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Toads in the backyard: why do invasive cane toads (*Rhinella marina*) prefer buildings to bushland?

Edna González-Bernal^{1,2} · Matthew J. Greenlees¹ · Gregory P. Brown¹ · Richard Shine¹

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Abstract Like many invasive species, cane toads (*Rhinella marina*) in Australia concentrate in the disturbed habitats created by human activity, rather than in pristine areas. We surveyed cane toads in the wet–dry tropics of the Northern Territory to assess the abundances, body sizes, sexes, behaviour, hydration state and feeding rates of toads around buildings compared to those in areas remote from buildings, and conducted experimental trials to assess the effects of building-related variables (lights and increased toad densities) on the foraging success of toads. Toads around buildings were smaller than bushland conspecifics, and adult sex-ratios were female-biased. Toads were more sedentary around buildings than in the bush, but their feeding rates (based on direct observations and faeces production post-capture) were similar. That similarity, despite twofold-higher densities of competing toads around building, reflected the strong enhancement of feeding rates due to artificial lights attracting insects (in our experimental trials, a threefold increase regardless of the number of competing toads). Toads collected from around buildings were apparently in better hydric condition. Thus, access to water also may attract toads to buildings. The relative scarcity of adult male toads around buildings likely reflects waterbody-centred reproductive activities, whereas the concentration of females and juveniles around buildings is driven largely by access to the insects attracted by artificial light. We conclude that buildings enhance the

persistence of cane toad populations and may facilitate their spread.

Keywords Artificial light · Habitat use · Human disturbed sites · Seasonality · Invasive species

Introduction

The ecological impact of invasive species on the native biota is a major conservation issue worldwide, and has stimulated extensive research on the biology of invading populations (Holway 1998; Courchamp et al. 2003; Greenlees et al. 2006; D'Amore et al. 2010; Lesser and Slattery 2011). One of the most fundamental considerations when attempting to predict or quantify any impact, is understanding habitat use by the invader. All species use habitats non-randomly, and the distribution of an invasive organism across the landscape can have substantial effects on its ecological impact; for example, an invader that avoids rainforest likely will have little effect on rainforest endemics (D'Amore et al. 2010; Delnatte and Meyer 2012). Many of the most troublesome invasive species have relatively broad patterns of habitat use, but often with clear preferences for certain kinds of habitat (Johnson et al. 2008; Fuller et al. 2011). Perhaps the most common pattern is for invaders to prefer the disturbed areas around human habitations (Sacchi et al. 2002; Lake and Leishman 2004; Colunga-Garcia et al. 2010; Gavier-Pizarro et al. 2010). Activities such as urbanization, farming and mining often result in a distinctive suite of biophysical characteristics that render those areas unsuitable for native taxa, and available for colonization by commensal taxa that have been translocated to the new region by human interference (Colunga-Garcia et al. 2010; Ficetola et al. 2010; Ekka and Behera 2011).

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Although many authors have noted the tendency of infamous urban invaders such as rodents, cockroaches and sparrows to proliferate in highly disturbed habitats, the details of that colonization remain unclear for most invasive species. Even for an invader with a strong preference for human-modified habitats, that preference may well be stronger in some age classes than others, in some seasons than others, or in one sex rather than the other (McIntyre 2000; Rose and Nagel 2006). We can quantify any such non-random processes by comparing the phenotypic traits of individuals found in disturbed vs undisturbed habitats. In addition, we can conduct experimental studies to test hypotheses about the nature of the advantages that attract invaders to these disturbed areas. The present paper describes an analysis of this kind on invasive cane toads (*Rhinella marina*) in tropical Australia. Even within its native Central American range, *R. marina* chiefly is found around human habitation (Zug and Zug 1979). Several authors have noted that cane toads prefer disturbed habitats for feeding and spawning, and rarely penetrate far into dense forest (Hagman and Shine 2006; Pearson et al. 2009). To our knowledge, only one previous study with invasive cane toads has compared phenotypic traits of toads from different environments (Zug et al. 1975). We are not aware of any other work to quantify the phenotypic traits of toads in disturbed vs undisturbed habitats, or to experimentally test ideas about the benefits to toads of urban life.

Materials and methods

Study species

Cane toads (formerly *Bufo marinus*) are large [up to 100–150 SUL (snout-urostyle length)] anurans native to tropical and subtropical areas of the American continent. They were released in Australia in 1935 as a biocontrol for insect pests of sugar cane. Since then they have colonized more than a million square kilometers of the continent, negatively impacting many native species. Cane toads exploit anthropogenically disturbed sites in both their native (Zug and Zug 1979) and introduced distributions (Letnic et al. 2014).

