Pest control by the public: Impact of hand-collecting on the abundance and demography of cane toads (*Rhinella marina*) at their southern invasion front in Australia

Matthew Greenlees a, b, Gregory P. Brown a, Richard Shine a, b, *

*Department of Biological Sciences, Macquarie University, New South Wales, 2109, Australia
bSchool of Life and Environmental Sciences, University of Sydney, New South Wales, 2006, Australia

**Abstract**

The population dynamics of an alien species can be heterogeneous across a geographically widespread invasion—and thus, the effectiveness of alternative control methods can vary. Research in tropical Australia has concluded that hand-collecting adult cane toads (*Rhinella marina*) is unlikely to offer a useful means of control, because the offtake rates needed to significantly reduce toad abundance are not achievable. Our data from southern (temperate-zone) Australia are more encouraging. We captured, marked and released toads in sites soon to be “toad-busted” by volunteer groups, and compared the animals that were collected to those known to be present. The volunteers disproportionately collected adult rather than subadult toads, probably because larger animals are easier to find. A single night’s “toad-busting” by volunteers removed 28%–47% of local toads. If conducted several times a year, and combined with recently-developed methods to curtail recruitment (pheromone-based trapping of larvae), that offtake could massively reduce toad abundance and perhaps, eradicate isolated populations at the southern margins of the cane toad invasion.

© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Invasive species threaten native taxa in many parts of the world, and have been implicated as a primary cause of extinctions (e.g., Clavero and García-Berthou, 2005; Woinarski et al., 2019). Invaders also impose economic and other societal impacts, prompting massive investment into programs to eradicate introduced species (e.g., Grarock et al., 2014; Keller et al., 2014). Much of that investment has occurred without clear evidence as to the effectiveness of alternative methods of control, resulting in inefficiencies (e.g., Buhle et al., 2005; Shine, 2018; Shine et al., 2018). To remedy that situation, we should attempt to identify optimal methods to cull invasive species (e.g., King and Powell, 2011). To answer that question, we need to combine demographic models with empirical data sets; and ideally, to monitor the population before and after implementation of the control method (e.g., Lazenby et al., 2015).

Importantly, the optimal approach for control efforts may differ not only among species, but even among populations and through time. For example, seasonal aggregations or shifts in demography may render control effects especially effective at
specific times (e.g., Govindaraju et al., 2005), and a particular method may be better-suited to some habitat types than to others (Schuchert et al., 2014). Additionally, the dynamics of range expansion vary through space and time even within a single invasion — for example, individuals may disperse more rapidly in some regions than others, and as a function of time since colonisation (Lindström et al., 2013; Pizzatto et al., 2017). Thus, control methods should be fine-tuned to local situations.

The most obvious way to reduce the abundance of invasive animals is via direct means such as hunting or trapping. For many alien species, that approach has been a popular form of control (Newsome et al., 2017). However, although direct culling can extirpate some kinds of organisms, it is ineffective with others. For example, density-dependence in rates of growth and survival may result in culling freeing the survivors from intraspecific competition, thereby conferring resilience (Grarock et al., 2014; King and Powell, 2011; Thresher and Bax, 2006). As a result, approaches that combine multiple avenues of attack, perhaps aimed at different life stages, may be more effective (e.g., Beaty and Salice, 2013; Pepin et al., 2017a,b). Again, however, there is a dearth of empirical information on the effectiveness of such methods (Newsome et al., 2017). Evaluations of culling programs often have been based simply on the numbers of animals removed (Porteus et al., 2019) or on comparisons between areas with different levels of culling (e.g., Grarock et al., 2014). A more robust approach is to assess the abundance and demographic characteristics of a population before and after episodes of culling, or to compare pre-existing populations to the offtake of individuals during culling (e.g., Berry et al., 2014; Lazenby et al., 2015).

One invasive species that has been the target of intensive control effort is the cane toad (Rhinella marina), an American amphibian that has been spreading through Australia since the species was introduced to that continent in 1935 (Shine, 2018). These highly toxic toads have fatally poisoned many native predators, stimulating managers to reduce the abundance of toads (Tingley et al., 2017). By far the most popular technique has been catching by hand, whereby collectors (either professional or volunteer) “toad-bust” by searching for active toads at night by torchlight (Fig. 1a). Community groups claim to have collected millions of toads in this manner, and government-employed teams have culled tens of thousands more (Shine et al., 2018).

