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Resources and their distribution can influence social behaviour at translocation sites: lessons from a lizard.

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Abstract

In a translocation program, the social interactions among released individuals can influence both the stress levels and the tendency for the individuals to remain at the site where they have been released. In hard releases stress from social interactions may lead to early dispersal away from the release site. In soft releases, where individuals are confined together for periods of time at the release site, before ultimate release, stress levels from social interactions may become even higher as individuals are unable to move away. In this study we investigated how the abundance and distribution of a fundamental habitat resource, refuge burrows, can influence social behaviour, probable stress levels, and subsequent translocation success, of the endangered Australian pygmy bluetongue lizard, *Tiliqua adelaidensis*, in simulations of translocation releases. We suggest that understanding the social organization of any endangered species, and whether it can be manipulated, will be an important component of planning a translocation release program.

Keywords: Behaviour, *Tiliqua adelaidensis*, Burrow density, translocation, burrow layout

Introduction

A common aim of conservation management is to maintain or increase the local population density of an endangered species, at presently occupied sites, or at currently unoccupied sites, and translocation or reintroduction programs are commonly considered (Crandall, Bininda-Emonds, Mace *et al.*, 2000; Fernández-Olalla, Martínez-Abraín, Canut *et al.*, 2012; Todd, Nicol & Koehn, 2004). In translocations, a potential dilemma is that, on the one hand, high densities among the group of individuals released, could increase the chance that at least some individuals might survive, persist at the release site, and establish a new population or contribute to the existing population. But, on the other hand, a high release density could increase competitive and social interactions among the released group, or with existing conspecific residents. Those interactions might increase levels of stress, and increase the chance of rapid dispersal away from the release site (Anders, 2006; Fletcher, 2007; Goymann & Wingfield, 2004; Morris, 2003), or reduce fecundity and juvenile survival among individuals that stay (Clutton-Brock, Albon & Guinness, 1987). For instance, we previously reported that reducing supplementary food caused lizards, newly introduced to an area, to stay active more, to spend more time basking, and to disperse more quickly from a simulated translocation site (Ebrahimi & Bull (2012). Here we focus on the short period immediately following a translocation release, and the social interactions in that period that might determine whether an individual will stay close to where it is released or disperse away from the release site.

Animal social interactions can be affected by a range of ecological factors (Alexander, 1974; Bronikowski & Altmann, 1996; Lancaster, Jessop & Stuart-Fox, 2011) such as shelter, food and vegetation density (Graves & Duvall, 1995; Johnson, Kays, Blackwell *et al.*, 2002; Tanner & Jackson, 2012). Adverse social interactions, affecting translocation success, might be reduced by manipulating one or more of those factors. Understanding the influence of habitat resource distribution and availability is crucial. A low density of resources could increase the frequency of social interactions (Lancaster *et al.*, 2011). For instance solitary scorpions, under conditions of reduced shelter and food, increased their agonistic interactions, leading to an increase in mutilations and deaths, (Warburg, 2000). The level of social stability in animals can be influenced both by the level of available resource, and by the way the resource is distributed (Carr & Macdonald, 1986; Ditchkoff, Saalfeld & Gibson, 2006; Reynolds & Bruno, 2013).

Successful translocations aim to keep the initial group of individuals in habitat close to the release site (Mihoub, Robert, Le Gouar *et al.*, 2011; Rickett, Dey, Stothart *et al.*, 2013). Dispersal is likely to take animals to poorer habitat, to disperse individuals and make it harder for them to find mating partners, and to make monitoring the success of the management strategy more difficult. To achieve this low dispersal goal, one factor we need to understand is how the spatial distribution of resources within a release location affects social interactions and the tendency of individuals to remain where they are released. From a management perspective we need to know whether we can manipulate the distribution of resources to improve retention success.