Study area and climate

The floodplain of the Adelaide River, 60 km east of Darwin in the Northern Territory, consists of low-lying flat ground used primarily for agricultural production. Buildings are scattered through the landscape, and often surrounded by irrigated lawns. The area lies within the wet-dry tropics, with high temperatures year-round (mean

monthly maxima exceed 30 °C in every month), but with >75 % of the 1300 mm annual rainfall occurring in a brief monsoonal wet season from December to March. Most native anurans have adapted to the precipitation regime by adopting a long annual inactivity period during the dry season from April to November (Brown and Shine 2007; Tracy et al. 2007). Cane toads colonized the area in 2005, and remain active year-round but with reduced rates of activity, dispersal, feeding and growth during the drier months (Brown et al. 2011). Even when other native anuran species [green tree frogs (*Litoria caerulea*), red tree frogs (*L. rubella*) and Roth's tree frogs (*L. rothii*)] in addition to an invasive gecko, (*Hemidactylus frenatus*) are commonly encountered in human-modified habitats in the area, they do not directly interact with cane toads as all these species use vertical elements of the habitat (i.e., walls) almost exclusively.

Field surveys

We conducted surveys late in the dry season (November 2009), the time when toads are likely to be under the greatest hydric stress (Brown et al. 2011) and also during the wet season (March 2010) when conditions are more favourable. Our surveys were conducted at ten sites within a 30 km radius: five with artificially illuminated buildings (two at Beatrice Hill Farm 131°18'12"E, 12°37'16"S, three at Corroboree Park 131°29'10"E, 12°45'56"S) and five "bushland" areas that were at least 1 km from the nearest lighted building (Fogg Dam Conservation Reserve 131°17'45"E, 12°33'26"S, Leaning Tree Lagoon Nature Park 131°25'10"E 12°42'43"S, Harrison Dam Road 131°19'48"E 12°35' 29"S, Beatrice Hill Farm Road 131°17'49"E 12°36'57"S, and Anzac Parade, 131°18'48"E 12°34'58"S). Within each of the two main built-up areas, the replicated sample sites were less than 200 m apart and likely represented a single population within each area. At built-up sites we collected toads within 3 m of buildings that were artificially illuminated. At the bushland sites, we collected toads along roads (the habitat where we most frequently see toads in the wider landscape: see Brown et al. 2006).

To avoid confounding site type with local weather conditions, we surveyed multiple sites (including both habitat types) on the same nights [adult toads are exclusively nocturnal in activity (Freeland and Kerin 1991; Pizzatto and Shine 2008)]. Every time a toad was found, temperature and relative humidity measurements were taken. As only one person conducted all the surveys, these measurements were taken as synchronously as possible between different sites instead of simultaneously. As soon as a toad was found, the observer approached to within 2 m without disturbing it, and recorded the number of feeding

movements (recognized by lunging and tongue extrusion), and the distance moved by the toad during the next 2 min. We also recorded the number of toads within 1 m and within 10 m of the focal toad. Then, the focal toad was collected and returned to our nearby field laboratory in an individually numbered cloth bag.

The next morning each toad was sexed, measured (SUL and body mass) and any faeces in the bag were collected and air-dried. Each toad was then placed into a plastic bin containing both a large pool of water and a dry side (giving the toad equal access to both dry and wet conditions). Each toad was left in this container for 60 min and allowed to hydrate if it so desired. Toads do not hydrate by drinking, but instead gain moisture through a ventral skin patch by sitting in water or on damp substrates (Christensen 1974; González-Bernal et al. 2012). After 60 min, all individuals were reweighed. We considered a toad's decision to enter and remain in water as an indication of its hydric condition. We used the mass change of the toad over that period as an indirect indication of its hydration status, under the assumption that a severely dehydrated toad would be likely to take up more water than a fully hydrated individual.

Experimental trials

In contrast to toads in farmland, toads around buildings have access to insects that are attracted to artificial lights, but also have to compete for those insects with a higher density of conspecific toads. To quantify the effects of artificial light and competitor density on toad feeding rates, we constructed 12 outdoor enclosures consisting of vertical metal walls driven into the ground. Each enclosure measured 2.4×1.2 m, with walls 0.8 m high, and contained a pool of water. Light globes (25 W) were hung above half of the enclosures to attract insects; the other half were not illuminated. We collected toads from our field sites (see above) and kept them without food for 48 h to standardise their hunger levels. We then added 1, 2 or 4 toads to each enclosure, such that mean body sizes (SULs and masses) did not differ significantly between treatments (all $P > 0.48$). The body sizes of these toads ranged from 60 to 117 mm SUL, and from 23 to 201 g. Toads were allowed to feed overnight within the enclosure and the following morning, all of them were humanely euthanised. Afterwards, the number and mass of prey in their stomachs were recorded. We conducted a total of six experimental trials, three during the wet season and three during the dry season.

