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Shrinking before our isles: the rapid expression of insular dwarfism in two invasive populations of guttural toad (*Sclerophrys gutturalis*)

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Island ecosystems have traditionally been hailed as natural laboratories for examining phenotypic change, including dramatic shifts in body size. Similarly, biological invasions can drive rapid localized adaptations within modern timeframes. Here, we compare the morphology of two invasive guttural toad (*Sclerophrys gutturalis*) populations in Mauritius and Réunion with their source population from South Africa. We found that female toads on both islands were significantly smaller than mainland counterparts (33.9% and 25.9% reduction, respectively), as were males in Mauritius (22.4%). We also discovered a significant reduction in the relative hindlimb length of both sexes, on both islands, compared with mainland toads (ranging from 3.4 to 9.0%). If our findings are a result of natural selection, then this would suggest that the dramatic reshaping of an amphibian's morphology—leading to insular dwarfism—can result in less than 100 years; however, further research is required to elucidate the mechanism driving this change (e.g. heritable adaptation, phenotypic plasticity, or an interaction between them).

1. Introduction

Islands have a long history of piquing the interest of evolutionary ecologists, owing to the frequent stark contrasts between insular and mainland populations (e.g. divergent behavioural and morphological traits) [1–3]. These island-specific features can arise from adaptation by natural selection [4–6], phenotypic plasticity [7] or an interplay between them—accelerating adaptation towards localized 'optimal' phenotypes [8]. Examining adaptive processes within these natural laboratories has contributed extensively to our understanding of evolution [1,8] and the concept of island syndromes (i.e. repeated convergent island-specific traits across species and locations [3,9]). Some of the more commonly recognized traits associated with island syndromes involve reduced antipredator behaviour, longer life spans, lower reproductive outputs and dramatic changes in body size (e.g. the 'island rule'—insular dwarfism in large-bodied species and island gigantism in small-bodied species) [3,6,9,10].

For many taxa associated with the island syndrome, phenotypic change occurs after colonizing islands through island biogeographic processes [11,12], like the oversized and fearless Dodos (*Raphus cucullatus*) of Mauritius or the miniature hippopotamuses (*Hippopotamus creutzburgi*) and elephants (*Mammuthus creticus*) of Pleistocene Crete [3]. Yet within the modern era, anthropogenic introductions of species outside their native range occur far more frequently [13]. The establishment and success of invasive species represent additional opportunities where we can

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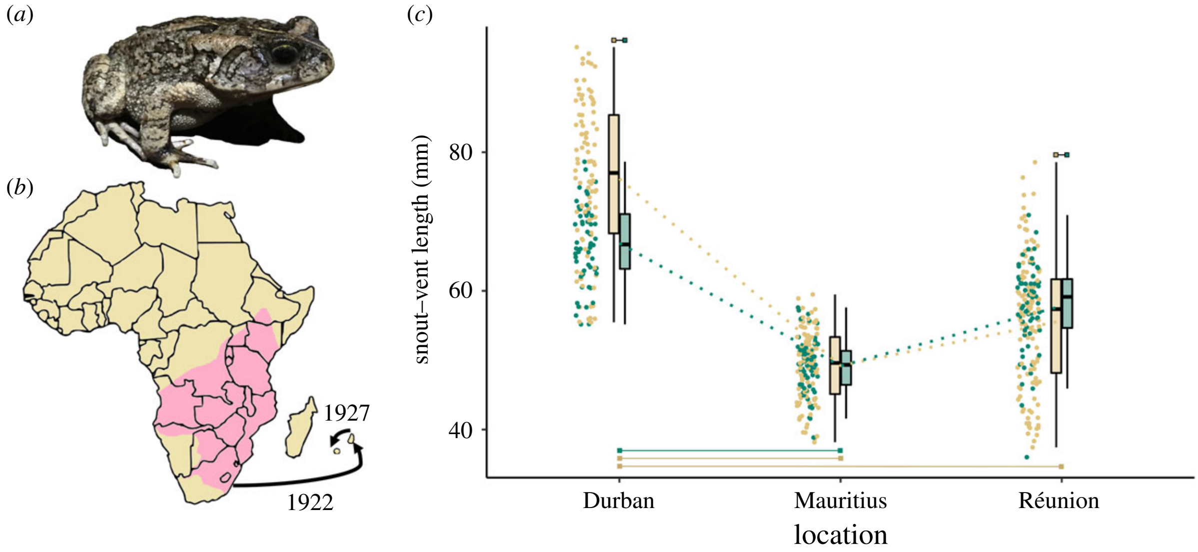