As in many other animal translocations, reptiles tend to disperse from the site where they are released (Dodd & Seigel, 1991; Germano & Bishop, 2009). Additionally, the social system of many reptile species is primarily solitary (Leu, Kappeler & Bull, 2011; Visagie, Mouton &

Bauwens, 2005), meaning that aggregations following translocation release are likely to induce dispersal. Lizards also live in heterogeneous habitats, for instance requiring both shelter refuges and open areas for thermal basking (Gálvez-Bravo, Belliure & Rebollo, 2009), so will need a complete range of their habitat resources at release sites.

We investigated these issues in simulated translocation releases of the endangered pygmy bluetongue lizard, *Tiliqua adelaidensis* in South Australia. The lizards currently occupy a few isolated fragments of native grassland, with genetic evidence suggesting very little recent migration between patches (Smith, Gardner, Fenner *et al.*, 2009). Fordham, Watts, Delean *et al.* (2012) have shown that, for realistic climate change scenarios, translocations may be the best management option to retain viable populations of this endangered species into the future.

An essential resource for this species is the single entrance, narrow, vertical burrows, constructed by lycosid and mygalomorph spiders, which the lizards use as refuges. They spend most of their time either refuged in the burrow, or using the burrow entrance to bask, and as an ambush site to catch their invertebrate prey (Hutchinson, Milne & Croft, 1994; Milne, Bull & Hutchinson, 2003b). They rarely leave their burrows, even during aggressive burrow defence against rival conspecifics (Fenner & Bull, 2011). Artificial burrows added to current population sites augment existing populations (Souter, Bull & Hutchinson, 2004) and could be provided at a release site in a translocation program. In that case a successful translocation would rely on the lizards remaining within an area where burrows were provided.

In our study we used artificial burrows as the resource, and investigated how the availability and distribution of burrows affected the behaviour of lizards in simulated translocation releases. We were specifically interested in the immediate responses of lizards in the first days after a release, and examined aspects of their behaviour and tendency to move. Our aim was to develop an understanding about the design of a release site, and the location of resources within that release site, that might minimise the chance of lizards moving from the site, or experiencing stressful social interactions at the site, in the days immediately following the release.

Methods

We used 16 *T. adelaidensis* (8 male and 8 female) that had been captured from two populations near Burra, South Australia (33° 42' S, 138° 56' E), and held in individual plastic boxes (52.5 × 38 × 31) at room temperature (25 °C) and fed excess meal worms.

We conducted three experiments using four circular cages (15 m diameter) that were located in the grounds of Monarto Zoo, South Australia (35° 06' S, 139° 09' E). Each cage had a 1 m high-galvanised iron wall and bird-proof wire roofs. The four cages were located in a line, about 5 m apart. Throughout each experiment, lizards were confined to a central 4 m diameter circular area within each cage using a 20 cm high black plastic wall (Ebrahimi & Bull, 2013). We constructed artificial burrows from 30 cm lengths of 3 cm diameter wooden dowling with a 2 cm diameter hole drilled out of the centre. In previous studies lizards have readily accepted these artificial burrows both in the field and in cages (Ebrahimi, Fenner & Bull, 2012; Milne, Bull & Hutchinson, 2003a). We used an auger to make 30 cm deep and 3 cm diameter holes in the ground and hammered the artificial burrows into these holes until they were flush with the ground surface. The number and arrangement of burrows in the central part of each cage varied with the treatment in each of three experiments, as described below.

In these experimental conditions we were attempting to simulate the conditions in the first few days of a soft release translocation. Although the confined area that we used of just over 12 m^2 was small, lizards in natural populations rarely move more than a few centimetres from their permanent burrow refuge, and agonistic interactions only occur when conspecifics approach to within 5 cm of an occupied burrow (Fenner & Bull, 2011). Our broad hypothesis was that social interactions would be most likely during the first few days after release, as the lizards establish their burrow ownership, and that the density and the arrangement of the burrows in the release site will influence the intensity of those social interactions, and the subsequent levels of normal behaviours in the lizards.