Data analysis

We used ANOVA to examine patterns in toad traits (body length, mass and condition, density, feeding rate, faeces

production, hydration state, movement) as a function of season (wet vs dry) and habitat (building vs bushland). Preliminary analyses revealed that including toad body sizes did not affect any of our main results (effects of season, lights, competitor density), so for simplicity we report only analyses that omit the body-size data. We defined any toad <90 mm SUL as a juvenile, based on (Zug and Zug 1979). To quantify a toad's body condition (mass relative to length), we used residual scores from the general linear regression of \ln body mass against \ln SUL. We used temperature and humidity measurements to calculate vapor pressure deficit (VPdeficit), which represents the difference between the amount of moisture in the air and the amount of moisture that saturated air can hold. VPdeficit is a measure of the drying capacity of the air (Ludwig 1945); higher VPdeficit increases transpiration and thus, the Vpressure calculation enables us to evaluate the desiccation risk experienced by a toad in each site (Carey 1978; Fletcher et al. 2007).

For our experimental data, we used ANOVA to evaluate the effects of season, artificial illumination and competition on feeding rates (dry and wet mass of prey, and the number of prey items in the stomach) of toads in outdoor enclosures. All analyses were run in JMP 9 (SAS Institute, Cary, NC).

Results

Field surveys

We obtained data for a total of 347 toads (99 dry season bushland, 79 dry season buildings, 94 wet season bushland, 75 wet season buildings).

Body sizes

The toads found around buildings were smaller, on average, than were those found in bushland, and this difference was greater in the wet season than the dry season (mean values: wet season = 93.6 mm SUL around buildings, vs 102.2 mm in bushland; dry season = 93.1 vs 110.4 mm, respectively). These differences were significant for body length (ANOVA season effect $F_{1,343} = 8.05$, $P < 0.005$; habitat effect $F_{1,343} = 90.60$, $P < 0.0001$; interaction $F_{1,343} = 10.15$, $P < 0.002$) and body mass (season effect $F_{1,343} = 24.02$, $P < 0.001$; habitat effect $F_{1,343} = 49.24$, $P < 0.0001$; interaction $F_{1,343} = 13.63$, $P < 0.004$). Because the main effects were consistent (toads larger in wet season than dry season, and larger in bushland than around buildings), these main effects are biologically interpretable despite the significant interaction terms (Fig. 1a, b).

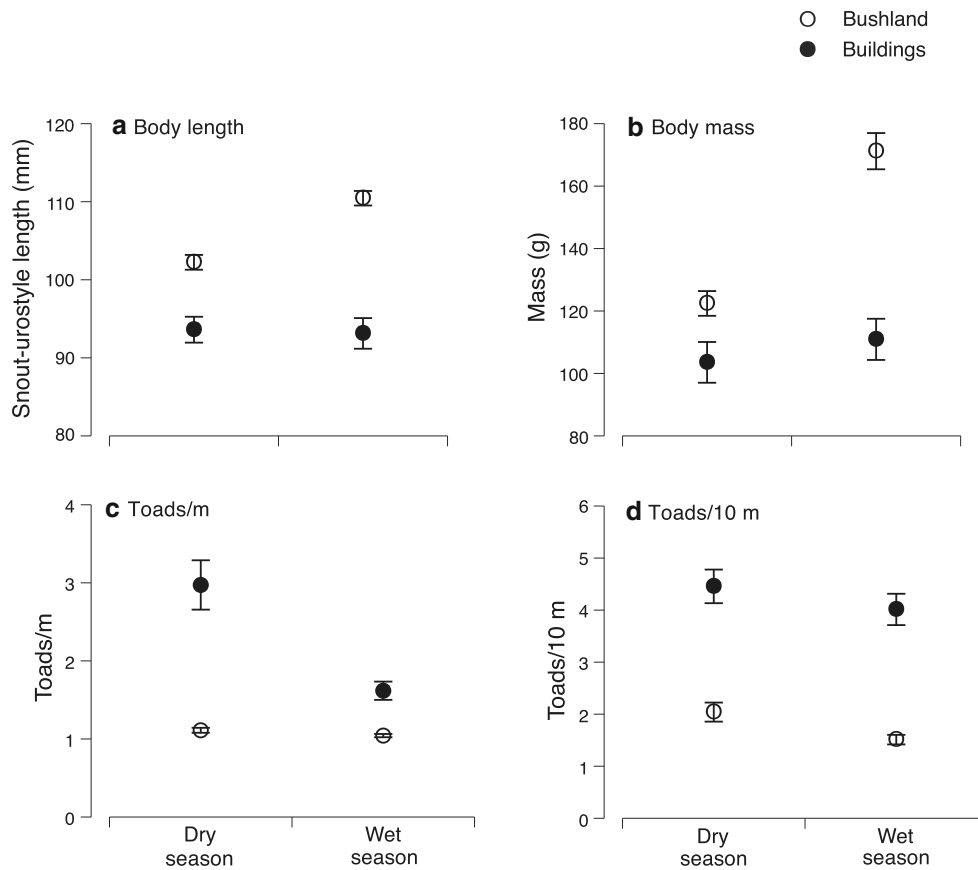


Fig. 1 Body sizes and densities of cane toads around buildings, and in nearby bushland areas, during the wet season and the late dry season in tropical Australia (Adelaide River floodplain). Toads collected around buildings were smaller in length (**a**) and mass (**b**),

