

Article

Cane toads beneath bird rookeries: utilization of a natural disturbance by an invasive species

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Abstract

Many invasive species exploit anthropogenically disturbed habitats, but most of those taxa evolved long before humans. Presumably, then, an ability to use natural (non-anthropogenic) disturbances pre-adapted invaders to a world later degraded by people. Studies on invasive species in naturally disturbed habitats thus can clarify the ancestral niche of invaders. In the Australian tropics, metallic starlings *Aplonis metallica* nest communally in emergent rainforest trees during the wet-season, and invasive cane toads *Rhinella marina* join other predators (mammals, birds, reptiles, and other anurans) to exploit the food resources beneath those trees. Compared to conspecifics found along nearby roads through the forest, cane toads beneath bird-nesting trees occur at higher densities, and are smaller in body size. The sex ratio is female-biased, and recapture records suggest that females may be philopatric at these sites (whereas recaptures were rare for both sexes found along the roads). Some toads were found under the same trees in successive wet-seasons. Spooling showed that distances moved per night were similar along the road versus under the trees, but toads under trees showed lower net displacements. Diets also differed (based upon scat analysis), with tree toads feeding more on beetles and less on ants. These nutrient-rich hotspots are exploited primarily by adult females and juvenile toads, whereas adult males congregate at breeding sites. By magnifying pre-existing intraspecific divergences in habitat use, bird rookeries may enhance population viability of cane toads by enabling critical age and sex classes to exploit food-rich patches that are rarely used by adult males.

Key words: ancestral niche, communal nesting, niche partitioning, pre-adaptation, spatial ecology.

Invasive species belong to many phylogenetic lineages, and arise in (and invade) many different habitats and geographic regions (Baker 1974; Kolar and Lodge 2001). Nonetheless, invaders exhibit consistent ecological and life-history traits (Marchetti et al. 2004; Devin and Beisel 2007). One of the strongest correlates of invasion success is an ability to thrive in anthropogenically disturbed habitats, which are typified by structural simplicity and high resource levels (Hansen and Clevenger 2005; MacDougall and Turkington 2005). A specialization on anthropogenically disturbed habitats is seen in many plants (Baker 1974), invertebrates (Bolger et al. 2000), fish (Nicol

et al. 2004), amphibians (Wang and Li 2009), reptiles (Chapple et al. 2015), birds (Lim et al. 2003), and mammals (Nogales et al. 2006). That consistency is paradoxical, however, because most or all of these “colonizing” taxa separated from related species millions of years before the appearance of *Homo sapiens* in the fossil record (200,000 years ago; Watson et al. 1997). Presumably, the invaders already possessed their distinctive ecological attributes at that time, so those attributes cannot be adaptations to exploit anthropogenic disturbance. Instead, modern-day invaders thrived in areas that resembled those that were later created by our activities, and so

were pre-adapted to human-degraded habitats. To understand how invaders evolved, we need to study them in habitats disturbed by natural processes such as fire, floods, and hurricanes. However, the large spatial scale of such processes often complicates interpretation. Ideally, we need to study a disturbance process that operates on a small spatial scale, enabling individual organisms to readily move between the disturbance and the rest of the habitat.

In the wet tropics of northeastern Australia, metallic starlings *Aplonis metallica* migrate from New Guinea each year to nest in massive aggregations in emergent rainforest trees (Natusch et al. 2016). The ground beneath those trees is enriched by bird faeces and dead nestlings, creating nutrient-rich patches within the rainforest. Predatory mammals, birds, reptiles and amphibians gather to exploit those resources (Natusch et al. 2016). High densities of soil invertebrates and flying insects beneath the trees (Natusch et al. 2016) provide abundant prey for insectivores like the invasive cane toad *Rhinella marina* (Linnaeus, 1758). Our other papers discuss the ecology of snakes in this area, and the ecological impacts of bird colonies on a suite of native and invasive taxa (Natusch et al. 2016, 2017a,b). In the current article, we compare ecological traits of toads collected beneath bird-nesting trees with conspecifics collected along nearby roads. Although densities of cane toads typically are higher in anthropogenically disturbed areas than in more pristine sites (e.g., Zug and Zug 1979; González-Bernal et al. 2015), we found the reverse situation: toads were more abundant beneath the bird rookeries than in adjacent anthropogenically created roadside habitat. Accordingly, we investigated the ways in which toads (like other vertebrate and invertebrate taxa, both invasive and native: Natusch et al. 2016, 2017a,b) exploit the rich nutrient source created by communally nesting birds. *A priori*, we predicted that such resource hotspots would increase toad abundance and philopatry (and thus, reduce distances moved), and skew demographic traits towards sections of the population (e.g., juveniles, adult females) whose activities largely focus on foraging rather than (as for adult males) breeding.