The first experiment tested the effect of burrow density on lizard behaviour. The alternate treatments are shown in Fig 1A and 1B. Two cages had high burrow density. We distributed 41 artificial burrows evenly around the central area, as previously described (Ebrahimi & Bull, 2012), one in the middle, and then 8, 16 and 16 burrows in three concentric rings. In this arrangement burrows were on average 63 (SE = 0.01) cm apart. The other two cages had low (10) burrow density, with 2, 4 and 4 artificial burrows in three concentric rings, and spaced between 100 and 120 cm apart. For this experiment, we ran three four day trials in each cage. Each trial commenced at 0700 h on the first day, when four lizards were released at the same time onto the ground in the centre of the experimental area of the cage. The three sets of trials in this first experiment started on Jan 13, Jan 19 and Jan 25, 2010. Lizards were returned to their plastic boxes, and were fed three mealworms for the two days between trials. For each trial there were different combinations of four lizards in each cage, selected from the 16 available lizards, although individual cages retained their treatment status across trials.

In the second experiment we tested the effect of the closeness of the release locations to each other. The alternate treatments are shown in Fig 1C and 1D. Each cage had 41 burrows in the experimental area. In two cages the 41 burrows were arranged in concentric rings as in the high density treatment of experiment one, and three lizards were released at the start of each four day trial into three burrows, in a triangular formation, that were 150 cm from each other. In the other two cages, 38 burrows were arranged as above, but lizards were released into three additional burrows that had been moved to a central triangular formation, within 50 cm of each other. Three sets of trials started on Feb 2, Feb 8 and Feb 14 2010 with lizards removed from the cages for two days in between trials as before. For each trial, there were different combinations of three lizards for each cage, selected from the 16 lizards.

The third experiment considered the influence of burrow clustering. The alternate treatments are shown in Fig 1E and 1F. Each cage had 41 burrows. Burrows in two cages were evenly spaced as before (63 cm apart), while burrows in the two other cages were clustered. For clustering, we placed one burrow at each apex of a centrally located equilateral triangle with 2.5 m sides. Then we placed nine burrows 10.4 cm apart around the circumference of a 15 cm radius circle around each apex, creating three clusters of 10 burrows. Another 11 burrows were placed singly around the experimental area, each 75 cm from any other burrow . At the start of trials, three lizards were released in each cage 250 cm apart in the three apex burrows of the clustered arrangement, and 150 cm apart as in experiment two, in the evenly spaced burrow arrangement. Thus lizards were initially released further apart in the clustered burrow treatment than in the evenly spaced burrow treatment. Three trials started on Mar 5, Mar 11 and Mar 17, 2010. The selection of three lizards for each trial was the same as in experiment two.

Note that all of the experiments were conducted several months after the spring mating period for these lizards (Oct-Nov) (Fenner & Bull, 2009; Hutchinson *et al.*, 1994) and we did not consider that sexual differences played an important part in the responses we observed. We consider that this period of the year would be the optimal time for translocations as stressful interactions involved with mating behaviour would be infrequent.

We mounted four surveillance cameras (Longse: LICS23Hf, 3.5 mm lens) above the central area of each cage, with a combined field of view that covered the entire experimental area. On each day of each trial we used the cameras to record all lizard activity during daylight hours from 0700 to 1800 h onto a 16-channel h.264 DVR (ESW26), powered by four 12 V batteries. From the playback, we derived seven behavioural parameters that allowed us to compare the behaviour of the lizards in each treatment. These were total activity time, basking time, number of movements, number of burrow changes, the number of fights, the mean distance between lizards, and the distance between burrows when there was a burrow change.