and at higher densities: we recorded more toads within 1 m of the focal toad (**c**) and within 10 m of the focal toad (**d**). Graphs show mean values and associated standard errors

Proportion of juvenile toads

Juveniles comprised a larger proportion of the total sample in collections made around buildings (42 juveniles among 79 animals collected around buildings during the dry season, =53 %; wet season, 30 of 76 = 39 %), than for collections made in bushland (dry season, 21 of 99, =21 %; wet season, 3 of 94, =3 %; likelihood ratio test from logistic regression, habitat effect $\chi^2_1 = 58.53$, $P < 0.0001$; season effect $\chi^2_1 = 18.21$, $P < 0.0001$; interaction effect $\chi^2_1 = 5.59$, $P = 0.01$). The significant interaction effect is due to buildings being more important for juveniles during the dry season than during the wet season.

Adult sex ratio

Excluding juvenile toads (because their sex is unknown), we found a higher proportion of female toads around buildings [23 of 37 (62 %) in the dry season, 31 of 46 (67 %) in the wet season] than in bushland [34 of 78 (43 %) in the dry season, 46 of 91 (50 %) in the wet season; likelihood ratio test from logistic regression, habitat

effect $\chi^2_1 = 7.05$, $P = 0.008$; season effect $\chi^2_1 = 0.83$, $P = 0.36$; interaction effect $\chi^2_1 = 0.008$, $P = 0.92$]. Female toads are more likely to use buildings than males, during both wet and dry seasons.

Density

Toads were more abundant around buildings than in bushland, and this difference was more pronounced in the dry season than the wet season (Fig. 1c, d). The density patterns were similar for number of toads within one metre of the focal animal (dry season = bushland 1.1, buildings 3.0, wet season = bushland 1.04, buildings 1.6; ANOVA season effect $F_{1,340} = 22.53$, $P < 0.001$; habitat effect $F_{1,340} = 66.09$, $P < 0.0001$; interaction $F_{1,340} = 18.40$, $P < 0.001$; Fig. 1c). The same pattern was seen for number of toads within 10 m of the focal animal, but the interaction between season and habitat type was not statistically significant at this larger spatial scale (dry season—bushland 2.0, buildings 4.4, wet season—bushland 1.51, buildings 14.0; ANOVA season effect $F_{1,344} = 4.84$, $P < 0.04$; habitat effect $F_{1,344} = 114.71$, $P < 0.0001$; interaction

$F_{1,344} = 0.04$, $P = 0.85$). That is, the number of toads within ten metres of the focal animal was higher in the wet season and around buildings, but with no significant interaction between these two effects (Fig. 1d).

Abiotic conditions

Areas where we found toads around buildings were closer to water sources than were the areas where we found toads in bushland (35 and 294 m, respectively; $F_{3,340} = 81.99$, $P < 0.0001$; season effect $F_{3,340} = 0.11$, $P = 0.73$; interaction $F_{3,340} = 1.91$, $P = 0.16$) during both wet and dry seasons. Similarly, the building-associated areas that supported toads were moister and cooler than areas where we found toads in the bushland (as reflected by VPdeficit measures 103 and 128, respectively, Fig. 2a). The disparity was greater in the wet season than the dry season, but the direction of differences between the two habitat types was consistent (vapor pressure deficit, season effect $F_{3,344} = 21.9$, $P < 0.0001$; habitat effect $F_{3,344} = 72.21$, $P < 0.0001$; interaction $F_{3,344} = 10.37$, $P = 0.001$) Thus, the main effects are interpretable despite the significant interaction terms (Fig. 2a).

