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Author for correspondence:
Richard Shine
e-mail: rick.shine@sydney.edu.au

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Evolutionary biology

Is the enhanced dispersal rate seen at invasion fronts a behaviourally plastic response to encountering novel ecological conditions?

Lachlan J. Pettit, Matthew J. Greenlees and Richard Shine

School of Life and Environmental Sciences, University of Sydney, Sydney, New South Wales 2006, Australia

LJP, 0000-0002-2628-1416; MJG, 0000-0002-8679-0925; RS, 0000-0001-7529-5657

As a population expands into novel areas (as occurs in biological invasions), the range edge becomes dominated by rapidly dispersing individuals—thereby accelerating the rate of population spread. That acceleration has been attributed to evolutionary processes (natural selection and spatial sorting), to which we add a third complementary process: behavioural plasticity. Encountering environmental novelty may directly elicit an increased rate of dispersal. When we reciprocally translocated cane toads (*Rhinella marina*) among study sites in southern Australia, the transported animals massively increased dispersal rates relative to residents (to an extent similar to the evolved increase between range-core versus invasion-front toad populations in Australia). The responses of these translocated toads show that even range-core toads are capable of the long-distance dispersal rates of invasion-front conspecifics and suggest that rapid dispersal (rather than evolving *de novo*) has simply been expanded from facultative to constitutive expression.

1. Introduction

The speed at which invasive species spread into new areas often increases through time because traits that enhance dispersal rate accumulate in the invasion vanguard [1]. For example, invasion-front individuals may have larger flight muscles (butterflies), feet (voles), wings (beetles) or lighter seeds (conifers) than do conspecifics from range-core areas [2–5]. Invasion-front individuals also may move more often, move further per move and follow straighter paths. The accumulation of dispersal-enhancing traits at expanding range edges has been attributed to evolutionary processes; natural selection (via fitness benefits to faster dispersal [6]) and spatial sorting (via the non-adaptive concentration of 'fast-dispersal' alleles through successive founder events at the leading edge in each generation [7,8]). A third (and complementary) explanation for rapid dispersal at range-edges has been neglected. Rates of dispersal may increase as a direct (behaviourally plastic) response to encountering novel environments at the expanding population edge. Lacking information on the distribution of critical resources (food, water, refuge from predators and abiotic extremes), an individual that finds itself in uncharted waters may benefit from increasing its dispersal rate [9].