Figure 1. Guttural toads (*a*) are native to mainland Africa (shaded pink [23] in *b*) and were introduced from Durban, South Africa, to Mauritius in 1922 and then to Réunion in 1927 (*b*). Between these locations, snout–vent length (SVL; mm) differed based on location and sexes (*c*). Depicted are raw SVL for each location by sex (females in beige and males in green). Significant differences in female and male toads between locations are shown using a beige and a green line, respectively, along the *x*-axis with squares at the ends. Sex-specific differences at each location are shown with a black line with beige and green squares at the ends located above the boxplots. The figure depicts raw data points on the left with corresponding boxplots.

observe rapid phenotypic changes [14,15]. Given the role humans play in the spread of invasive species [13] and the recurrent negative impacts [16], detailed information on the origin, timeframes and local ecological interactions is generally well known. This can provide fine-scale temporal and genetic details not always available to more traditional island evolutionary studies. Invasions may also be replicated across multiple locations, owing to repeating anthropogenic causes (e.g. transportation networks and deliberate introductions [13]), allowing for parallel investigations into island-derived phenotypic change to provide deeper insights.

Compared with other vertebrate groups (e.g. birds, mammals, and reptiles) [1–10], amphibians have received less attention regarding island-derived morphological changes [17–19]. This taxonomic bias is surprising, as studies on mainland amphibians have greatly advanced our understanding of rapid phenotypic change during invasions [20] and dramatic changes in size (e.g. miniaturization) have naturally evolved numerous times across several lineages [21,22]. Here, we examine the morphology of guttural toads (*Sclerophrys gutturalis*) within their invasive populations on the islands of Mauritius and Réunion, after almost 100 years of colonization, and compare them with their known mainland source population in South Africa [23]. We test whether relatively parallel toad invasions have resulted in comparable phenotypic divergence in overall body size, skull shape and limb lengths. Based on preliminary reports from Mauritius [24], and following trends seen in other bufonid populations invading tropical islands [18], we predict that guttural toads on both islands will exhibit reductions in overall body size, when compared with the native mainland counterparts, and their skull shape and limb lengths to scale proportionately.

2. Methods

(a) Study system

Guttural toads are large bufonids, up to 140 mm snout–vent length (SVL) [25], with a broad distribution in sub-Saharan Africa [23] (figure 1*a*,*b*). These toads also have invasive populations in Mauritius, Réunion and Cape Town (South Africa; see electronic supplementary material for more details), with a molecular analysis confirming that all three invasive populations have the same native source population originating near Durban, South Africa and that the founding populations on Mauritius and Réunion had a relatively high degree of genetic diversity [23]. Their deliberate introduction to Mauritius occurred in 1922, and toads were subsequently moved from Mauritius to Réunion in 1927 [23,26] (figure 1*b*), resulting in both invasions experiencing island-specific selective pressures for roughly 47 generations [27].

Mauritius and Réunion are similarly sized islands, 2040 km^2 and 2512 km^2 respectively [23], that have tropical climates. Ecologically, both are considered biodiversity hotspots that are rich in endemics [28] and lack any recent evolutionary history with bufonids (pre-1920's [26]). Although not identical, these islands represent two relatively similar ecosystems, sharing a wide diversity of flora and fauna, including invertebrate communities [29–31] (prey for toads [24]) and similar toad predators (mostly non-native vertebrates [26]).