Movement distances and feeding rates

Toads around buildings were generally sedentary (mean displacements over 2 min averaged <0.5 m in both seasons) whereas toads on roads in the bushland moved about more extensively (means of 1.1 m in the wet season, 1.5 m in the dry season). Thus, analysis showed that toad displacements differed between habitat types ($F_{1,344} = 9.90$, $P < 0.002$) but not between seasons ($F_{1,344} = 0.54$, $P = 0.461$; interaction $F_{1,344} = 0.46$, $P = 0.50$). The number of prey-attack attempts by focal toads within our 2-min observation periods did not differ significantly as a function of either season (0.73 during the dry season and 0.66 during the wet season) or habitat type (0.61 on bushland and 0.78 on buildings; season effect $F_{1,344} = 0.14$, $P = 0.71$; habitat effect $F_{1,344} = 0.75$, $P = 0.39$; interaction $F_{1,344} = 0.65$, $P = 0.24$; Fig. 2b). Our alternative measure of feeding rate was the dry mass of faeces produced during the night after capture; for this variable, values were higher in the wet season than the dry season ($F_{1,342} = 6.86$, $P < 0.01$) but were not affected by habitat in either season ($F_{1,342} = 0.10$, $P = 0.75$; interaction $F_{1,342} = 0.001$, $P = 0.98$; see Fig. 2c).

Body condition

Cane toads were in better body condition during the wet season than the dry season ($F_{2,344} = 8.93$, $P < 0.003$), and the ones around buildings tended (albeit non-significantly) to be heavier-bodied as well ($F_{2,344} = 3.14$, $P = 0.08$; interaction $F_{2,344} = 0.001$, $P = 0.99$; Fig. 3a).

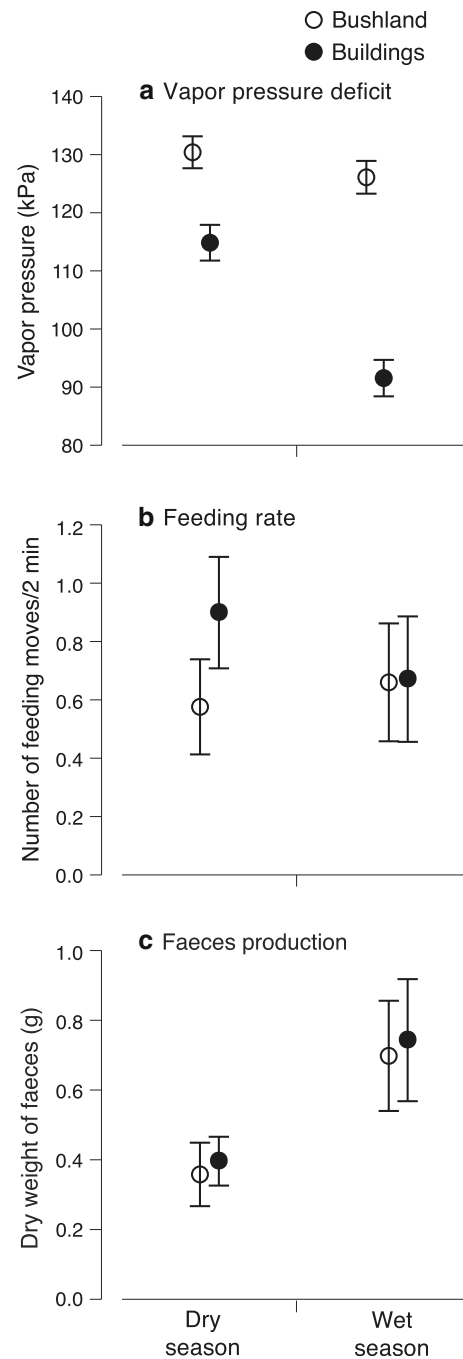


Fig. 2 **a** Vapor pressure deficit (kPa), around buildings and in nearby bushland areas during the wet season and the late dry season in tropical Australia (Adelaide River floodplain). **b** The number of foraging moves by focal cane toads during 2-min observation periods, and **c** faeces production by toads in the night after capture. Graphs show mean values and associated standard errors

Hydric balance

When given the opportunity to rehydrate, field-collected toads from the dry season, and from bushland areas during the wet season, tended to gain significantly in mass. In

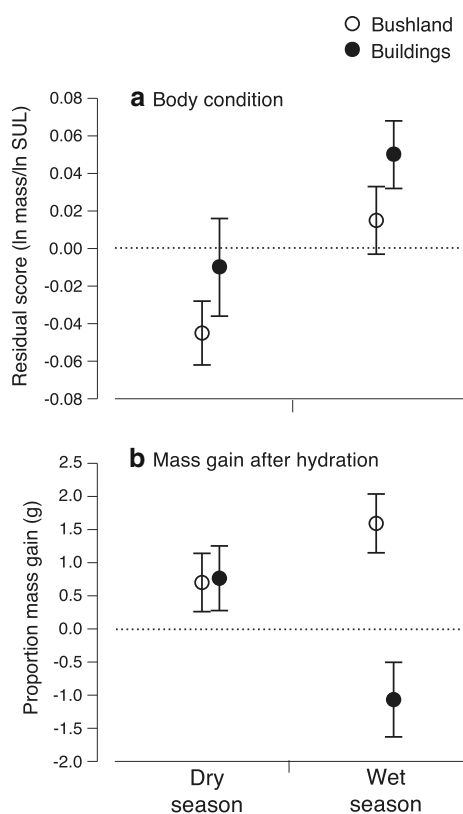


Fig. 3 **a** Body condition (residual scores from the linear regression of \ln mass vs \ln SUL) and **b** hydration state (as indicated by water uptake post-capture) of cane toads collected from around buildings, and in nearby bushland areas, during the wet season and the late dry season in tropical Australia (Adelaide River floodplain). Graphs show mean values and associated standard errors