Activity time was defined as the period from when the lizard head first emerged from a burrow in a day to when the lizard retreated into its burrow for the last time on that day. In this definition activity time could include periods when the lizard had retreated into a burrow during the day, if it subsequently re-emerged later on the same day. In the first experiment, in which lizards were released onto the ground early on the morning of the first day, we allowed lizards to retreat to their first burrow before starting to monitor for the first emergence. We defined basking as when a lizard remained partly emerged at its burrow entrance. We calculated basking time (min h^{-1}) as the time (in minutes) that a lizard spent basking in a day, divided by 11, the number of hours filmed per day. Basking time did not include time when the lizard had retreated into its burrow.

We defined a lizard as having moved if it fully emerged from the burrow and then retreated to same burrow. During movements, we observed lizards walking around their burrow, basking while fully emerged, foraging for invertebrate prey, or defecating. We counted the number of times that each lizard made one of these movements on each day in each trial. We defined a lizard as changing burrows if it emerged from one burrow, and then located, and retreated into another burrow. When two lizards approached each other on the ground surface, there was always an agonistic interaction involving the lizards scuffling, or one running from the other. We counted each agonistic interaction as a fight. For distance between lizards, we located the burrow occupied by each lizard at the end of each day, in each cage, and took the average of the distances between each pair of individuals. Finally we measured the straight-line distance between burrows following a burrow change, and derived two measures for a lizard if it made two or more burrow changes in a day, the sum of all of the distances moved in the day, and the average distance of each move. We used both measures in separate analyses, and found no difference in the results, so here only report results using the average distance per move. .

We derived parameter values from each of the four days of video recording in each trial. We conducted preliminary analyses using mixed effects models, and including individual lizards as a random factor, and found no significant effect of either individual lizards or of lizard sex on the behavioural parameters in any of the three experiments. We then used repeated-measures analysis of variance (ANOVA) for each behavioural parameter, in each experiment, with day (1-4) and trial (1-3) as within- subjects factors and treatment (burrow density (experiment one), release location (experiment two) and burrow clustering (experiment three)) as the between-subjects factors. In these analyses, we used the Greenhouse-Geisser correction where data were non- spherical.

Because the same lizards were used, although in different combinations and in different cages, in all three trials of experiment one, and because we selected 12 of the 16 lizards for each trial in the last two experiments, lizards may have become familiar with the experimental layout as the trails progressed. If that familiarity influenced their responses to the alternative experimental treatments in each experiment we would have expected to see significant trial x treatment interaction effects from the analyses.

Continuous temperature records were taken every day by two digital thermometers, placed in the shade at each end of the line of cages. We also used temperature recordings from a weather station at Pallamana Aerodrome (35° 04' S, 139° 13' E), 10 km from Monarto Zoo.

Results

Among the lizard behaviours recorded in each experiment, basking was consistently the most commonly observed, and fighting the least commonly observed (Table 1).

Although the analyses (Table 2) showed a number of significant relationships between behavioural parameters and day or trial number, there were no correlations with ambient temperature (using either the daily mean, the daily maximum or the daily minimum temperature). Nevertheless we believe those significant effects of trial and day represented differences in ambient conditions or in the physiological condition of the lizards over different times.

Table 2 also shows no significant interactions between treatment and trial for any behavioural parameter in any experiment. Any increasing familiarity with the experimental arrangement over successive trials in an experiment, did not influence the responses of the lizards to the alternative treatments.

Experiment 1

The number of movements, the number of burrow changes, and the distance of burrow changes all showed significant main effects of burrow density (Table 2). Lizards moved more (3.73 ± 0.02 moves/lizard/day) but changed burrows less (0.06 ± 0.006 changes/lizard/day) when burrows were at low density, than when burrows were at high density (1.88 ± 0.02 moves/lizard/day; 0.50 ± 0.008 changes/lizard/day). When lizards changed burrows the distance moved was further when burrows were at low density (101 ± 0.09 cm), than when burrows were at high density (215 ± 0.08 cm). Activity time and basking time were not affected by the experimental treatment, although they varied among days (as did the changing burrow distance), or on different days among trials (Table 2), probably as a result of differences in ambient conditions. For distance between lizards at the end of each day, there was a significant three way interaction (burrow density x trial number x day; Table 2). This reflected a trend at least in trial 1, for lizards to move further apart from each other between day one and day two in the high density burrow treatment, while those separations had already been achieved by the end of day one in the low burrow density treatment (Fig 2). Mean distance between pairs of the four lizards in each cage seemed to stabilise by day 4 at between 1.4 – 1.8 m apart in all treatments and trials.