(b) Data collection

We caught adult guttural toads from multiple sites in Mauritius (two sites; $n = 158$ toads), Réunion (two sites; $n = 186$) and in and around Durban, South Africa (four sites; $n = 151$) between June 2019 and March 2020 (see electronic supplementary material for the region and sex-specific details). Upon capture, we recorded each toad's collection site and sex, and took morphological measures of SVL, jaw width, jaw length, forearm length (combining upper and lower forearm lengths), hindlimb length (combining upper and lower hindlimb lengths) and foot length, using a set of digital callipers (±0.01 mm). All measurements were taken by the same researcher (JB-G) on the toad's left side (unless prior injury prevented it; $n = 2$) to avoid interobserver variation.

(c) Statistical analysis

Owing to known sexual size dimorphism in anurans, including bufonids [32], we accounted for sex-specific differences in our analyses. Before analyses, all morphological traits were $\log_{10}$ transformed to ensure allometric relationships were linear [33].

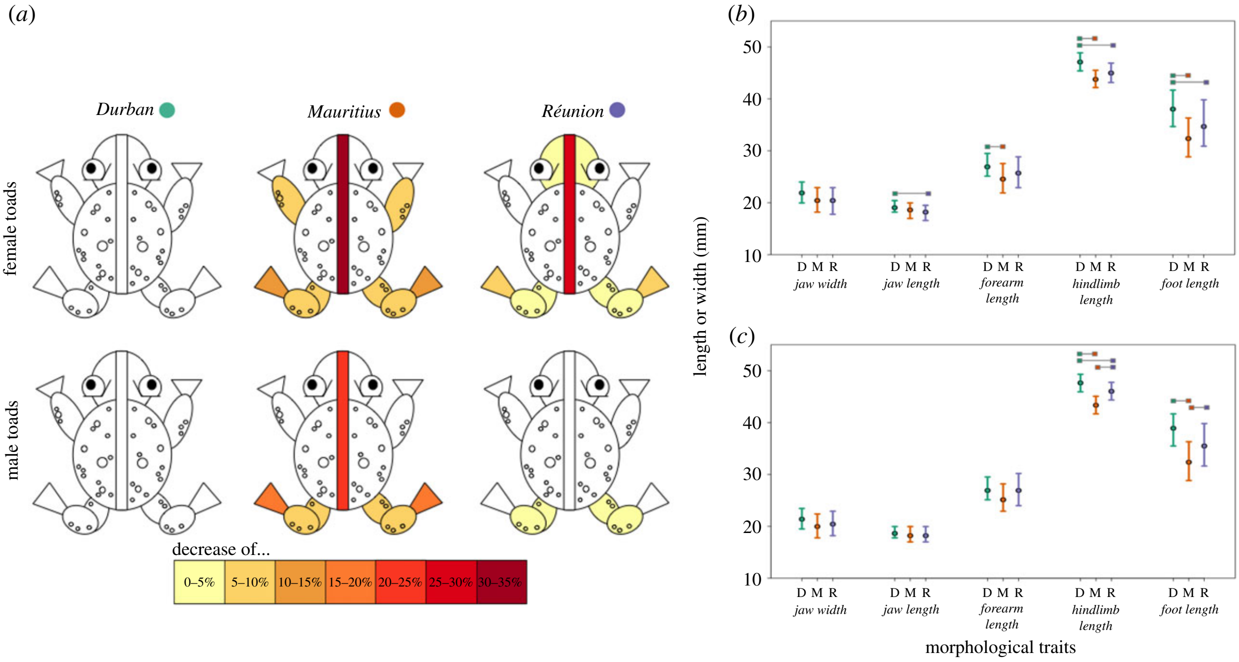

Figure 2. The degree to which morphological traits decreased in reference to female and male toads from the native, source population in Durban (*a*). Snout–vent length (SVL) is represented using a rectangle along the toad's midline. Percentage decreases in morphological traits were calculated separately for each sex and were based on statistically significant differences between estimated marginal means (EMM [35]) generated from their respective LMM. In addition, morphological trait (jaw width, as well as jaw, forearm, hindlimb and foot lengths) EMM and 95% confidence intervals are shown for female (*b*) and male toads (*c*) from Durban ('D', green), Mauritius ('M', orange) and Réunion ('R', purple). Significant differences between locations are shown using grey straight lines that are ended with squares reflecting the colours of each location.