contrast, toads collected around buildings during the wet season lost mass over this period (Fig. 3b), probably through urination. Our indirect measure of hydration status thus suggest that toads collected from different sites and in different seasons exhibit different levels of dehydration. Analysis showed a significant interaction between season and habitat on rates of water uptake (interaction $F_{2,342} = 7.96$, $P < 0.006$). A better measure of water uptake comes from toads that selected the wet rather than dry side of the rehydration container, and did not defecate during the rehydration period. Restricting analysis to these toads ($n = 173$, out of a total of 342 tested), water gain relative to initial body mass was greater for toads from bushland than from buildings, in both seasons ($F_{3,170} = 16.71$, $P < 0.0001$; season $F_{3,170} = 3.16$, $P = 0.077$; interaction $F_{3,170} = 0.99$, $P = 0.32$). This pattern suggests that toads from around buildings were in a better hydric state than were conspecifics from bushland areas. Although most toads urinated when picked up in the field, our results should be treated with caution because we did not empty the bladders of all the individuals before weighing them.

Experimental trials

The presence of artificial lights enhanced feeding rates of toads in our outdoor enclosures. Feeding rates (as based on gut contents) were higher in the wet season than the dry season (wet mass of prey, $F_{1,159} = 30.57$, $P < 0.001$; dry mass, $F_{1,159} = 25.83$, $P < 0.001$; prey number, $F_{1,159} = 6.97$, $P < 0.01$). Compared to conspecifics in non-illuminated enclosures, toads that had foraged in lighted enclosures consumed a greater mass of insects in terms of wet mass ($F_{1,159} = 19.12$, $P < 0.001$) and dry mass ($F_{1,159} = 22.57$, $P < 0.001$), as well as in terms of prey numbers ($F_{1,159} = 25.49$, $P < 0.001$; see Fig. 4). The number of toads in an enclosure did not significantly affect any of these feeding-rate measures (for variables including number of toads, all main effects and interactions $P > 0.18$).

Discussion

Especially during the prolonged (8-month-long) dry season in the Northern Territory tropics, the areas around buildings offer conditions very different from those that prevail over most of the surrounding landscape. Not only do buildings offer many shelter sites that protect animals from predators and abiotic, thermal and hydric, extremes, but they also provide ready access to fresh water (from dripping air-conditioners, dog bowls, recently-watered lawns) as well as an abundant supply of insects that are attracted to artificial lights (Mckinney 2006; Truxa and Fiedler 2012). Importantly, Australian culture has retained traditional English devotion to residential gardens, even under climatic conditions where those gardens require vast amounts of irrigation (Tait et al. 2005). Although the conditions that invasive cane toads encounter in the bushland are very different (and seasonally more xeric) than any they would encounter within their native range (Brown et al. 2011), the conditions around buildings likely are more similar to those within the native range—and very similar to those around buildings in the native range. Thus, for a translocated species that utilizes disturbed habitats even within its ancestral home as does the cane toad—(Zug and Zug 1979; Lever 2001), human activities create a familiar environment that may largely eliminate the need for the invader to deal with novel abiotic challenges within the invaded range.

In our study area, cane toads utilized areas around buildings in preference to bushland areas both in the wet season and the dry season (Fig. 1). Unsurprisingly, the aggregation tended to be stronger during the dry season, when ambient temperatures and humidity pose the greatest challenges for anurans in this area (Brown et al. 2011).