Materials and Methods

Study species

Cane toads (*Rhinella marina*; *Bufo marinus* in earlier literature) are native to South and Central America, but have been translocated to many countries around the world in attempts to control troublesome insect pests (Lever 2001). The toads were released in northeastern Australia (~1,000 km south of our study area) in 1935, and expanded their range to colonise our study area near the tip of Cape York by 1995 (Urban et al. 2007). Adult cane toads can grow to >1 kg, but typically average around 100–300 g (Phillips et al. 2007). Female cane toads lay large clutches of small eggs in ponds, and the resulting tadpoles metamorphose at small sizes (<0.1 g) within a few weeks (Zug and Zug 1979; Lever 2001). All terrestrial phases of cane toads have generalized diets, mostly feeding on small insects (e.g., Zug et al. 1975; Ingle and McKinley 1978; Evans and Lampo 1996), but take occasional vertebrate prey also (Lever 2001). The toxic bufadienolide defences of toads have caused catastrophic mortality of endemic anuran-eating predators in Australia (Shine 2010).

Cane toads have been reported to utilize anthropogenically disturbed habitats rather than more pristine sites both in the native range (Zug and Zug 1979) and in their invaded range (González-Bernal et al. 2016; Ward-Fear et al. 2016). The sexes differ in habitat use, with male cane toads often reported to spend long periods

beside spawning sites, calling for mates, whereas juveniles and females move more widely through the terrestrial habitat away from waterbodies (e.g., González-Bernal et al. 2015; Ward-Fear et al. 2016). In most populations that have been studied, cane toads are relatively sedentary (typically moving <20 m per night: see reviews by Pettit et al. 2016; Ward-Fear et al. 2016). At invasion fronts, however, individual toads sometimes move much further (up to >1 km per night: Phillips et al. 2007; Lindström et al. 2013; Pettit et al. 2016).

Study system

The Lockerbie Scrub is an isolated patch of rainforest within a woodland mosaic, at the extreme northern tip of Cape York Peninsula in Queensland, Australia. To the north, 150 km across Torres Strait, lies Papua New Guinea. Mean monthly temperatures vary from 26°C to 28°C year-round, but rainfall is concentrated in a 4-month “wet-season” (December–April) each year (mean rainfall in February = 475 mm, in August <20 mm: Meat and Livestock Association 2016). Our survey area comprised 10,000 ha of woodland and rainforest in and around the Lockerbie Scrub. Local roads are unpaved, and have low traffic volumes (especially at night, when adult cane toads are active).

Each wet-season, vast numbers of metallic starlings *Aplonis metallica* arrive in the Lockerbie Scrub and nest communally in emergent rainforest trees (Natusch et al. 2016). The birds attract an array of local predators that feed on fallen nestlings, and invertebrates in the guano-enriched soil beneath the tree (Natusch et al. 2016; see Figure 1). Because feral pigs *Sus scrofa* kill any seedlings that grow in this nutrient-rich soil, each bird-colony tree usually has an area of open ground beneath it measuring ~140 m² (Natusch et al. 2017b). During the season when birds are breeding, the open ground beneath each bird-nesting tree often contains predatory mammals (dingos *Canis lupus dingo*), birds (scrub-fowl *Megapodius reinwardt*, cockatoos *Cacatua galerita* and *Probosciger aterrimus*), snakes (*Boiga irregularis*, *Liasis fuscus*, *Morelia amethystina*, and *Stegonotus cucullatus*), and amphibians (*Rhinella marina* and *Litoria infrafrenata*). We located 27 active starling colonies scattered throughout the Lockerbie Scrub survey area (Natusch et al. 2016). Most starling colonies were >3 km from one another. A few of those trees were located near to our survey roads (<50 m separation), although most were several hundred metres from the nearest road. Over the course of three nesting seasons (total of 1,353 nocturnal visits to trees) we have recorded 6098 anurans (although many of those animals doubtless were recorded multiple times). Ninety-eight per cent of these records were invasive cane toads *Rhinella marina*, whereas the rest were native frogs (white-lipped tree frogs *Litoria infrafrenata* $n=75$; northern banjo frogs *Limnodynastes terraereginae* $n=15$; marbled frogs *Limnodynastes convexiusculus* $n=12$; green tree frogs *Litoria caerulea* $n=11$). We also frequently recorded cane toads on the sides of a 28-km unpaved road that we drove along to reach the nesting trees ($n=1,372$ records). The roads traverse many habitat types, and cross small streams, so our road-based sample should reflect the wider population of cane toads found along roads within our study area.

