–492
- Doody J, Castellano C, Rhind D, Green B (2013) Indirect facilitation of a native mesopredator by an invasive species: are cane toads re-shaping tropical riparian communities? *Biol Invasions* 15:559–568. <https://doi.org/10.1007/s10530-012-0308-8>
- Doody J, Mayes P, Clulow S et al (2014) Impacts of the invasive cane toad on aquatic reptiles in a highly modified ecosystem: the importance of replicating impact studies. *Biol Invasions* 15:2303–2309. <https://doi.org/10.1007/s10530-014-0665-6>
- Doody J, Soanes R, Castellano CM et al (2015) Invasive toads shift predator–prey densities in animal communities by removing top predators. *Ecology* 96(2544–2554):15031 0115152000. <https://doi.org/10.1890/14-1332.1>
- Estes JA, Terborgh J, Brashares JS et al (2011) Trophic downgrading of planet Earth. *Science* 333:301–307
- Feit B, Letnic M (2015) Species level traits determine positive and negative population impacts of invasive cane toads on native squamates. *Biodivers Conserv* 24:1017–1029. <https://doi.org/10.1007/s10531-014-0850-z>
- Feit B, Dempster T, Gibb H, Letnic M (2015) Invasive cane toads' predatory impact on dung beetles is mediated by reservoir type at artificial water points. *Ecosystems* 18:826–838. <https://doi.org/10.1007/s10021-015-9865-x>
- Florance D, Webb JK, Dempster T et al (2011) Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proc R Soc B* 278:2900–2908
- Gooden B, French K, Turner PJ (2009) Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia. *For Ecol Manag* 257:960–967. <https://doi.org/10.1016/j.foreco.2008.10.040>

- Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge
- Green B, King D (1978) Home range and activity patterns of the sand goanna, *Varanus gouldii* (Reptilia: Varanidae). *Wildl Res* 5:417–424
- Greenlees MJ, Brown GP, Webb JK et al (2007) Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? *Austral Ecol* 32:900–907. <https://doi.org/10.1111/j.1442-9993.2007.01778.x>
- Griffiths A, McKay J (2007) Cane toads reduce the abundance and site occupancy of Merten's water monitor (*Varanus mertensi*). *Wildl Res* 34:609–615. <https://doi.org/10.1071/WR07024>
- Guillera-Arroita G, Lahoz-Monfort JJ, MacKenzie DI, Wintle BA, McCarthy MA (2014) Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models'. *PLoS ONE* 9:e99571
- Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616
- James C (2003) Response of vertebrates to fence-line contrasts in grazing intensity in semi-arid woodlands of eastern Australia. *Austral Ecol* 28:137–151
- James CD, Landsberg J, Morton SR (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. *J Arid Environ* 41:87–121. <https://doi.org/10.1006/jare.1998.0467>
- Jessop T, Kearney M, Moore J et al (2013a) Evaluating and predicting risk to a large reptile (*Varanus varius*) from feral cat baiting protocols. *Biol Invasions* 15:1653–1663
- Jessop T, Letnic M, Webb JK, Dempster T (2013b) Adrenocortical stress responses influence an invasive vertebrate's fitness in an extreme environment. *Proc R Soc B*. <https://doi.org/10.1098/rspb.2013.1444>
- Letnic M, Dickman C, Tischler M et al (2004) The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *J Arid Environ* 59:85–114. <https://doi.org/10.1016/j.jaridenv.2004.01.014>
- Letnic M, Koch F, Gordon C et al (2009) Keystone effects of an alien top-predator stem extinctions of native mammals. *Proc R Soc B* 276:3249–3256. <https://doi.org/10.1098/rspb.2009.0574>
- Letnic M, Webb J, Jessop T et al (2014) Artificial water points facilitate the spread of an invasive vertebrate in arid Australia. *J Appl Ecol* 51:795–803. <https://doi.org/10.1111/1365-2664.12232>
- Letnic M, Webb JK, Jessop TS, Dempster T (2015) Restricting access to invasion hubs enables sustained control of an invasive vertebrate. *J Appl Ecol* 52:341–347
- Losos JB, Greene HW (1988) Ecological and evolutionary implications of diet in monitor lizards. *Biol J Linn Soc* 35:379–407