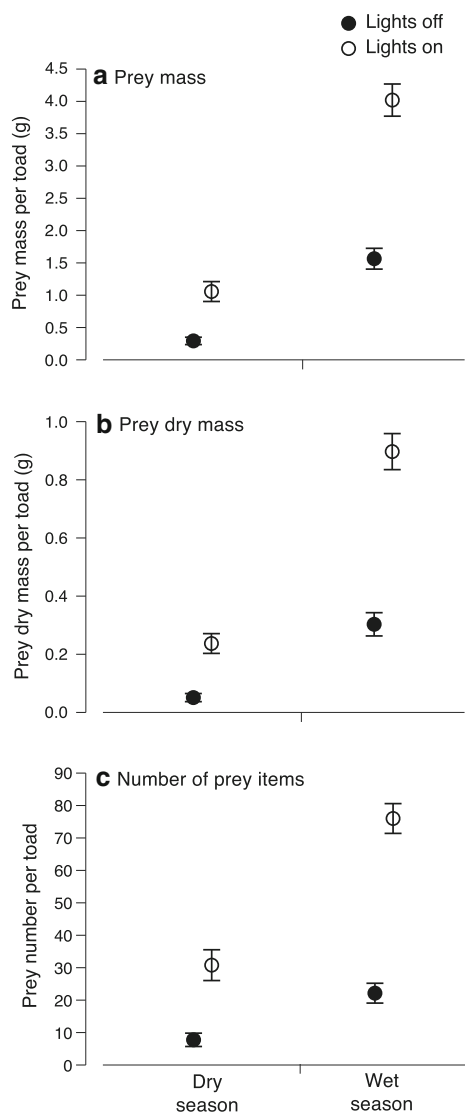


Fig. 4 Prey items dissected from the stomachs of cane toads in experimental enclosures, as a function of whether or not the enclosure contained a light to attract insects. Toads in lighted enclosures consumed more prey than did conspecifics in unlighted enclosures, in terms of prey mass (a), dry mass of prey (b) and number of prey items (c). These trials were conducted during the wet season and the late dry season in tropical Australia (Adelaide River floodplain). Graphs show mean values and associated standard errors

Importantly, the toads found around buildings were not a random subset of the larger population that we sampled in surrounding areas. Instead, the populations of toads around buildings were dominated by smaller rather than larger toads (Fig. 1a, b), and by females rather than males. Amphibians have low resistance to evaporative water loss across the skin (Lillywhite 1971, 2006; Jorgensen 1997; Tingley and Shine 2011). The high ratio of surface area to volume in a small anuran exacerbates this problem (Young et al. 2005), forcing juvenile toads to restrict their activities to times and places that provide moist microhabitats

(Schwarzkopf and Alford 1996; Child et al. 2008, 2009). Also, high feeding rates may be particularly advantageous for smaller toads, by enabling them to grow rapidly to a body size that reduces their vulnerability both to desiccation and to predation (Jorgensen 1988). Thus, the moist and food-rich habitats around buildings may be of more benefit to younger, smaller toads than to older, larger conspecifics.

Advantages related to small body size cannot explain why the adult toads around buildings were mostly females, because female cane toads grow larger than males (Zug and Zug 1979). The most plausible reason for this sex-ratio bias is that spawning occurs only at waterbodies (because cane toads have aquatic eggs and larvae: Lever 2001), where males gather and call to attract females (Wells 1977). Unlike many species of native frogs, cane toads in tropical Australia breed over a prolonged period (Crossland 2000) and thus, breeding males may spend long periods engaged in this activity. The strongly male-biased sex ratio around breeding ponds (Davies and Halliday 1978), which often are located in bushland far away from buildings, thus translates into a female bias in adult sex ratios in commensal populations of cane toads.

The cane toads that we observed in bushland areas moved about two or three times as far during our observation periods as did their conspecifics that we observed around buildings. That disparity likely reflects two processes. The first is that toads on roads in the bushland were unlikely to remain in that area long-term, because of a lack of suitable shelter and moisture. Instead, toads use roads as movement corridors (Brown et al. 2006). Second, prey items were undoubtedly less concentrated on roads than under artificial lights (which often attracted thousands of flying insects, especially during the wet season: González-Bernal, personal observation). Toads on roads often hopped from one insect to another, whereas toads under lights often remained in one place and seized prey items as they alighted near them (González-Bernal et al. 2011). This disparity might also be accentuated by a plausibly adaptive behaviour to reduce water loss in juveniles. Activity elevates evaporative loss through the skin, especially in smaller individuals. Thus, juveniles around buildings, even with constant access to water, might reduce this evaporative loss by reducing their movements (Heatwole et al. 1969). Although the roads where we sampled bushland toads technically represent modified habitat, they do not provide subsidies of moisture or insect-attracting light. Toads preferentially forage in open areas, and roads in bushland merely provide convenient settings in which to observe active toads. Number of feeding movements by toads did not differ between habitat types, reflecting similar prey availabilities. The major difference was that in bushland, toads have to move further between successive prey items.