Methods

To identify the attributes of cane toads that were exploiting a natural (non-anthropogenic) form of ecological disturbance (the open ground beneath bird-nesting trees), we compared the attributes of toads found at these sites (henceforth, “tree toads”), to those of



Figure 1. (A) An emergent rainforest tree with nests of metallic starlings, showing bare ground beneath the tree; (B) aggregation of predators at night beneath a bird-nesting tree, and (C) a cane toad *Rhinella marina* eating a nestling starling beneath a bird-nesting tree. Photographs by R. Shine (A), D. Natusch (B), and D. Lettoof (C).

conspecifics found nearby along the edges of roads through the forest (henceforth, “road toads”). Both types of sites are examples of “ecological disturbance”, but they differ in whether that disturbance was created “naturally” (by nesting birds) or anthropogenically (by road construction). The comparison is not ideal, because the areas beneath bird colonies and along roads differ greatly in shape (oval versus linear). However, detectability of adult toads was close to 100% in both of these very open habitats (Natusch et al. 2017a, 2017b). Neither of these habitat types is typical of the surrounding forest, and both are “disturbed” (but in different ways). We could not sample toads in the “undisturbed” forest, because we saw them there only rarely. That low rate of encounter partly reflects difficulty of detection, but a more important bias is that cane toads avoid dense vegetation, instead preferring open areas (both in the native range and in invaded areas: Lever 2001; González-Bernal et al. 2015). Thus, the only places where we could sample toads were the two types of disturbed areas: one affected by bird colonies and the other by human activities.

On most nights during the bird-nesting season (average of > 5 nights per week), we surveyed 2–12 bird-nesting trees plus associated roads. The trees were 20–200 m from the nearest road, so we walked into the trees (1930–2300 h) and counted cane toads as well as other fauna. These surveys were conducted over bird-nesting seasons in three successive years (2013–14, 2014–15, and 2015–16). Over a subset of this period (1 March to 5 April 2015), we carried out a more intensive study. During that one-month period we hand-captured all toads found under trees, plus an approximately equal number from small sections of nearby roads (i.e., we collected a

sample of toads along the road sections adjacent to each bird-nesting tree). The sections of roads surveyed were 0.2–2 km in length, depending upon their proximity to starling colony trees in the nearby forest.

Captured toads were housed individually in cloth bags for 48 h, and any faeces produced over that time were preserved for later analysis (identification of prey fragments). Because only fragments were available, we were able to identify prey items only to broad levels (often, only to Family; in total, 12 categories were recognized). Toads were measured (snout–urostyle length [= SUL]) and individually marked (toe-clipped; up to three toes per toad) before being released at their site of capture. Sex was determined based on skin rugosity, color, and the release call (Lever 2001). We could not reliably determine sex for animals <90 mm SUL, so classed these as juveniles. Toads recaptured on subsequent nights were recorded but not returned to the laboratory, so each individual is represented only once in each dataset for faecal samples or morphology.

To quantify movements, we attached cotton spools to 26 toads (13 tree toads [12 F, 1 M], 13 road toads [8 F, 5 M]) using bead-chain waistbelts (see Ward-Fear et al. 2016 for detailed methods). The toads were then released, and we returned the following day to measure their overnight movements and remove the belts. From the cotton trail, we recorded total distance travelled, and net displacement (distance from origin to end of trail).

We conducted statistical analyses of these data using JMP Pro 11.0 (SAS Institute, Cary, NC, USA). Where required, we log-transformed variables to satisfy the assumptions of normality and variance homogeneity. To compare toads from beneath the bird-

nesting trees to those found along the road, we used ANOVA or ANCOVA for continuous variables (size, movements, dietary composition) and logistic regressions for nominal variables (sex, recapture).