To test that idea, we reciprocally translocated invasive cane toads (*Rhinella marina*) among sites, and radio-tracked them to compare the distances travelled by resident animals (released at their original capture site) with translocated individuals (released in an unfamiliar area). Previous research allows us to compare the movements of our experimental animals with those exhibited by 'resident' toads in range-core and range-edge populations [10].
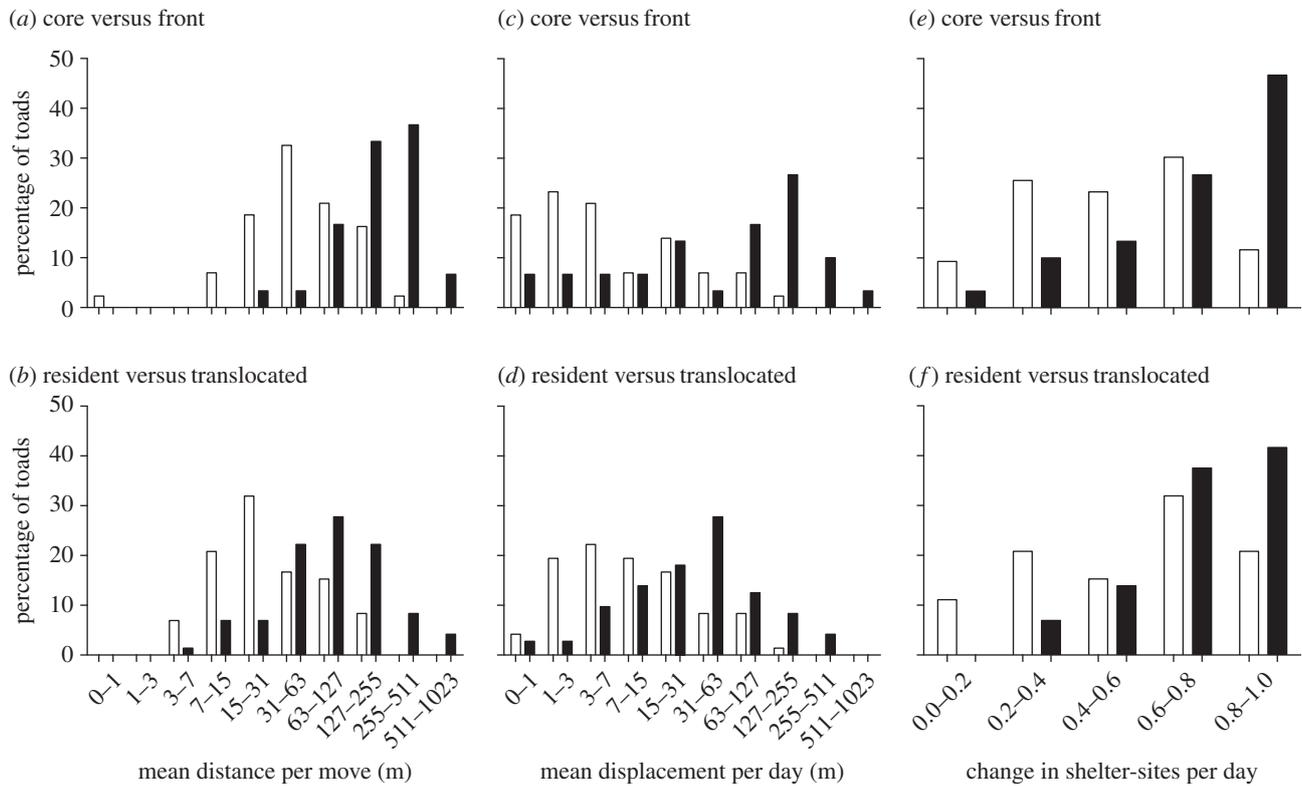
Figure 1. Frequency distributions of dispersal-relevant traits of radio-tracked cane toads. Upper panels (a,c,e) depict change over evolutionary timescales (QLD versus NT), whereas lower panels (b,d,f) show the effects of experimental translocation on toad movements in a single study area (northeastern NSW). Invasion-front toads (NT; filled bars) moved further per move (a), displaced further per day (c) and changed shelter-sites more often (e) than did QLD core-range toads (open bars). In (b,d,f), translocated NSW toads (filled bars) moved further per move (b), displaced further per day (d) and changed shelter-sites more often (f) than did resident NSW toads (open bars). The impact of translocation thus was broadly similar to the divergences seen between range-core and invasion-front toads.

2. Material and methods

Cane toads are large bufonid anurans from Latin America. Released in northeastern Queensland (QLD) in 1935 [11], toads reached our study sites in northeastern New South Wales (NSW) approximately 30 years ago [12]. We radio-tracked toads at eight sites across Yuraygir, Bundjalung and Bungawalbin National Parks, and thereafter located them daily for 5 days. Half of the 144 toads were released at their original capture sites, and the other half were released at a novel site. Orthogonal to that treatment, half the toads were subjected to 48 h of captivity before release (simulating long-distance dispersal by truck), whereas the others were released less than 3 h post-capture. The duration of captivity had less effect than translocation and thus is not incorporated into this analysis (see the electronic supplementary material for details). We quantified distances moved based on daily observations of diurnal shelter locations of toads over 5 days. For comparison, we used data from the study of Alford et al. [10] based on 43 toads tracked for 6–56 days in the species' Australian range-core in northeastern QLD (close to the original 1935 release sites) in 1992–1993, and 30 range-edge toads tracked on a coastal floodplain in the Northern Territory (NT) in 2005. For detailed descriptions of methods and sites, see Alford et al. [10] and the electronic supplementary material.

(a) Analysis

We calculated three dispersal-relevant parameters for each toad: (i) mean distance per move (cumulative distances travelled divided by the number of times a toad changed diurnal shelter site); (ii) mean displacement per day (total linear distance between the release point and final position divided by the number of days; thus, a toad that travelled in a loop would have a displacement of zero); and (iii) changes in shelter sites (the number of shelter sites divided by number of observations). Non-normally distributed data were analysed using Kruskal–Wallis tests. Pairwise comparisons were performed with Steel–Dwass all-pairs tests. All statistical tests were performed in JMP Pro 11.