Despite the widespread use of hand-collecting to reduce the abundance of cane toads, researchers have questioned the feasibility of this technique. Mathematical models suggest that culling is unlikely to reduce local densities long-term, especially in situations (such as at the tropical invasion front) where individual toads disperse long distances and hence, can rapidly recolonise areas after culling has concluded (Beaty and Salice, 2013; McCallum, 2006; Thresher and Bax, 2006). In the only empirical study of this process, Somaweera and Shine (2012) reported strong declines in toad abundance as a result of culling, but rapid recovery to pre-culling levels. However, both modelling and data are more encouraging for the impact of hand-collating on toads in small isolated populations. As long as offtake rates are very high (e.g., >25% of the population per month: McCallum, 2006), culling might extirpate such isolates. Case studies on a small island in Bermuda (Wingate, 2011) and an industrial suburb within a large city in Australia (Greenlees et al., 2018) reported successful eradication of cane toads based primarily upon hand-collating. Although those studies provide useful data, they do not directly address the proportion of the population that is removed by a specific culling effort, nor the degree to which hand-collating affects demographic subgroups (e.g., by sex or group size). Disproportionate offtake of some demographic groups may either exacerbate or reduce the impacts of culling on the viability of the targeted population (e.g., Beaty and Salice, 2013; Lampo and De Leo, 1998).

To address those gaps in knowledge, we conducted capture-mark-recapture studies on populations of invasive cane toads in sites that were scheduled for “toad-busts” by local councils and volunteer groups. By comparing parameters of populations to the offtake during culling, we could quantify both the impact of culling on overall abundances, and on relative abundance of different demographic classes. We worked near the southern invasion front of cane toads in Australia, in an area of northern New South Wales where toads are expanding their range only slowly, and where populations are discontinuous and hence, might be vulnerable to extirpation by targeted control.

2. Materials and methods

2.1. Study sites

2.1.1. Koala Beach

This 5-ha site (–28.372786, 153.554692) centres on a sediment retention pond retained after the construction of a coastal housing estate in the late 1990s and early 2000s. On one side of the 3-ha pond, a mown lawn runs along a residential street. A walking and cycling track runs around the pond, 20 m from the water, bordered by low-lying swamp with dominant trees being Melaleuca quinquenervia and Allocasuarina littoralis. Banksia robur (shrubs) have also been planted extensively. At this site, toads were collected by volunteers who had responded to locally posted advertisements. Most of the volunteers were young (7–14 years of age) and inexperienced in toad-busting, with a few adults; 20 to 26 people attended each event. Koala Beach was toad-busted on Dec 4, 2011 and Feb 15, 2012.

2.1.2. Yamba Golf course

This golf course (–29.443451, 153.358406) in the Yamba Golf and Country Club covers 40 ha with multiple water features and drainage lines. Most of the area is sparsely vegetated except for scattered Melaleuca quinquenervia. The periphery contains some small patches of coastal vine thicket, though is mostly bordered by urban and light industrial development.
Fig. 1. Photographs of a “toad-bust” in progress, showing (a) collectors, (b) toads in hand, and (c) the night’s catch prior to euthanasia. Photographs by Scott Lenton, with permission.
2.1.3. Micalo Island

Micalo Island (-29.444880, 153.312321) is a large (930 ha) island situated in the Clarence River estuary. It is used primarily for grazing cattle, so much of the island is cleared pasture, with a decommissioned prawn farm taking up a small area of the southern end of the island. It is sparsely vegetated other than scattered patches of Allocasuarina littoralis and a small plantation of sugar cane. Much of the free-standing water on the island is brackish due to tidal inundation, but a few dams and channels retain fresh water. During our study, we were able to access approximately one third of the island.

At both Yamba and Micalo Island, toads were collected by a group (the Clarence Valley Conservation in Action Volunteers) who carry out such activities on Friday evenings between October and April. Most volunteers were over 50 years of age, but five were under the age of 20. All of the older members had participated in >20 previous toad-busts. The number of volunteers per evening ranged from 10 (Micalo Island) to between 13 and 20 (Yamba Golf Course). Micalo Island was toad-busted on March 15, 2019, and Yamba Golf Course on Jan 18, 2019 and March 22, 2019.

2.2. Methods for data collection

Commencing 2–4 days prior to the scheduled toad-bust, two people (M.G. plus a trained volunteer) traversed the site with head-torches for approximately 5 h per night (2000 h–0100 h AEDST) on two successive nights searching for toads. Metamorph cane toads (<25 mm snout-urostyle length [SUL]) typically are active diurnally (Pizzatto et al., 2008) and were not recorded or captured. On the first night of surveys, the SUL of every captured toad was measured, and sex was determined by the presence of nuptial pads, skin dichromatism and rugosity, and/or a release call (Kelehear and Shine, 2019). Individuals that could not confidently be determined to be either male or female were recorded as subadult; most of these animals were <70 mm SUL (range 25–81 mm). All captured toads were given a unique mark by clipping the terminal 1–2 mm of up to two toes on each foot (usually, fewer) and then released at their point of capture, with the process taking <1 min. Toe-clipping has minimal impact on behaviour or locomotor performance of cane toads (Hudson et al., 2017). On the second evening, surveys were undertaken in an identical manner except that previously-collected ( toe-clipped) individuals had their identity recorded and were immediately released, whereas unmarked toads were processed as above. The two nights of surveys were consecutive and occurred within three nights of the scheduled toad-bust.