Results

Densities of toads

During the one-month period of intensive study, we recorded an average of 0.05 toads/m² of open ground under the bird-nesting trees ($SE = 0.003$, range = 0–0.25; a maximum of 35 toads under a single tree). In comparison, we found an average of 0.0001 toads/m of road along nearby road sections ($SE = 0.00003$, range = 0–0.0005; a maximum of 96 toads in a single road survey). Even if we (conservatively) assume that the only usable habitat for each “road toad” was a 1-m-wide strip running along each side of the road, toads were more concentrated under the bird-nesting trees than along the roads, by a factor of at least 100 (one-way ANOVA with capture location [road vs. tree] as the factor: $F_{1,282} = 44.9$, $P < 0.0001$).

Sexes and body sizes of toads

Of 85 road toads captured during the intensive field period in 2015, 41 (48%) were females; in contrast, 67 of 84 tree toads were females (80%; log-likelihood ratio $\chi^2 = 18.69$, $df = 1$, $P < 0.0001$). Because female cane toads grow larger than males (Lever 2001), we included sex as well as location as factors in an ANOVA to examine body sizes. Adult females averaged larger than males overall ($F_{1,140} = 7.68$, $P < 0.01$), and within each sex, adult toads found along the road were larger than adult toads found under trees ($F_{1,140} = 21.44$, $P < 0.0001$). The size disparity between the sexes was similar in tree toads versus road toads (adults only; interaction $F_{1,140} = 0.15$, $P = 0.70$; Figure 2A).

Philopatry of toads within a season

Of 171 individually marked toads, 47 (27%) were recaptured on at least one subsequent night. Of 85 marked toads found on the road, we recaptured 1 of 44 males (2%) and 2 of 41 females (5%). All recaptures were on roads not under bird-nesting trees. In contrast, we recaptured 6 of 18 male tree toads (33%) and 37 of 68 female tree toads (54%). All were found under the same tree where they were initially marked. Logistic regression showed that the probability of recapture was higher at trees than on the road ($\chi^2 = 33.33$, $df = 1$, $P < 0.0001$) but was not influenced by sex ($\chi^2 = 1.48$, $df = 1$, $P = 0.22$; interaction location*sex, $\chi^2 < 0.001$, $df = 1$, $P > 0.98$). The maximum number of captures per toad was 2 on the road, and 8 under the trees.

Philopatry of toads between successive seasons

Of 84 toads captured beneath trees during the intensive field period in 2015, we recaptured only 4 individuals the following season despite large numbers of toads (up to 30 beneath single trees) continuing to utilize the trees. All recaptured individuals were females. We did not recapture any originally marked road toads the following season.

Movements of toads

Based on spool-tracking, the total distances moved by toads did not differ between tree versus road individuals (means 216 versus 175 m; $F_{1,25} = 2.23$, $P = 0.15$; sex effect and interaction NS) but net displacements were lower for tree toads (51 versus 139 m;