Using linear mixed effect models (LMM), we examined whether there were differences in adult toad SVL between locations, sex and an interaction between location and sex. In the LMM, we also included the random intercept of the collection site to incorporate dependency among toads from the same population.

We then used separate LMM that contained the same fixed, interaction and random effects as the LMM analysing SVL to examine differences in five other morphological traits (jaw width, jaw length, forearm length, hindlimb length and foot length). In addition, these LMM included the fixed factor of SVL to test for potential changes in these five morphological traits that are disproportionate to any changes in toad SVL. Post-hoc we tested for multiple comparisons between study locations and sexes correcting *p*-values using the Scheffe procedure [34] (see electronic supplementary materials for additional details).

3. Results

All model outputs and additional information on the location and sex-specific differences in morphology are presented in the electronic supplementary materials.

(a) Female toads

Female toads from Mauritius and Réunion had significantly shorter SVL than Durban by 33.9% and 25.9%, respectively (figures 1*c* and 2*a*). Controlling for SVL, Réunion females had significantly shorter jaw lengths than females from Durban (by 4.5%) and Mauritius females had significantly shorter forearms than Durban females (by 8.8%; figure 2). Also, females from Mauritius and Réunion had significantly shorter hindlimbs and feet than Durban females, independent of reductions in their SVL (figure 2). Mauritius female hindlimbs and feet were shorter than those of Durban females by 7.1% and 14.9%, respectively (figure 2). Réunion female hindlimbs and feet were shorter than those of Durban females by 4.5% and 8.8%, respectively (figure 2).

(b) Male toads

Male toad SVL from Mauritius was significantly shorter (22.4%) than those of Durban males (figures 1*c* and 2*a*), a trend not seen with Réunion males. Males from Mauritius and Réunion had shorter hindlimbs (by 9.0% and 3.4%, respectively) than Durban males, disproportionate to differences in their SVL (figure 2). In addition, males from Mauritius and Réunion differed in their hindlimb length; males from Mauritius have hindlimbs that are 5.8% smaller than Réunion males. Foot length of Mauritius males was 16.8% shorter, also accounting for SVL, than that of Durban males (figure 2) and Mauritius male foot length was significantly shorter than the foot length of Réunion males (by 8.8%).

4. Discussion

Mauritius and Réunion guttural toad populations have experienced substantial reductions in overall body size compared with their source population in Durban; however, the extent of change varies between the sexes and islands. We observed further reductions in skull and limb lengths, accounting for SVL, but these too varied between sexes and locations. Notably, we observed significant reductions in hindlimb length, disproportionate to SVL, across both sexes and islands compared with mainland counterparts. Owing to the high degree of genetic diversity on both islands [23] and historical practices for deliberately introducing large numbers of amphibian biocontrol agents [26,36], we assert that our findings are not a result of founder effects (for more details, see electronic supplementary materials), yet we are unable to determine the evolutionary mechanisms of this change (e.g. adaptation or phenotypic plasticity). Even if this 'island morphology' is, or originally was, a product of phenotypic plasticity, this still can result in heritable adaptations arising through avenues such as 'plasticity-first' adaptation [37], heritable phenotypic plasticity [38], or by acting as a stopgap allowing populations to persist long enough for natural selection to take place [39,40]. Overall, what we are able to report is a highly rapid response (less than 100 years) compared with previous studies on island-derived changes in amphibian body size that report timescales for colonization and isolation that are two to five orders of magnitude longer [17–19,41]. This suggests that dramatic changes in body size, related to island populations, can arise rapidly soon after establishment.