We attended the subsequent toad-busts (which commenced at ∼ 2000 h AEDST and typically lasted around 2 h) but as observers only (i.e., we did not collect toads). Volunteers caught and processed toads in their usual ways, in the same sites as we had used for the initial surveys. At the end of the evening we retained all of the animals that had been collected, checked them for toe-clips, and rechecked their sexes and sizes before returning them to the toad-busters for humane euthanasia (NSW legislation does not allow cane toads to be released into the wild).

2.3. Statistical analysis

2.3.1. Number of toads

We estimated the effectiveness of toad-busting in two ways:

1. the proportion of previously-marked toads that were captured in toad-busts; and
2. the number of toads caught in the toad-busts as a proportion of the estimated total population sizes of toads in the area.

To estimate toad population sizes during the five recapture experiments at the three sites we used the POPAN implementation of MARK (White and Burnham, 1999). For each of the five analyses we ran a set of 8 mark-recapture models where survival (phi), recapture rate (p) and “probability of entrance” (pent; a measure of recruitment, in this case immigration rather than reproduction, because of the short timeframe) were either constant over time or allowed to vary across capture sessions. The population size parameter was constrained to be constant over time. Because the recapture sessions in each experiment were short (3–6 days), the most appropriate model was one in which survival, probability of entrance and population size (N) remained constant over time but where recapture rate (p) was allowed to vary across nights. Encouragingly, this model was either the top model or shared equal support with the top model (i.e., ΔAICc < 2.0).

2.3.2. Sex ratio and age classes of toads

To quantify non-random patterns in the impact of toad-busting on different demographic classes, we compared the attributes (sexes, body sizes) of toads that we had captured beforehand to those collected during toad-busts at the same sites. We used logistic regression in SAS for this purpose, using data for all toads captured during the volunteer toad-busts as well as at least one preceding night during surveys. The independent variables were toad sex and body size (SUL), plus their interaction, as well as the number of nights on which each toad had been caught previously during initial mark-recapture surveys (1 or 2). If the interaction term was non-significant (p > 0.05), it was deleted and main effects were recalculated. We included capture session (toad-bust #) as a random factor to avoid pseudoreplication. We used ANOVA to compare mean body sizes of toads in successive toad-busts within each site.
3. Results

3.1. Number of toads

We obtained data from 2539 captures of 2034 toads (so, mean = 1.25 captures per toad, range 1–3). Of those captures, 1206 (47%) were made during our surveys, and the remaining 1333 (53%) were made during toad-busts (Table 1). The relative numbers of toads first captured before versus during the toad-busts ranged from 43 to 59% among our five capture sessions.

3.2. Estimated population sizes

Based on recapture rates, we calculated that the total population of cane toads (within the size range that we surveyed) was approximately 306 and 389 for the two sessions at Koala Beach, 1708 and 1108 for the two sessions at Yamba Golf Course, and 295 at Micalo Island (see Table 2 for confidence limits on those estimates, based on the modelling approach outlined by White and Burnham, 1999). Given the areas over which collecting occurred, these total numbers translate into densities (respectively) of 61, 78, 43, 28 and 0.96 toads per ha. Full output details of each model are provided in Table 3.

3.3. Effectiveness of toad-busting

We quantified the impact of toad-busting in two ways. First, the proportion of marked toads that were recaptured during toad-busts was 29% overall (355 of 1206 marked toads were re-caught), ranging from 22 to 34% among the five toad-busts. Those proportions varied among demographic classes also. The proportion of marked subadults that was recaptured averaged 21%, whereas corresponding figures for adult toads were 31% for adult females and 36% for adult males.

Second, the numbers of toads removed per toad-busting session averaged 36% of the total population at that site based on our mark-recapture data. Calculated in this way, effectiveness was 38% and 28% for the toad-busts at Yamba Golf Course (644 of 1708 toads; 311 of 1108 toads), 32% and 36% for the two toad-busts at Koala Beach (98 of 306; 140 of 389), and 47% at Micalo Island (140 of 295).