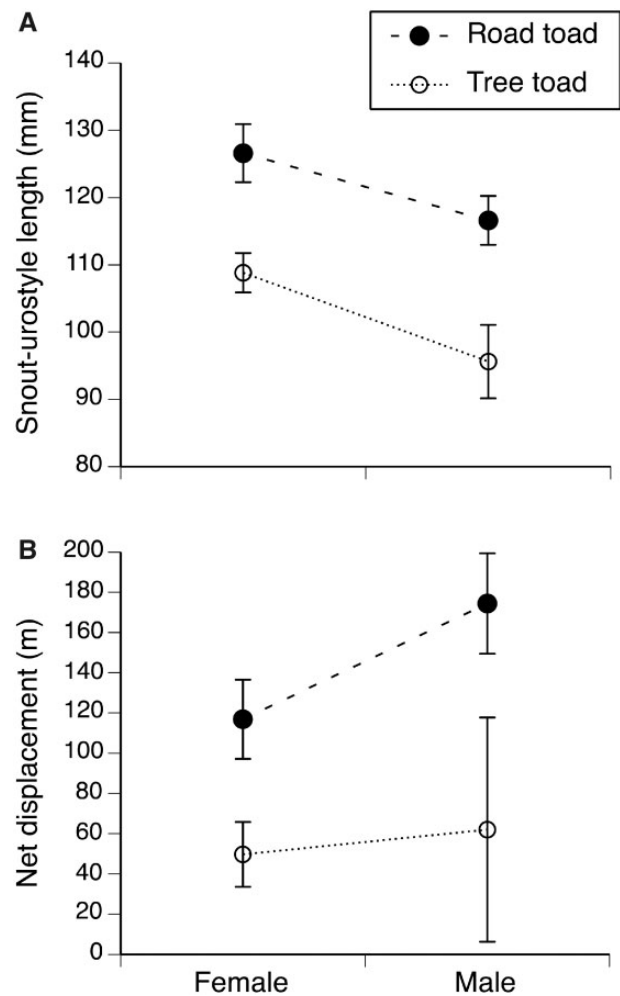


Figure 2. Comparisons between male and female cane toads captured under bird-nesting trees, and conspecifics found beside nearby roads, in terms of (A) body sizes (snout-urostyle lengths), and (B) net displacements per night (total distance between release point and recapture point; based on cotton-spooling). Mean values are shown with associated standard errors.

$F_{1,25} = 15.47$, $P < 0.001$; sex effect and interaction NS; see Figure 2B). Thus, an ANCOVA with location as the factor, total distance moved as the covariate, and displacement as the dependent variable, shows that tree toads displaced shorter distances even after variation in overall distances moved was included in the analysis (location, $F_{1,24} = 11.91$, $P < 0.003$).

Dietary composition of toads

We obtained faecal samples from 57 toads (25 from tree toads, 32 from road toads), generating a total of 1,051 identifiable prey items. Of those items, all but three were invertebrates, primarily Coleoptera (beetles, $n = 447$) and Hymenoptera (ants, $n = 353$), but also Isoptera (termites, $n = 140$), Orthoptera ($n = 60$), Myriapoda ($n = 19$), Arachnida (Scorpiones, $n = 18$), Blattodea ($n = 5$), Diptera ($n = 2$), Heteroptera ($n = 2$), Diplura ($n = 1$), and Neuroptera ($n = 1$). The only vertebrate prey were three blindsnakes (*Ramphotyphlops braminus*, 465–630 mm body length; two in one toad), although we also observed numerous toads consuming starling chicks that had fallen from their nests (Figure 1C).

Preliminary analyses revealed no significant effects of toad sex or body size on dietary composition (i.e., relative numbers of prey

