

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

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METHODS

Translocation trials

Adult cane toads (snout-urostyle lengths > 85 mm [mean \pm SE = 139.4 \pm 5.3 mm], mass range 70–513 g) were reciprocally translocated in a series of trials between October 2015 and January 2016 among four heath and four woodland sites in the Northern Rivers region of New South Wales (NSW), Australia (Table 1).

Table 1. *Descriptions of sites used in cane toad (Rhinella marina) translocation telemetry trials in the Northern Rivers region of NSW. The “translocated” column displays the number of toads translocated from that site, and the numeral in parentheses is the site ID (from the second column) to which toads were translocated.*

National Park	(ID) Site	Latitude	Longitude	Habitat	Translocated
Bungawalbin	(1)Ironbark trail	29°05'05"S	153°07'35"E	Woodland	4 (2)
Bungawalbin	(2)Lagoon trail	29°05'49"S	153°09'41"E	Woodland	4 (1), 4 (3)
Bundjalung	(3)Mororo east	29°20'24"S	153°15'30"E	Woodland	4 (2), 5 (4), 4 (5), 4 (7)
Bundjalung	(4)Lewis lane	29°21'13"S	153°13'24"E	Woodland	4 (3), 4 (5)
Yuraygir	(5)Redcliff road	29°34'28"S	153°19'30"E	Heath	4 (3), 4 (4), 4 (7), 3 (8)
Yuraygir	(6)Coastal road	29°34'56"S	153°19'28"E	Heath	1 (8), 3 (7)
Yuraygir	(7)Quarry road	29°36'48"S	153°18'53"E	Heath	4 (3), 4 (5), 4 (6)
Yuraygir	(8)Bosches road	29°37'20"S	153°18'53"E	Heath	4 (5)

For each trial, we hand-collected four toads at night from two sites and kept them in captivity (placed in calico bags with woodchips, housed in an insulated box [28 x 30 x 56 cm], experienced two to four h of vehicle transport) for ~ 48 hours (high transport stress). A further four toads were collected from the same sites two nights later (low transport stress). Upon collection, we weighed and measured each toad and attached a radio-transmitter (PD2; Holohil, Ontario, Canada) and iButton temperature logger (model DS1921G-F5; Maxim Integrated Products, Sunnyvale, CA), with the combined mass (< 7 g) below the

recommended limit of < 10% of total body mass [1]. Immediately following the second collection, toads from both transport stress treatments were randomly assigned to a “resident” or “translocated” treatment. “Resident” toads were returned to their original site and capture location, while “translocated” toads were reciprocally translocated between paired sites.

In total, 144 (90 female, 54 male) toads were included in trials, with approximately equal numbers exposed to a low *versus* high transport stress treatment and released to a familiar *versus* novel site in heath *versus* woodland habitats (Table 2). Trial order was randomised to remove any confounding effects of season. We quantified toad dispersal traits over five days based on daily observations of diurnal shelter locations.

Table 2. *Number of resident and translocated toads used in trials within each habitat combination and mean translocation distance. An equal number of toads were exposed to low and high transport stress treatments throughout each group, except that 12 of 23 toads translocated heath to heath, and 13 of 25 translocated woodland to woodland, were “low stress”.*

Trial Type	Residents	Translocated	Mean translocation distance (km)
Heath to heath	24	23	4.6
Woodland to woodland	24	25	11.2
Heath to woodland	12	12	28.9
Woodland to heath	12	12	28.9

Range-core and range-edge toads

We obtained data on dispersal from the cane toad radio-tracking trials (tracked for 6-56 days) reported in Alford *et al.* [2]. We assigned two Northern Queensland populations tracked in 1992-93 as range-core toads, and one population of Northern Territory toads tracked at the invasion front in 2006 as range-edge toads.

Analysis - Translocation trials

We calculated three dispersal-relevant parameters for each toad: (1) mean distance per move (cumulative distances travelled divided by the number of times a toad changed diurnal shelter site); (2) mean displacement per day (total linear distance between the release point and final position divided by the number of days; such that a toad that returned to its initial release point by the end of the five-day period would receive a score of zero); and (3) daily rate of changes in shelter-sites (the number of shelter sites divided by number of observations).

The main text provides results of analyses that include both toads used in the current study, and those tracked in the earlier study by Alford et al. [2]. Here, we present analyses based on toads from the current study only, and incorporate duration of retention prior to release as an additional factor.

We used linear mixed effects models fit by restricted maximum likelihood estimation (REML) to explore the main effects of simulated transport stress (low or high), translocation status (resident or translocated) and their interaction on the transformed dispersal-related variables; $\log_{10}(1 + \text{mean distance per move})$, $\log_{10}(1 + \text{mean displacement per day})$, $\arcsin \sqrt{\text{change in shelter-sites}}$. Collection site and release site were included as random effects to account for variation between sites. Transformations allowed data to meet parametric test assumptions with the exception of change in shelter-sites where normality could not be achieved (Shapiro-Wilk $P < 0.05$). Results are robust to violations of normality provided sample sizes are large [3, 4].

RESULTS

Toads translocated to novel habitats moved further per move [resident - low stress mean = 48.1m (8.5 SE); resident – high stress 45.2 m (8.5 SE); translocated – low stress 92.0 m (12.9 SE); translocated - high stress 158.3 m (27.3 SE)], displaced further per day [resident - low stress 19.1 m (4.6 SE); resident – high stress 19.1 m (4.2 SE); translocated – low stress 35.2 m (5.9 SE); translocated - high stress 83.4 m (15.9SE)] and changed shelter sites more frequently [resident - low stress 0.65 (0.05 SE); resident – high stress 0.66 (0.04 SE); translocated – low stress 0.80 (0.03 SE); translocated - high stress 0.85 (0.03 SE)] than did resident toads (all $P < 0.0001$; Table 3). Toads that experienced high transport stress displaced further per day ($P = 0.04$), but mean distances per move and changes in shelter-sites were not significantly different to those seen in low-transport-stress toads, nor was there a significant interaction between translocation and transport stress (all $P > 0.05$).

Table 3. *Main effects of transport stress and translocation on the transformed mean distance per move, mean displacement per day and changes in shelter-sites of adult cane toads (Rhinella marina). Collection site and release site were included as random effects. Boldface font denotes significant results ($P < 0.05$). Untransformed values are reported in-text for ease of interpretation.*

	df	<i>F</i>	<i>P</i>	Parameter estimate	Standard error
Mean distance per move					
Translocation	1, 129.9	40.94	<0.0001	0.2178	0.0340
Transport	1, 129.8	1.63	0.20	0.0434	0.0340
Translocation x transport	1, 129.8	3.33	0.07	0.0621	0.0340
Collection site				0.0011	0.0060
Release site				0.0078	0.0093
Mean displacement per day					
Translocation	1, 135.1	33.69	<0.0001	0.2426	0.0418
Transport	1, 135.1	4.35	0.04	0.0872	0.0418
Translocation x transport	1, 135.1	2.97	0.09	0.0720	0.0418
Collection site				0.0017	0.0054
Release site				0.0030	0.0077
Changes in shelter-sites					
Translocation	1, 129.4	18.33	<0.0001	0.1153	0.0269
Transport	1, 129.3	1.09	0.30	0.0282	0.0269
Translocation x transport	1, 129.3	0.50	0.48	0.0191	0.0269
Collection site				0.0010	0.0054
Release site				0.0074	0.0082

Data accessibility: Data available from the Dryad Digital Repository:

<http://dx.doi.org/10.5061/dryad.bk5s3> [5]

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