Another way to explore effectiveness of toad-busting is to look at the changes in numbers, sexes and sizes of toads collected in consecutive collections at the two sites that were each used twice. At Koala Beach, the number of toads collected increased from the first session to the second (N=227, 343), but the proportions of males, females and subadults did not change significantly (logistic regression $\chi^2 = 0.75$, 2 df, $p = 0.69$; see Fig. 2). Mean body size showed no significant shift in females (88.1 vs. 90.0 mm SUL; $F_{1,399} = 2.85$, $p = 0.09$), but males were smaller in the second session (92.2 vs. 88.1 mm SUL; $F_{1,111} = 8.43$, $p < 0.005$) whereas subadults were larger (65.9 vs. 71.3 mm; $F_{1,230} = 34.61$, $p < 0.0001$). At Yamba Golf Course, the total numbers collected fell from 1158 to 542. The relative proportion of subadult animals increased from the first to the second session (29 vs. 38%; $\chi^2 = 21.54$, 2 df, $p < 0.0001$; see Fig. 2). Mean body sizes were unchanged for females (92.7 vs. 92.6 mm SUL; $F_{1,223} = 0.001$, $p = 0.97$) but males averaged larger at the second sampling session (85.9 vs. 88.9 mm SUL; $F_{1,757} = 27.44$, $p < 0.0001$) whereas subadults were smaller (62.8 vs. 53.3 mm SUL; $F_{1,538} = 59.82$, $p < 0.0001$; see Fig. 3).

3.4. Sex ratio and age classes of toads

Overall, 928 toads (37%) were classed as subadults, 926 (36%) as adult males, and 685 (27%) as adult females (Table 1). The Micalo Island sample was dominated by subadult toads (58%), whereas the other sites had more adults than subadults (Fig. 2).

Table 1

| Locality  | Koala 1 | Koala 2 | Yamba 1 | Yamba 2 | Micalo |
|-----------|---------|---------|---------|---------|--------|
| Dates     | Dec 2011| Feb 2012| Jan 2019| Mar 2019| Mar 2019|
| (a) Surveys|         |         |         |         |        |
| Numbers of toads | 129 | 203 | 514 | 231 | 129 |
| Males     | 23 | 43 | 231 | 117 | 30 |
| Females   | 53 | 77 | 149 | 53 | 25 |
| Subadults | 53 | 83 | 134 | 61 | 74 |
| Mean SUL (mm) | 81.10 | 82.58 | 80.78 | 82.20 | 68.14 |
| (b) Toad-busts|         |         |         |         |        |
| Numbers of toads | 98 | 140 | 644 | 311 | 140 |
| Males     | 17 | 30 | 304 | 107 | 24 |
| Females   | 139 | 56 | 139 | 60 | 34 |
| Subadults | 42 | 54 | 201 | 144 | 82 |
| Mean SUL (mm) | 81.76 | 83.96 | 78.97 | 70.84 | 70.28 |
3.5. Body-size distributions of toads

Overall, adult female toads averaged larger than conspecific males, with subadults smaller (respective mean values 89.67, 86.65, 63.32 mm SUL; F\textsubscript{2,1062} = 731.41, p < 0.0001). The mean body sizes within each group were similar between survey samples and toad-bust samples, but data from the first session at Yamba Golf Course show that female toads and subadult

| Location      | Estimated population size ±SE | 95% confidence limits | Date of surveys and toad-busts | # of toads busted | % population busted |
|---------------|-------------------------------|-----------------------|-------------------------------|------------------|---------------------|
| Koala Beach 1 | 306 ± 66                      | 227–509               | Dec 2011                      | 98               | 32.0                |
| Koala Beach 2 | 389 ± 48                      | 321–516               | Feb 2012                      | 140              | 36.0                |
| Micalo Island | 295 ± 53                      | 241–480               | Mar 2019                      | 140              | 47.4                |
| Yamba 1       | 1708 ± 88                     | 1554–1900             | Jan 2019                      | 644              | 37.7                |
| Yamba 2       | 1108 ± 226                    | 796–1720              | Mar 2019                      | 311              | 28.1                |

Table 2
Estimated population sizes and effectiveness of five “toad-busting” events at our study sites in northeastern New South Wales.

Table 3
Summary of Mark-recapture model selection for each of the toad-busting data-sets. Model names indicate whether each parameter (phi [probability of survival], p [probability of recapture], pent [probability of entry], and \(N\) [population size]) was constant over time (\(\cdot\)) or varied over time (t). Other columns show the population size estimated from each model, and model-fitting values AICc (corrected Akaike information criterion), delta AICc, number of parameters and model deviance.