- Lunney D, Barker J (1986) Survey of reptiles and amphibians of the coastal forests near Bega, NSW. *Aust Zool* 22:1–9. <https://doi.org/10.7882/AZ.1986.001>
- Mack RN, Simberloff D, Mark Lonsdale W et al (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. *Oecologia* 139:359–375. <https://doi.org/10.1007/s00442-004-1518-2>
- Olsson M, Wapstra E, Swan G et al (2005) Effects of long-term fox baiting on species composition and abundance in an Australian lizard community. *Austral Ecol* 30:899–905. <https://doi.org/10.1111/j.1442-9993.2005.01534.x>
- Paltridge R (2002) The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildl Res* 29:389–403
- Parker I, Simberloff D, Lonsdale W et al (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Pasanen-Mortensen M, Pyykönen M, Elmhagen B (2013) Where lynx prevail, foxes will fail—limitation of a mesopredator in Eurasia. *Glob Ecol Biogeogr* 22:868–877. <https://doi.org/10.1111/geb.12051>
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509
- Read J, Scleri V (2014) Ecological implications of reptile mesopredator release in arid South Australia. *J Herpetol* 49:64–69
- Risbey DA, Calver MC, Short J et al (2000) The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildl Res* 27:223–235
- Robinson QH, Bustos D, Roemer GW (2014) The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. *Ecology* 95:3112–3123
- Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol Invasions* 8:927–939. <https://doi.org/10.1007/s10530-005-5103-3>
- Roemer GW, Donlan CJ, Courchamp F (2002) Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proc Natl Acad Sci USA* 99:791–796. <https://doi.org/10.1073/pnas.012422499>
- Roy HE, Adriaens T, Isaac NJB et al (2012) Invasive alien predator causes rapid declines of native European ladybirds. *Divers Distrib* 18:717–725. <https://doi.org/10.1111/j.1472-4642.2012.00883.x>
- Royal JA, Nichols JD (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790
- Royle JA, Nichols JD (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790
- Sax DF, Stachowicz JJ, Gaines SD (2005) Species invasions: insights into ecology, evolution and biogeography. Sinauer Associates Incorporated, Sunderland
- Shine R (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Q Rev Biol* 85:253–291
- Simon KS, Townsend CR (2003) Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshw Biol* 48:982–994
- Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshw Biol* 55:152–174. <https://doi.org/10.1111/j.1365-2427.2009.02380.x>

- Sutherland DR (2011) Dietary niche overlap and size partitioning in sympatric varanid lizards. *Herpetologica* 67:146–153
- Terborgh J, Estes J (2010) Trophic cascades: predators, prey and the changing dynamics of nature. Island Press, Washington, DC
- Thoresen JJ, Towns D, Leuzinger S, Durrett M, Mulder CP, Wardle DA (2017) Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure. *Ecol Appl* 27:1190–1198
- Tingley R, Phillips BL, Letnic M, Brown GP, Shine R, Baird SJ (2013) Identifying optimal barriers to halt the invasion of cane toads *Rhinella marina* in arid Australia. *J Appl Ecol* 50:129–137
- Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realized niche shift during a global biological invasion. *Proc Natl Acad Sci U S A* 111:10233–10238. <https://doi.org/10.1073/pnas.1405766111>
- Underwood AJ (1990) Experiments in ecology and management: their logics, functions and interpretations. *Aust J Ecol* 15:365–389
- Vanhooydonck B, Van Damme R (2003) Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. *Funct Ecol* 17:160–169
- Vitousek P, D'Antonio C (1997) Introduced species: a significant component of human-caused global change. *N Z J Ecol* 21:1–16
- White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. *Divers Distrib* 12:443–455. <https://doi.org/10.1111/j.1366-9516.2006.00265.x>