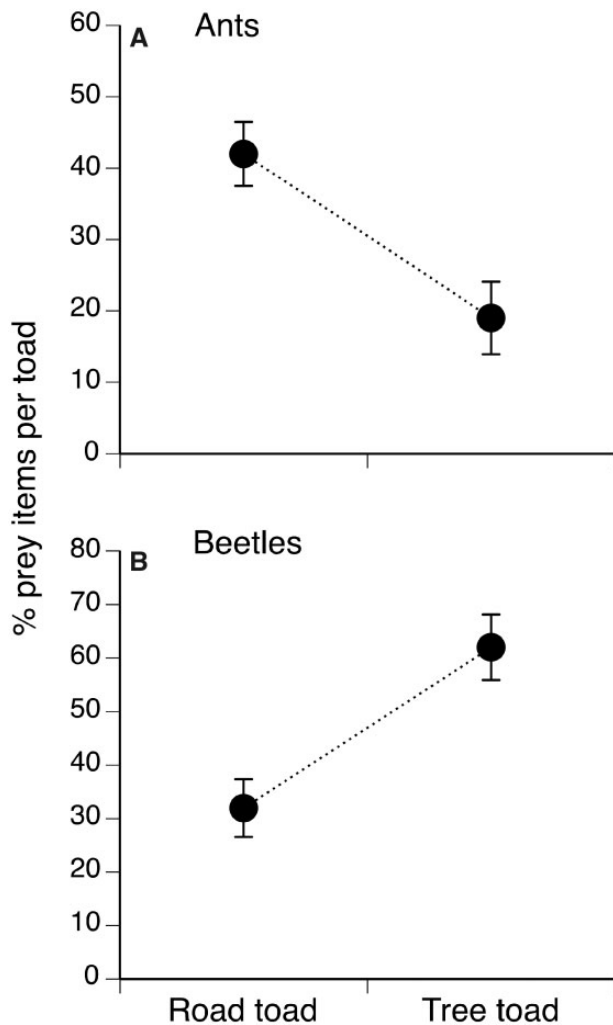


Figure 3. Comparisons of prey items identified from 25 cane toads captured under bird-nesting trees, versus 32 conspecifics found beside nearby roads, in terms of the proportion of the diet composed of ants (A) and beetles (B). Total sample sizes were 353 ants and 447 beetles. Mean values (per toad) are shown with associated standard errors. Percentages are shown for ease of interpretation, but analyses reported in the text were based on absolute numbers (ln-transformed).

items in each of the 12 categories; all $P > 0.05$). The mean number of prey items identified per faecal sample was similar for tree toads and road toads (means of 15.9 versus 20.4, respectively; $F_{1,569} = 1.31$, $P = 0.26$) but dietary composition differed (repeated-measures ANOVA with prey Family as the repeated measure; toad location $F_{12,39} = 2.15$, $P < 0.04$; see Figure 3). That divergence was driven largely by a higher proportion of ants in road toads, and beetles in tree toads (Figure 3). If we repeat the analysis using data for only beetles and ants, the tree versus road divergence remains significant ($F_{2,50} = 3.80$, $P < 0.03$): toads collected on the road had fed more often on ants, and less often on beetles, than had toads collected under bird-colony trees.

Discussion

Like many invasive species, cane toads are most abundant in anthropogenically disturbed habitats, both in the species' native range (Zug and Zug 1979; Isaacs and Hoyos 2010) and in its invaded

range in Australia (Pearson et al. 2009), and elsewhere (Zug et al. 1975; McKeown 1996). Many authors have attributed this pattern to human-modified areas offering enhanced availability of water (Florance et al. 2011; Tingley et al. 2013) and nutrients (e.g., insects attracted to artificial lights, dung beetles in cattle faeces: González-Bernal et al. 2013), coupled with reduced competition and predation by local fauna (Cabrera-Guzmán et al. 2013).

The response of cane toads to “natural” (non-anthropogenic) disturbance has attracted less scientific attention. In Australia, however, toads have been recorded to move into recently burned areas (Virrki 2014). Cane toads consistently select relatively open areas at night, which may allow these sit-and-wait predators to detect edible insects more easily than in a densely vegetated area (Zug and Zug 1979; Lever 2001; González-Bernal et al. 2011). As a result, cane toads use “natural” open areas such as the sandy banks of streams, and paths or close-cropped grassland created by wallabies (Mayer et al. 2015; R. Shine, personal observation). The ground beneath bird-nesting trees similarly offers an open flat area, because vegetation is removed by foraging pigs and native brush turkeys (Natusch et al. 2016). The primary attraction of bird-nesting trees for cane toads is nutritional, however: similarly open, flat areas within the forest (and especially, along the roads) have far lower densities of toads than do the bird-nesting trees (see above). The aggregations of cane toads beneath bird-nesting trees offers a strong contrast to the scarcity of native frogs in such sites; in total, we recorded 4,165 cane toads and only 69 frogs under bird-colony trees (Natusch et al. 2016). Predation by cane toads on adult native frogs appears to be very rare (Shine 2014), and the snake species attracted to bird-colony trees have not been recorded to eat frogs (unpublished data), suggesting that avoidance of predation risk cannot explain the low numbers of native frogs at these sites. Instead, the invasive anuran appears to be better at locating and exploiting these resource hotspots than are the other amphibian taxa that occur in the area.

Cane toads that we found beneath bird-nesting trees differed in mean body sizes and sex ratios from toads that we found along nearby roads. The sample from trees comprised 80% female (versus close to 50% female on roads), and included many smaller toads (Figure 2A). This sex bias may reflect differential philopatry, at least within a season, although sex differences in movement patterns were not statistically significant within the small sample of animals that we spool-tracked. Adult female toads were found repeatedly under the same tree, whereas males under trees dispersed within a few days at most. Despite the small sample, this pattern was broadly confirmed by the greater number of females recaptured beneath trees after one year. For specimens found on the road, displacement rates were higher (and thus, recapture rates were lower).