| Location      | Estimated population size ±SE | 95% confidence limits | # of toads busted | % population busted |
|---------------|-------------------------------|-----------------------|------------------|---------------------|
| Koala Beach 1 | Model                         | Pop. Size Estimate (SE) | AICc Delta AICc Parameters Deviance |
|               | Phi(t) pent(t) N(.)           | 221.5 (20.5)          | 253.48            | 0.00 |
|               | Phi(.) pent(.) N(.)           | 305.8 (66.2)          | 253.49            | 0.01 |
|               | Phi(t) pent(t) N(.)           | 336.6 (92.8)          | 254.31            | 0.83 |
|               | Phi(t) pent(t) N(.)           | 219.4 (23.7)          | 255.61            | 2.13 |
|               | Phi(.) pent(.) N(.)           | 295.0 (29.9)          | 259.35            | 5.87 |
|               | Phi(.) pent(.) N(.)           | 311.1 (35.6)          | 280.41            | 26.93 |
|               | Phi(.)(t) pent(.) N(.)        | 308.9 (31.0)          | 287.00            | 33.52 |
|               | Phi(.)(t) pent(t) N(.)        | 311.9 (31.4)          | 280.41            | 33.52 |
|               | Phi(t) pent(.) N(.)           | 382.9 (25.4)          | 388.27            | 0.00 |
|               | Phi(t) pent(.) N(.)           | 388.5 (47.7)          | 388.57            | 0.30 |
|               | Phi(t) pent(.) N(.)           | 306.4 (17.4)          | 390.03            | 1.77 |
|               | Phi(t) pent(.) N(.)           | 385.9 (27.0)          | 390.19            | 1.93 |
|               | Phi(t) pent(.) N(.)           | 388.0 (49.8)          | 390.65            | 2.38 |
|               | Phi(t) pent(.) N(.)           | 304.0 (22.7)          | 392.11            | 3.84 |
|               | Phi(t) pent(.) N(.)           | 371.8 (23.5)          | 400.23            | 11.96 |
|               | Phi(t) pent(.) N(.)           | 368.2 (23.1)          | 400.84            | 12.57 |
| Yamba 1       | Model                         | Pop. Size Estimate (SE) | AICc Delta AICc Parameters Deviance |
|               | Phi(.) pent(.) N(.)           | 1708.1 (87.9)         | 885.86            | 0.00 |
|               | Phi(t) pent(.) N(.)           | 1500.2 (108.8)        | 887.70            | 1.84 |
|               | Phi(t) pent(.) N(.)           | 1655.6 (125.9)        | 887.85            | 1.99 |
|               | Phi(t) pent(.) N(.)           | 1432.3 (120.1)        | 889.65            | 3.79 |
|               | Phi(t) pent(.) N(.)           | 1860.1 (104.4)        | 903.86            | 18.01 |
|               | Phi(t) pent(.) N(.)           | 1963.4 (101.5)        | 906.46            | 20.60 |
|               | Phi(t) pent(.) N(.)           | 1734.3 (86.8)         | 940.25            | 54.39 |
|               | Phi(t) pent(.) N(.)           | 1832.9 (88.9)         | 951.65            | 65.79 |
| Yamba 2       | Model                         | Pop. Size Estimate (SE) | AICc Delta AICc Parameters Deviance |
|               | Phi(.) pent(.) N(.)           | 1369.8 (214.5)        | 370.27            | 0.00 |
|               | Phi(t) pent(.) N(.)           | 1315.3 (154.6)        | 371.44            | 1.17 |
|               | Phi(t) pent(.) N(.)           | 1168.0 (225.6)        | 371.67            | 1.40 |
|               | Phi(t) pent(.) N(.)           | 745.9 (88.1)          | 372.56            | 2.29 |
|               | Phi(t) pent(.) N(.)           | 1143.6 (254.0)        | 373.03            | 2.76 |
|               | Phi(t) pent(.) N(.)           | 708.0 (95.1)          | 374.54            | 4.27 |
|               | Phi(t) pent(.) N(.)           | 1141.3 (113.4)        | 409.55            | 39.28 |
|               | Phi(t) pent(.) N(.)           | 1254.3 (119.8)        | 416.62            | 46.35 |
| Micalo Model  | Model                         | Pop. Size Estimate (SE) | AICc Delta AICc Parameters Deviance |
|               | Phi(.) pent(.) N(.)           | 370.0 (60.7)          | 232.87            | 0.00 |
|               | Phi(t) pent(.) N(.)           | 381.6 (64.9)          | 233.86            | 0.99 |
|               | Phi(t) pent(.) N(.)           | 293.2 (53.0)          | 234.11            | 1.25 |
|               | Phi(t) pent(.) N(.)           | 246.9 (8.5)           | 234.85            | 1.98 |
|               | Phi(t) pent(.) N(.)           | 300.8 (56.0)          | 235.56            | 2.70 |
|               | Phi(t) pent(.) N(.)           | 250.3 (17.7)          | 236.92            | 4.05 |
|               | Phi(t) pent(.) N(.)           | 399.0 (42.2)          | 244.59            | 11.73 |
|               | Phi(t) pent(.) N(.)           | 393.3 (61.5)          | 250.81            | 17.95 |