Experiment 2

In the second experiment there were significant main effects of treatment for two behaviours (Table 2). Lizards changed burrows more often (0.97 ± 0.01 changes/lizard/day) and had more fights (0.04 ± 0.004 fights/lizard/day) when they were released closer to each other, than when released further apart (0.22 ± 0.009 changes/lizard/day; 0.003 ± 0.001 fights/lizard/day). There was no interaction effect with day of trial, indicating that these differences remained consistent even after the lizards were allowed time to adjust their spatial proximity. The number of moves had a significant treatment x day effect (Table 2), with lizards released closer to each other always moving more, but that difference changing with the day of the experiment (Fig 3a). Similarly, distance between lizards had a significant treatment x day effect (Table 2) with lizards released closer together increasing their distance apart over successive days, while those released far apart retained that distance over the four day trials (Fig 3b). The three lizards in each cage achieved mean separations of between 1.4 and 1.8 m by the end of day 4, although those released closer, were still closer together by day 4 (Fig 3b). Activity time, basking time and distance moved when changing burrows were not significantly affected by the treatment in these trials, only varying with day and trial number, as in experiment one.

Experiment 3

In this experiment there were significant main effects of treatment on basking time, movement and distance moved when changing burrows (Table 2). Lizards spent more time basking (22.04 ± 0.06 min/h^{-1}) and made fewer movements (2.94 ± 0.04 moves/lizard/day) in the clustered arrangement (when lizards were released further apart), than in the evenly spaced arrangement (11.68 ± 0.06 min/h^{-1}; 5.66 ± 0.04 moves/lizard/day). When lizards changed burrows they moved shorter distances when burrows were clustered (41.9 ± 0.30 cm) than when burrows were evenly spaced (106.81 ± 0.30 cm). There were also significant day x treatment effects for the number of burrow changes, for the number of fights and for the distance apart between lizards (Table 2). In each case the largest difference between treatments was on day 1, with reduced differences on later days (Fig 4). Thus there were more burrow changes (Fig 4a), less fights (Fig 4b), and greater distance apart (Fig 4c) on day 1 when burrows were clustered. Other effects of day and trial probably reflected changes in ambient conditions.

Discussion

Reptile species often select habitats based on the availability and quality of refuge shelters (Beck and Jennings, 2003, Heatwole, 1977, Pianka, 1966) and for many species, the because many of the availability of permanent, secure refuges is crucial for their persistence (Langkilde, Connor and Shine, 2003). For a wider range of taxa, the provisioning of release sites with adequate refuge resources will be a vital component of the success of any translocation program, particularly in the period soon after release when individuals are adjusting to novel features of the releases site (Gedeon, Boross, Németh *et al.*, 2012, Griffith, Scott, Carpenter *et al.*, 1989).

Our first experiment reflected this requirement for abundant refuge resources. When lizards were presented with low burrow densities in experiment 1, they made more movements out and back to the same burrow, changed burrows less often, but moved further when changing burrows than at high burrow densities. With more available burrows, lizards were probably more confident they could quickly assess closer unoccupied alternatives. Those burrow changes in both treatments led to a stabilisation of distance apart over the four days of the each trial.

One of the important problems in any translocation attempt is the stress of the released individuals soon after the release (Mihoub et al., 2009). One specific cause of stress can be from agonistic interactions with conspecifics (Drake et al., 2012; Letty et al., 2000; Teixeira et al., 2007). This stress can lead to post-release movement in the release habitat, with more exposure to climatic extremes and to predators, and more movement away from the release site. Examples of this include translocated birds (Kemink and Kesler, 2013) and snakes (Reinert and Rupert, 1999). The way that the available refuges are organised in a release site may have an important influence on the level of stress. Too few refuges, or refuges spaced too close together may lead to more frequent interactions for refuge ownership and higher stress levels.