3. Results

The movement parameters of translocated toads differed from resident toads, to a similar degree as range-edge toads differ from range-core toads (figure 1). Kruskal–Wallis tests showed that the four toad groups (NSW resident, NSW translocated, QLD range-core, NT range-edge) differed in mean distance per move ($\chi_3^2 = 68.5$, $p < 0.0001$), mean displacement per day ($\chi_3^2 = 45.6$, $p < 0.0001$) and the rate of changes in shelter-sites ($\chi_3^2 = 42.2$, $p < 0.0001$). Post hoc Dwass–Steel tests showed that translocated NSW toads resembled range-edge NT toads in mean displacement per day ($Z = 1.65$, $p = 0.35$) and shelter-site changes ($Z = 1.86$, $p = 0.24$), but the NT range-edge toads moved further per move ($Z = 4.35$, $p < 0.0001$). By contrast, resident NSW toads did not differ significantly from range-core QLD toads in daily mean displacement ($Z = 1.59$, $p = 0.38$) but travelled shorter distances per move ($Z = 3.08$, $p < 0.01$), and shifted shelter sites more often ($Z = 2.72$, $p = 0.03$).

The remaining post hoc comparisons supported the general result of the two major groupings described above. Translocated toads moved more often ($Z = 3.95$, $p = 0.0004$), displaced further per day ($Z = 5.12$, $p < 0.0001$)

and moved further per move than did resident NSW toads ($Z = 5.42$, $p < 0.0001$) or QLD range-core toads (mean displacement per day ($Z = 5.06$, $p < 0.0001$); proportion of movements ($Z = 6.26$, $p < 0.0001$); but not mean distance per move ($Z = 2.48$, $p = 0.06$)). Compared with range-edge NT toads, resident NSW animals moved less far per move ($Z = 6.86$, $p < 0.0001$) and displaced less far per day ($Z = 3.93$, $p = 0.0005$), but did not differ significantly in the frequency of shelter-site reuse ($Z = 1.37$, $p = 0.52$). Lastly, our reanalysis of Alford et al.'s [10] data supported their original conclusions: range-edge NT toads moved further per movement than did range-core QLD toads ($Z = 5.49$, $p < 0.0001$), displaced greater distances per day ($Z = 4.03$, $p = 0.0003$) and changed shelter-sites more often ($Z = 3.80$, $p = 0.0008$).

4. Discussion

Behavioural plasticity can influence the impact of evolution on phenotypic traits. For example, selection can modify mean values for a trait by changing an ancestrally facultative behaviour (only elicited by specific stimuli) into one that is permanently expressed. This 'genetic assimilation' [13] has occurred in many evolutionary transitions [14,15].

The rate of toad invasion through tropical Australia has accelerated dramatically, owing to evolved shifts in morphological, physiological and behavioural traits that enhance dispersal rate of individuals in the invasion vanguard [16–19]. Toads collected from the invasion front disperse further and faster than do toads from the range core [20]. Importantly, the offspring of field-collected adult toads raised under standard conditions manifest phenotypic traits (and thus dispersal rates) similar to those of their parents [19–21]. Thus, at least part of the toad acceleration must be owing to evolved (heritable) features of the phenotype.

Nonetheless, behavioural plasticity may also play a role. Rather than the rapid dispersal of invasion-front toads evolving as a novel trait value (not present in the ancestral population), the capacity for long-distance travel clearly is present but rarely manifested in populations of slow-dispersing toads from southern Australia. Despite their normally sedentary habits, the animals massively increased their dispersal rates when translocated to novel habitats. The relevance to invasional accelerations is clear. At an invasion front, individuals are (by definition) moving into novel environments. Like the translocated toads in our experiments, invasion-front toads lack information about the location of suitable sources of food, water or shelter. That situation may stimulate toads to move further per day than in familiar habitats.

But if range-core toads are capable of long-distance movement, why did the acceleration of invasion not occur until decades after toads first began spreading from coastal Queensland [16]? Plausibly, early colonists increased their dispersal rates in response to environmental novelty, yet were unable to sustain movements for long enough to increase the rate of range expansion. If so, the capacity to maintain rapid dispersal was the critical trait that evolved during the toad's invasion trajectory. Consistent with this idea, toads at the invasion front spend more time in 'dispersive mode' [22].

Our radio-tracking did not continue for long enough to detect any exhaustion or habituation effects. Presumably, translocated toads would eventually view their new homes as no longer novel, and thus reduce their movements. In re-introductions of endangered animals, familiarity with a site (gained by 'soft release' methods prior to actual release) reduces subsequent dispersal distances [23]. Hence, invasive toads may have evolved a diminution of that habituation response. That is, range-core toads only exhibit long-distance dispersal when encountering novel conditions; but invasion-front toads maintain a high dispersal rate regardless of environmental conditions. Repeating the translocation study on toads at the invasion front would be of great interest. We predict that such a manipulation would have little effect, because the animals there already encounter novel situations on a daily basis, and also may be dispersing at close to maximal rates [24].

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