3.5. Body-size distributions of toads

Overall, adult female toads averaged larger than conspecific males, with subadults smaller (respective mean values 89.67, 86.65, 63.32 mm SUL; F\textsubscript{2,1062} = 731.41, p < 0.0001). The mean body sizes within each group were similar between survey samples and toad-bust samples, but data from the first session at Yamba Golf Course show that female toads and subadults...
toads collected during surveys were larger than those taken in the subsequent toad-bust (means for female toads 94.6 vs. 86.0 mm; $F_{1,111} = 13.43, p < 0.001$; means for subadult toads 65.6 vs. 60.9 mm, $F_{1,333} = 10.19, p < 0.0001$). The same pattern for subadults was evident for the second session at Yamba Golf Course (means 57.8 vs. 51.4 mm, $F_{1,203} = 9.16, p < 0.003$; see Table 1). For all other comparisons (sessions, demographic classes), sizes of surveyed toads did not differ significantly from those of toad-busted individuals within each demographic class (all $p > 0.05$).

3.6. Vulnerability of toads to capture during toad-busts

Plausibly, attributes of individual toads (such as their location and/or behaviour) affect their probability of being seen and captured. We can assess this possibility by asking if the toads that we caught on both nights of our surveys were more likely to be caught during the subsequent toad-bust than were animals that we captured on only one night of our surveys. However, our logistic regression showed that toads collected on only one previous night were as likely to be collected by the toad-busters as were toads collected on both previous nights ($F_{1,1054} = 2.78, p = 0.10$). The collections made by volunteer toad-busters contained more males, and larger toads than did the collections made by experienced herpetologists in the preceding surveys (from logistic regression: sex effect $F_{1,1054} = 7.62, p < 0.006$; SUL effect $F_{1,1054} = 3.72, p < 0.025$).

4. Discussion

Our data confirm that feral cane toads can attain high abundances on the southern invasion front (to > 75 toads per ha), but also show that those numbers can be substantially reduced by hand-capturing. Two experienced people captured around 30% of adult toads by hand-capturing over two successive nights, and larger groups of volunteers (comprising inexperienced as well as experienced people) removed around 30–40% of previously-marked animals in a single evening.

Those offtake rates are higher than have been achieved with most other pest species. Thus, for example, attempts to cull foxes, cats and camels could rarely hope to eradicate a third of the adult population with a single nights’ effort (e.g., Newsome et al., 2017). The cane toad’s biology facilitates high capture rates. The animals are large and distinctive enough to identify relatively easily (but see Somaweera et al., 2010), are concentrated around human dwellings (González-Bernal et al., 2016), forage and call in open habitats, have highly reflective eyes that are readily detectable by flashlight, and allow close approach before fleeing (Shine, 2018). They move more slowly than do many other amphibians (or other types of feral animals), and lack defensive weapons (teeth, claws) that might discourage collectors. Although cane toads possess potent chemical defences, they rarely deploy those defences even when seized (Blennerhasset et al., 2019). Additionally, the nocturnal locations of active toads are highly predictable. These animals need to rehydrate frequently (at least once every few nights) and thus
Fig. 3. Body-size distributions of cane toads collected during five sessions (combined data from surveys plus toad-busts).
congregate around water sources (Letnic et al., 2015). This constellation of traits renders cane toads easy to capture in large numbers in short periods of time.

If one subset of animals (e.g., by sex or size) was more difficult to locate or capture, we might expect that group to be captured less often by citizen scientists than by experienced collectors. In practice, no such difference was evident. Hence, toads of both sexes and a wide range of sizes appear to be equally conspicuous to collectors using flashlight at night. However, ecological differences within a population of cane toads likely affect an individual’s probability of being captured. In cane toads as in many other species, habitat use is linked to phenotypic traits such as an animal’s sex, size, habitat, behaviour (“personality”), reproductive state and health (e.g., González-Bernal et al., 2014; Merrick and Koprowski, 2017). Most obviously, larvae are found in the water not on land, and metamorphs are active primarily by day rather than by night (Pizzatto et al., 2008). Hence, neither group is accessible to people searching by spotlight at night. Even if we restrict attention to adult toads, individuals found close to water are likely to be males not females (González-Bernal et al., 2015) and to be infected by lungworms (Finnerty et al., 2018).

Such biases may be relevant to the effectiveness of hand-collecting as a means of pest control, because the impact of culling on population viability depends upon the types of animals that are collected, as well as the total numbers removed (e.g., Newsome et al., 2017). Ideally, then, culling would fall heavily on demographic groups critical to population recruitment, such as reproductive females (Pepin et al., 2017a,b). In the case of cane toads, however, collectors usually target riparian areas, where toads are most abundant; and the individuals in such sites are likely to be males rather than females (González-Bernal et al., 2015). In contrast, adult female toads concentrate on feeding rather than breeding for most of the year, and hence are scattered throughout surrounding habitat (although, sometimes concentrated at resource hotspots: Lettoof et al., 2018; Silvester et al., 2019). Nonetheless, females have to return to waterbodies to hydrate as well as to breed, perhaps explaining why the sex-ratio bias in our samples was relatively modest (56% male).