In our experiment 2, with burrow density kept stable , lizards released closer to each other had more fights, more movements out and back to the same burrow, and more burrow changes than lizards released further apart. They reacted to the proximity of conspecifics with aggressive social behaviours, and with increased movement patterns that would put them at increased risk from predation. Again the burrow changes led to them ending further apart, particularly among the lizards released close together. In experiment 3 the clustered treatment had lizards both with a higher local density of burrows and with a greater initial distance apart than the evenly distributed burrow treatment. In the clustered arrangement, lizards moved in and out of their burrows less and basked more, suggesting they were less stressed, and more likely to settle where released. Confirming that interpretation, although the lizards with clustered burrows changed burrows more often on the first day of trials (as lizards did with higher burrow density in experiment 1) they had fewer fights with conspecifics and retained a distance apart of just over 200 cm, a level of separation that the lizards in evenly spaced burrows also rapidly achieved in this experiment. This was presumably achieved by the evenly spaced lizards (that were initially closer together) moving further when they changed burrows.

In summary our results suggested that pygmy bluetongue lizards rapidly adjust to the local density of burrows and to the proximity of conspecifics in those burrows. Any movements to change burrows in a real release will increase both exposure to predation, and the likelihood that lizards will leave the area where burrows have been provided and find themselves in habitat with less suitable refuges, thus reducing the chance of success of the translocation. Our experiments showed that lizards may be more likely to remain in the area where they are released if there is a high local density of burrows, so that exploratory moves can be short and secure, and if the distance apart from released conspecifics is relatively high, to reduce stress from agonistic interactions. In our study lizards basked more, a sign of unstressed behaviour, when released at 250 cm apart, than at closer distances.

More generally the study suggested that in any translocation program, resource availability and distribution at the release site could have profound and significant influences on behaviour of the released individuals in the critical first days after release in a new site. Other studies have indicated that low density of resources can encourage dispersal and migration in a range of different species (Bowler and Benton, 2005, Morales and Ellner, 2002, Wiener and Tuljapurkar, 1994). Specifically, Beck and Jennings (2003) reported that lizards were more likely to disperse from natural habitats with fewer shelter sites, or with poorer quality refuges, and a low density of shelter, food and other resources can increase agonistic interactions, stress and corticosterone levels (Lancaster *et al.*, 2011, Warburg, 2000).

If translocated animals are initially confined to familiarise themselves with local conditions, as in the soft release strategy often advocated for translocations, high local density may increase the chance of adverse social interactions. If we understand, for any species, how resource distributions at the release site can affect levels of interactions, then manipulations may become possible (Gedeon et al, 2012) to reduce the impact of those interactions on the stress both within an enclosure and at the wider release site. Our study suggests a benefit of exploring resource distributions at a release site before the translocation release is initiated, for a wider range of animal species where translocation strategies are being explored.

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Table 1. Number of cases of each activity recorded during each experiment.

Experiment	Activity				Total
	Basking	Movement	Changing burrows	Fights	
One	474	308	21	4	807
Two	381	378	65	6	830
Three	438	255	126	7	826

Table 2. Result of repeated-measures analyses of variance for each behavioural parameter in each experiment. Significant P value indicated in bold