The reduction in body size was more pronounced in Mauritius, both in effect size and occurring in both sexes, while in Réunion this trend was only significant for female toads. Sex-specific insular dwarfism in a reptile has been suggested to be related to localized differences in prey [42]; however, this remains to be tested for guttural toads. In general, our findings of reduced body size follow what has been seen in other tropical island populations of toads (e.g. ornate forest toad, *Rhinella ornata* [18]); however, it is in contrast with reports of amphibian island gigantism from temperate climates (e.g. green toads, *Bufo viridis* [41] and rice frogs, *Fejervarya limnocharis* [17]). Dichotomous shifts in island body size in mammals have been suggested to be related to taxonomic differences in ecology (e.g. local carrying capacity, resource specificity and/or trophic level) and original mainland body size [2,6], while in amphibians it may be related to an island's climate [17,18]. Island amphibians from more seasonal climates require larger body sizes to account for longer periods of inactivity and shorter reproductive seasons [17], based on the assumption that body size and condition positively correlate with reproductive output [43,44]. If this assertion is accurate, then tropical island toad populations that are active throughout the year, and able to breed over longer periods, may not have the same restrictions on morphology for breeding success during annual breeding events (e.g. a capital breeding strategy [45]). Examinations of the island syndrome have noted that insular populations can show increases in longevity with smaller reproductive outputs [3,10]. If this is also true for guttural toads, then the selective forces maintaining a large body size may have been relaxed, owing to the populations in Mauritius and Réunion engaging in smaller, but more frequent, reproductive bouts (akin to an income-breeding strategy [45]). This hypothesis does require further research into the evolutionary mechanism driving guttural toad's insular dwarfism, as well as uncovering any island-specific changes in life-history strategies and reproductive output.

We also see some variation between sexes and populations in limb and skull sizes, including a significant reduction in jaw length for female toads from Réunion compared with Durban and between-island differences in traits such as male foot length (see electronic supplementary materials for details). The most prominent change, however, was the significant reduction in hindlimb length across both sexes and islands. One possible cause of this could be a shift in selection associated with predator–prey interactions. The absence of the toads' native predators may have relaxed selection on the need to maintain large hindlimbs that provide longer bounds during escape [46–48], which could allow energy to be allocated elsewhere, such as more frequent reproductive events or other physiological processes (akin to the 'enemy release hypothesis' [49]). This reduction in limb length may also be associated with a reduced dispersal ability, similar to trends seen in island birds (e.g. flightlessness), as fitness benefits associated with investments in dispersal are diminished for insular populations [3,9,50]. As such, the reductions in body size and shape may be a result of selective forces favouring a less dispersive morphological phenotype [51]. Further research is required, however, comparing predatory selective pressures between mainland and island populations, as well as research on differences in locomotory performance and behaviour.

Miniaturization has repeatedly evolved within amphibian clades [21,22] and examples of dramatic shifts in amphibian body size have also been seen on islands [17–19,41] and mountains [52], yet these changes are typically reported within the context of thousands or millions of years. Our study suggests that a reduction in body size by up to a third can occur in less than a century—representing an exceptionally rapid expression of this trait. These findings mirror the rapid formation of distinct morphologies arising within lizard populations introduced to islands, either experimentally or through other anthropogenic activities [15,53,54]. If this holds true more broadly across other insular taxa, including those observed in the fossil record, then island-derived phenotypes may arise at a much faster rate than commonly assumed. We hope this study leads to further research attention being given to this relatively understudied invasive amphibian [55] within Mauritius and Réunion, particularly as this toad's introduction to these globally important biodiversity hotspots [28] may yield further insights into the pace at which islands can drive evolution.

Ethics. This work was conducted with authorization from Ezemvelo KwaZulu-Natal Wildlife (Ordinary Permit: OP 4072/2019) and Mauritian National Parks and Conservation Services (NP 46/3 V3), as well as with Stellenbosch University Research Ethics Committee clearance (ACU-2019-10386).

Data accessibility. The datasets and R code for this study are available from Open Source Framework (OSF) at https://osf.io/hw3fm/ (doi:10.17605/OSF.IO/HW3FM) [56].

Authors' contributions. J.B.-G. and J.M. conceived and designed the project. J.B.-G., J.L.R., C.W. and N.P.M. collected the data. J.L.R. led the statistical analysis and drafted the corresponding sections of the manuscript. J.B.-G. led the initial drafting of the manuscript. All authors contributed to, and have approved, the final manuscript and agree to be held accountable for the content of this paper.

Competing interests. We declare we have no competing interests.

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