In general, culling is unlikely to seriously deplete population densities for feral pests, especially if the species in question has a high reproductive rate (Newsome et al., 2017). As a result, offtake rates achievable by volunteer-driven control programs are often too low to reduce pest abundance over biologically meaningful areas or time periods (e.g., Grarock et al., 2014) or may even increase pest numbers overall (Lazenby et al., 2015). Mathematical models of closed populations of cane toads predict that in order for culling to reduce toad densities over the longterm, the offtake would need to be at least around 25% per month (McCallum, 2006) or 40% per year (Thresher and Bax, 2006). The authors of those studies concluded that such rates are unrealistically high, and hence hand-culling is unlikely to offer a useful way to control feral toads. We agree with that assessment for tropical Australia, especially near the invasion front where toads disperse very large distances and populations are continuously distributed — and hence, any reduction in local densities of toads is soon negated by immigration from surrounding areas (e.g., Somaweera and Shine, 2012). In contrast, our results at the southern front of the cane toad invasion suggest that a well-organised community group can remove around 30% of toads in a single evening’s toad-bust. Toads in this area are distributed discontinuously, with little immigration or emigration among sites (Pettit et al., 2017). Thus, regular toad-busting might drive local populations of adult cane toads to very low levels.

This approach could be made even more effective by combining it with methods of control that target aquatic stages of the life history. Most of the toad populations we studied had access to only a few waterbodies suitable for spawning (see Semeniuk et al., 2007). Thus, it would be feasible to deploy pheromone-baited traps to collect and remove larvae from those ponds (Crossland et al., 2012). In the absence of recruitment or immigration, high rates of culling of adult toads may achieve local extirpation. Large numbers of adult toads can also be trapped, using lights (to attract insects) and acoustic cues (advertisement calls of cane toads) (e.g., Muller and Schwarzkopf, 2018; Yeager et al., 2014).

The rates at which toads were collected in the present study (i.e., numbers per night) are broadly similar to those reported for collections in tropical areas by both professional and amateur “toad-busters” (e.g., Shine, 2018). For example, professional toad-collectors in tropical northwestern Australia culled around 30 toads per night per person, with a fivefold seasonal variation in capture rates (Shine et al., 2018). On a per-person basis, capture rates in the present study were somewhat lower than those figures from tropical Australia (5–24 toads per person per night), but higher than have been reported for an area in northeastern Queensland (0.06–1.5 toads per person per hour over a 10-week period: Muller and Schwarzkopf, 2018). The ability of the toad population to rebound from culling also is lower at southern sites, because of the cooler climate (restricting activity seasonally) and the discontinuous distribution of toads at the southern front (restricting immigration).

Importantly, the number of collectors was higher in our study than in the other two projects, because the proximity of “toad-busted” sites to large urban centres facilitated involvement by volunteers. The need for intensive and sustained volunteer effort means that toad-busting will work most effectively in places where isolated populations of toads exist close to urban conurbations. The southern front of the toad invasion fulfills this condition better than do the more sparsely-populated tropics. The success of local environmental authorities in attracting volunteers to toad-busting sessions, and to set up and maintain groups of committed people over periods of several years (e.g., Clarence Valley Conservation in Action) testifies to the feasibility of the approach. Analogous organisations, that bring people together regularly to tackle other environmental problems such as invasive weeds, offer further encouragement for this “citizen science” model. Volunteer toad-busters report high levels of enjoyment and satisfaction for this socially-acceptable form of hunting (Shine, 2018). The ethics of killing wild animals remain contentious, posing a potential obstacle (White and Whiting, 2000; Littin et al., 2014), but cane toads are widely vilified (Shine, 2018) and recent research has identified humane forms of euthanasia suitable for implementation by the general public (cooling then freezing: Shine et al., 2015). Lastly, community participation in toad-
busting provides an opportunity to disseminate information about conservation issues — such as the threat posed by invasive species, and the importance of maintaining biodiversity (Mau et al., 2007).

5. Conclusions

In summary, our mark-recapture studies provide a strong contrast to the conclusions from previous research in north-western Australia, where hand-collecting has been ineffective in controlling the spread of these pests (e.g., Peacock, 2007; Shine et al., 2018; Somaweera and Shine, 2012). Likewise, Muller and Schwarzkopf (2018) concluded that hand-collecting was relatively ineffective in northeastern Australia. However, southeastern Australia offers a very different landscape, climate, toad distribution and toad dispersal behaviour (e.g., Pettit et al., 2017). The combination of an abundant volunteer labour force, and a toad invasion front consisting of isolated groups of sedentary animals, enhances the feasibility of control methods that have had minimal impact in other parts of the cane toads’ Australian range. More generally, geographic variation in invasion dynamics and human populations can strongly affect the effectiveness of specific methods of control, and wildlife managers need to tailor their efforts to local situations.