	Effect		Activity time		Basking time		Movement		Burrow change		Fights		Distance of movement		Distance from conspecific		
		df	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	df	*F*	p
Experiment One	Treatment	1,14	2.54	0.133	2.11	0.168	5.20	**0.039**	6.85	**0.020**	3.50	0.082	6.41	**0.024**	1, 22	0.98	0.333
	Day	3,42	1.15	0.340	0.61	0.610	1.61	0.199	0.95	0.423	3.50	0.082	5.06	**0.004**	3, 66	7.14	**0.001**
	Trial	2,28	2.65	0.088	5.29	**0.024**	0.16	0.847	1.34	0.276	1.40	0.263	0.19	0.826	2, 44	1.34	0.270
	Day x treatment	3,42	0.64	0.592	0.76	0.520	0.61	0.612	1.26	0.300	3.50	0.082	0.35	0.788	3, 66	0.89	0.450
	Trial x treatment	2,28	0.80	0.458	0.67	0.518	1.20	0.314	0.08	0.992	1.40	0.263	0.29	0.745	2, 44	0.12	0.885
	Day x trial	6,84	5.75	**0.001**	2.69	0.078	0.43	0.852	1.46	0.245	1.40	0.224	1.95	0.082	6,132	6.73	**0.001**
	Day x trial x treatment	6,84	0.67	0.667	0.71	0.639	0.02	1.00	0.70	0.644	1.40	0.224	0.90	0.497	6,132	2.85	**0.012**
Experiment Two	Treatment	1,10	1.86	0.203	0.80	0.390	0.14	0.708	6.30	**0.033**	14.4	**0.003**	3.93	0.075	1,10	30.5	**0.001**
	Day	3,30	5.60	**0.004**	3.62	**0.024**	3.41	**0.030**	0.23	0.869	1.41	0.259	1.15	0.345	3,30	5.85	**0.003**
	Trial	2,20	0.17	0.838	0.16	0.847	1.48	0.251	2.31	0.128	0.15	0.861	0.48	0.626	2,20	1.69	0.209
	Day x treatment	3,30	0.29	0.830	0.27	0.846	5.62	**0.004**	0.23	0.869	1.61	0.208	0.19	0.899	3,30	4.73	**0.008**
	Trial x treatment	2,20	1.07	0.361	1.81	0.189	0.73	0.492	1.75	0.201	0.67	0.523	0.73	0.492	2,20	1.10	0.352
	Day x trial	6,60	4.48	**0.023**	3.76	**0.003**	0.67	0.668	2.36	0.120	1.61	0.208	3.97	**0.002**	6,60	0.26	0.952
	Day x trial x treatment	6,60	0.21	0.971	0.72	0.635	0.75	0.609	2.07	0.081	1.37	0.238	0.45	0.824	6,60	0.38	0.889
Experiment Three	Treatment	1,10	2.88	0.120	6.94	**0.025**	5.58	**0.040**	0.40	0.541	2.96	0.116	13.4	**0.004**	1,10	19.3	**0.001**
	Day	3,30	3.10	0.103	11.0	**0.001**	11.7	**0.001**	12.6	**0.001**	2.93	0.091	9.03	**0.001**	3,30	6.56	**0.002**
	Trial	2,20	0.15	0.858	4.05	**0.033**	0.16	0.851	0.57	0.575	1.81	0.327	1.21	0.316	2,20	1.43	0.262
	Day x treatment	3,30	0.72	0.545	0.78	0.515	0.54	0.656	3.26	**0.035**	2.93	**0.040**	0.48	0.695	3,30	3.95	**0.017**
	Trial x treatment	2,20	1.32	0.289	0.34	0.714	0.72	0.496	0.83	0.448	1.81	0.327	1.21	0.318	2,20	0.40	0.675
	Day x trial	6,60	0.92	0.486	2.45	0.081	1.31	0.356	0.72	0.493	2.38	0.052	4.17	**0.014**	3,30	0.72	0.628
	Day x trial x treatment	6,60	133	0.259	2.24	0.051	1.65	0.148	1.51	0.188	2.38	0.149	3.56	**0.026**	3,30	0.89	0.506