The lower net displacements of tree toads were due to a different pattern of movement rather than a decrease in total activity. Toads from the two types of locations moved similar distances overall, but the movements of road toads were more linear (along the road), whereas tree toads meandered about, remaining close to the initial point of release. Research at the invasion front has shown that toads often disperse along roads (apparently because roads and other open linear areas facilitate rapid displacement: Brown et al. 2006), and (despite the long period since colonisation) the animals in our study site used roads in the same way. Many of these animals may have been returning to familiar sites containing specific resources, as reported for cane toads in other populations (e.g., Boland 2004).

Despite their generalised diets, local populations of cane toads diverge in diets as a function of prey availability (Bailey 1976; Freeland et al. 1986; Grant 1996). Although we have no specific

data, casual observation suggests that beetles are far more common in the nutrient-rich soil under bird-nesting trees than on the hard open soil beside roads. Plausibly, then, availability drives the difference in prey types between tree toads and road toads. Bird-nesting trees also provide access to occasional large prey items such as nestling birds (Figure 1C); and in the same way, roads may offer access to road-killed animals (Lever 2001). Unusually among anurans, cane toads take stationary as well as moving prey (Lever 2001), so carrion may form a significant proportion of the diet at some times and in some places. Occasional predation by cane toads on nestling birds has been reported previously (Boland 2004; Beckmann and Pizzatto 2011).

Within the broader context of cane toad biology, the patterns we detected are an exaggerated development of pre-existing intraspecific divergence in habitat use. Commonly, cane toads of different sexes and ages are found in different microhabitats (González-Bernal et al. 2015). As in many anurans, adult males are concentrated around breeding sites close to water (Wells 2010). In contrast, females avoid such sites (thereby reducing harassment by males: Bowcock et al. 2009) and instead spend their time feeding in the matrix habitat between waterbodies. Female cane toads typically are found in forested areas that provide both food and protection from predators (González-Bernal et al. 2015). Consistent with those studies, we found that female toads were more common, and more philopatric, under bird-nesting trees than along more open roadside verges.

Regardless of the magnitude or nature of ecological disturbance to the habitat, cane toads gather around sources of food as well as sources of water. The carcasses of dead animals often are surrounded by several toads, feeding on insects attracted to the corpse (see photograph in Shine 2014); and beehives attract groups of toads also (Lever 2001; Silvester et al. 2017). Human disturbance magnifies that resource heterogeneity, because houses provide both water and food (e.g., dripping air-conditioner hoses, insects attracted to lights). In a study conducted in the wet-dry tropics of the Northern Territory, González-Bernal (2012) found that aggregations of toads around houses, especially during the tropical dry-season, disproportionately consisted of adult females and juveniles—just as we found for the bird-nesting trees. Thus, a trend for sex-biased and size-based exploitation of the resources available in disturbed habitats is a consistent theme in cane toad biology. The habitat heterogeneity caused by disturbance (whether it be due to bird-nests or buildings) exaggerates the degree of intraspecific niche partitioning (González-Bernal et al. 2015).

Although the specific habitat-choice behaviors of individual toads presumably reflect advantages to the individual (in survival, food intake, etc.), the phenomenon may have important consequences for population viability (Morales et al. 2010). A reduction in survival rates or feeding rates of adult males is unlikely to have severe effects at a population level, because reproductive rates potentially are far higher for male toads than for females (as is evident from highly male-biased sex ratios around breeding ponds: Wells 2010). The observed pattern of intraspecific niche partitioning gives female and juvenile toads disproportionate access to patches of well-watered, high-nutrient conditions. Thus, this system may have facilitated the success of the cane toad as an invasive species, especially during early stages of colonisation when numbers are low. Intraspecific niche partitioning directs the most demographically important population component (adult females) to localised patches of highly favourable conditions (Neuhaus and Ruckstuhl 2005). Under this scenario, a pre-existing divergence in habitat choice

among age and sex classes (in response to subtle habitat heterogeneity in undisturbed environments) pre-adapts cane toads to exploit the greater heterogeneity created by “natural” disturbance, and the even greater heterogeneity created by human activities (Skagen et al. 1991; Neuhaus and Ruckstuhl 2005). Similar analyses on habitat use by other invasive species would be of great interest, to see whether this hypothesis of invader pre-adaptation applies more widely.

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