Funding source

The funding sources did not play a role in the study design; data collection, analysis, or interpretation; writing of the report; or decision to submit the paper for publication.

Data statement

Data is available in Appendix A at the link below.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks to the Clarence Valley Conservation in Action (CVClA) ‘division’ of Landcare — especially Scott Lenton and family, Lorraine and Terry Watkins, Alan and Jan Armstrong, Bruce and Deborah Kane, Greg and Bryn Mashiah, Ann Creswell and all the dedicated, intrepid CVClA toad-busters. These people continue to donate considerable time to conserving biodiversity. We also thank Tweed Shire Council (especially Pamela Grey) for facilitating our research. Funding was provided by the Australian Research Council (with Linkage grant partners NSW Office of Environment and Heritage, NSW Roads and Maritime Services, NSW Department of Primary Industries), Tweed Council, Lismore More Council, and the Australian Wildlife Conservancy. M.G. thanks Trent McKenna for invaluable assistance in the field. All procedures were approved under The University of Sydney AEC protocol #2015/892.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01120.

Authors contributions

Matthew Greenlees: Conceptualization, Methodology, Validation, Investigation, Data curation, Writing - original draft, Visualization. Gregory Brown: Writing - review & editing, statistical tests, Supervision. Rick Shine: Conceptualization, Methodology, Writing - review & editing, Supervision.

References

Beaty, L.E., Salice, C.J., 2013. Size matters: insights from an allometric approach to evaluate control methods for invasive Australian Rhinella marina. Ecol. Appl. 23, 1544–1553. https://doi.org/10.1890/12-1298.1.
Berry, O., Tatler, J., Hamilton, N., Hilmer, S., Hitchen, Y., Algar, D., 2014. Slow recruitment in a red-fox population following poison baiting: a non-invasive mark-recapture analysis. Wildl. Res. 40, 615–623. https://doi.org/10.1071/WR13073.
Blennerhasset, R., Bell-Anderson, K., Shine, R., Brown, G.P., 2019. The cost of chemical defence: the impact of toxin depletion on growth and behaviour of cane toads (Rhinella marina). Proc. R. Soc. B 286, 19100867. https://doi.org/10.1098/rspb.2019.0867.
Buhr, E.R., Margolis, M., Ruesink, J.L., 2005. Bang for buck: cost-effective control of invasive species with different life histories. Ecol. Econ. 52, 355–366. https://doi.org/10.1016/j.ecolecon.2004.07.018.
Clavero, M., Garcia-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20, 110. https://doi.org/10.1016/j.tree.2005.01.003.
Tingley, R., Ward-Fear, G., Schwarzkopf, L., Greenlees, M.J., Phillips, B.L., Brown, G.P., Clulow, S., Webb, J., Capon, R., Sheppard, A., Strive, T., Tizard, M., Shine, R., 2017. New weapons in the Toad Toolkit: a review of methods to control and mitigate the biodiversity impacts of invasive cane toads (*Rhinella marina*). QRB (Q. Rev. Biol.) 92, 123–149. https://doi.org/10.1086/692167.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Hous. Theor. Soc. 46 (Suppl. ment), 120–138. https://doi.org/10.1080/00063659909477239.

White, P.C.L., Whiting, S.J., 2000. Public attitudes towards badger culling to control bovine tuberculosis in cattle. Vet. Rec. 147, 179–184. https://doi.org/10.1136/vr.147.7.179.

Wingate, D.B., 2011. The successful elimination of cane toads, *Bufo marinus*, from an island with breeding habitat off Bermuda. Biol. Invasions 13, 1487–1493. https://doi.org/10.1007/s10530-010-9925-2.

Woinarski, J.C.Z., Braby, M.F., Burbidge, A.A., Coates, D., Garnett, S.T., Fensham, R.J., Legge, S.M., McKenzie, N.L., Silcock, J.L., Murphy, B.P., 2019. Reading the black book: the number, timing, distribution and causes of listed extinctions in Australia. Biol. Conserv. 239, 108261. https://doi.org/10.1016/j.biocon.2019.108261.

Yeager, A., Commito, J., Wilson, A., Bower, D., Schwarzkopf, L., 2014. Sex, light, and sound: location and combination of multiple attractants affect probability of cane toad (*Rhinella marina*) capture. J. Pest. Sci. 87, 323–329. https://doi.org/10.1007/s10340-014-0555-9.