The greater abundance of insects due to artificial lights, and in the wet season compared to the dry season, is reflected in feeding rates of cane toads (Fig. 2b). The seasonal effect is straightforward: rates of faeces production show that toads ingested more prey during the wet season than the dry season (Fig. 2c). Analyses of stomach contents of cane toads in our study area have shown the same pattern (Brown et al. 2011). The approximate similarity in rates of feeding between bushland and backyard toads (as evidenced both by observed feeding movements, and by faeces production: Fig. 2b, c) likely reflects a balance between two competing trends: buildings not only offer higher food availability, but also increase the number of competing toads (Fig. 1c, d). Our experimental trials confirmed that the effect of lights on food availability can overcome the predicted density-dependent reduction in per-individual feeding rates at higher densities: individuals that foraged under artificial lights had higher feeding rates than did those that foraged in darkness, regardless of the number of conspecifics in their enclosure (Fig. 4). A similar facilitation of feeding rates by commensal animals likely is widespread. For example, an ability to exploit the rich sources of food provided by humans is key to the success of many invasive birds (Falk 1976). For cane toads in our study area, the artificial lights around buildings enhanced food access enough to eliminate any negative impacts of heightened competition with conspecifics.

Buildings also provided more favourable abiotic conditions, with local temperatures closer to toad preferences [approximately 24 °C (Johnson 1972) than would be true elsewhere, plus higher humidity]. Dry conditions induce toads to select temperatures that are lower than usual, presumably because of benefits to reducing rates of water loss (Malvin and Wood 1991). Thus, the availability of cool, moist sites during the tropical dry season may confer major advantages to toads. In keeping with this inference, our data on body condition and rates of water uptake post-capture are consistent with the idea that toads found around buildings were more fully hydrated than were toads found in bushland. Thus, exploitation of human habitats is likely vital to the persistence of cane toads during the dry season in some areas of Australia. Although this certainly facilitates their spread, the effect cannot readily be quantified. A similar pattern has been proposed for spiders, where constant temperature and humidity in transporting containers may enhance survival of smaller species and thus facilitate their arrival to new localities (Walther et al. 2009).

The trend for Australian cane toads to exploit the resources offered by buildings is a preadaptation to invasion, rather than a newly evolved trait adaptive to the increasingly arid areas colonized during the toads' recent expansion across the tropics. Even within well-watered areas of their native range, cane toads are typically found at

higher densities around human habitation than in less disturbed forest sites (Zug and Zug 1979; Lever 2001). Nonetheless, the rapid adaptive changes already documented in Australian cane toads [e.g., in dispersal rates and hydroregulation (Phillips et al. 2006; Tingley and Shine 2011)] suggest that it would be worth comparing the degree of building use by toads in their ancestral vs colonized ranges. In arid regions, toads may remain closer to waterbodies or other rehydration sources most of the time, whereas in more mesic areas they may be more widely spread through the landscape (Florance et al. 2011; Tingley and Shine 2011). More generally, preadaptation to human disturbance may contribute to the success of many invasive species (Hufbauer et al. 2012). For example, populations of the invasive ant *Wasmannia auropunctata* in its introduced range in New Caledonia are more similar, both in density and composition, to those native populations that are located in anthropogenic habitats (like forest edges along roads) than to those in natural habitats in French Guiana (Orivel et al. 2009).

In many of these “commensal” invasive species, the degree of dependence upon disturbed habitats may vary between age and sex classes, and shift seasonally, just as it does in cane toads (González-Bernal et al. 2015). Thus, to call a species “commensal” may be an oversimplification: exploitation of human-modified habitats may be critical or achievable for only some components of the population, and only for some parts of the year and/or in some parts of the geographic range. For cane toads, for example, the moist cool food-rich conditions offered by anthropogenically disturbed sites may be critical for juveniles, but largely irrelevant for adult males. Understanding the demographic distribution with respect to the landscape, or more precisely, how individuals with different phenotypic traits exploit different habitat types, may clarify the selective forces operating on habitat use (without introducing the confounding factors involved in interspecific comparisons) and may help to inform management tactics for controlling invasive species. For example, large aggregations of adult cane toads around waterbodies offer the easiest opportunity for wildlife-managers to collect and remove many individuals, but if most of those animals are males, the long-term effect on population numbers may be less than if a smaller number of females had been removed by collecting around buildings instead of waterbodies.

A detailed understanding of how commensal invasive species exploit human-modified habitat has a number of benefits. First, such knowledge allows for effective, targeted surveys to establish presence and implement control or eradication. Second, it contributes to fundamental understanding of temporal and spatial patterns of the distribution of the organism: characteristics increasingly appreciated as important in the control and eradication of

invasive species as well as in understanding their impacts. Finally, and potentially most usefully, should the animal in question (like cane toads in Australia) be a threat to endemic ecosystems or to human health, modification of habitat may be readily achievable. For example, excluding cane toads from anthropogenic water sources may be an effective control measure in arid Australia (Florance et al. 2011; Letnic et al. 2014). If we understand the habitat requirements of an invasive species, we may be able to reduce the numbers of that species by reducing the availability of the favoured habitat that we have created.

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