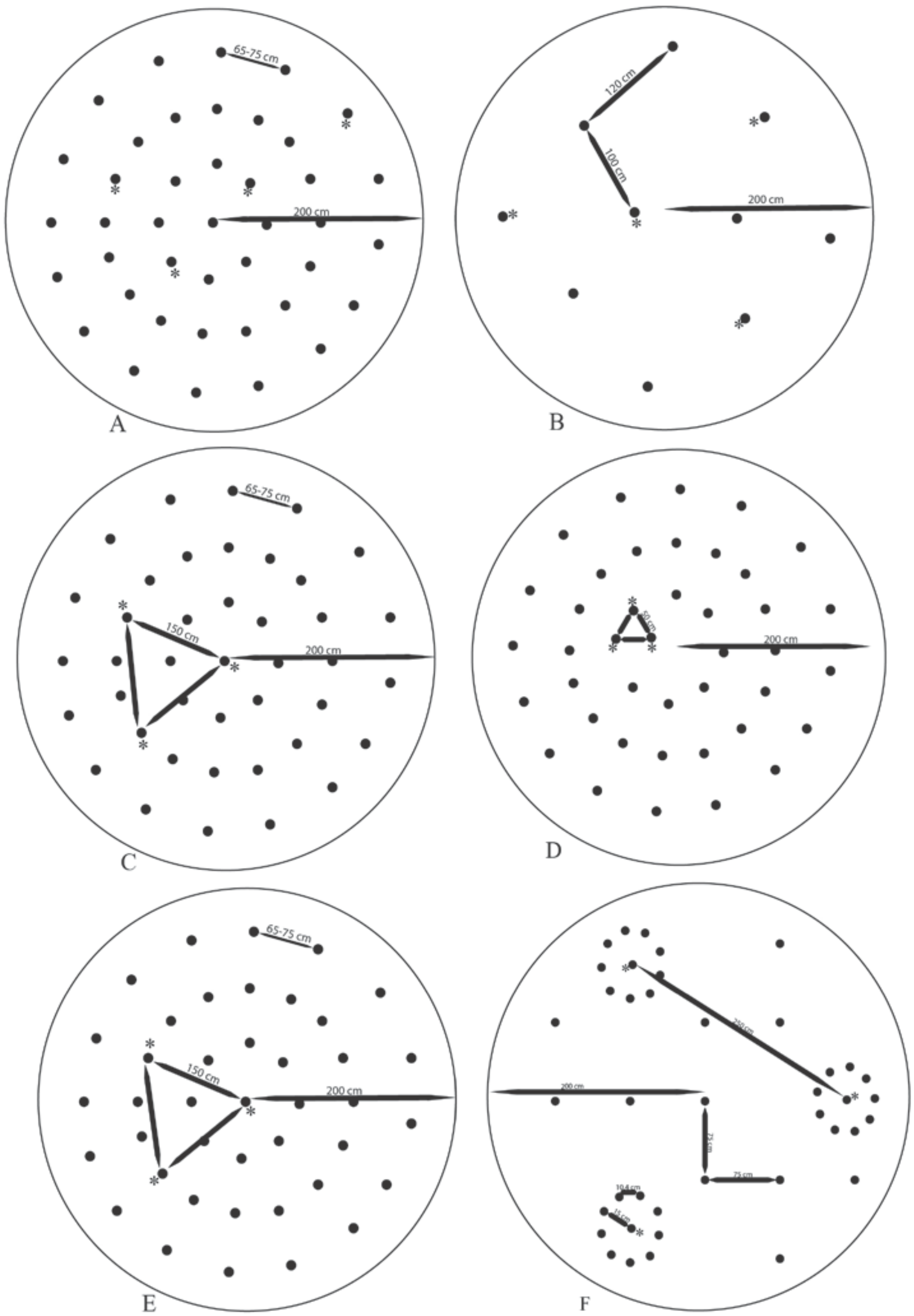

Fig 1. Layout of the two treatments in each experiment. Experiment 1, A and B; Experiment 2, C and D; Experiment 3, E and F. Stars near burrows are the release points.

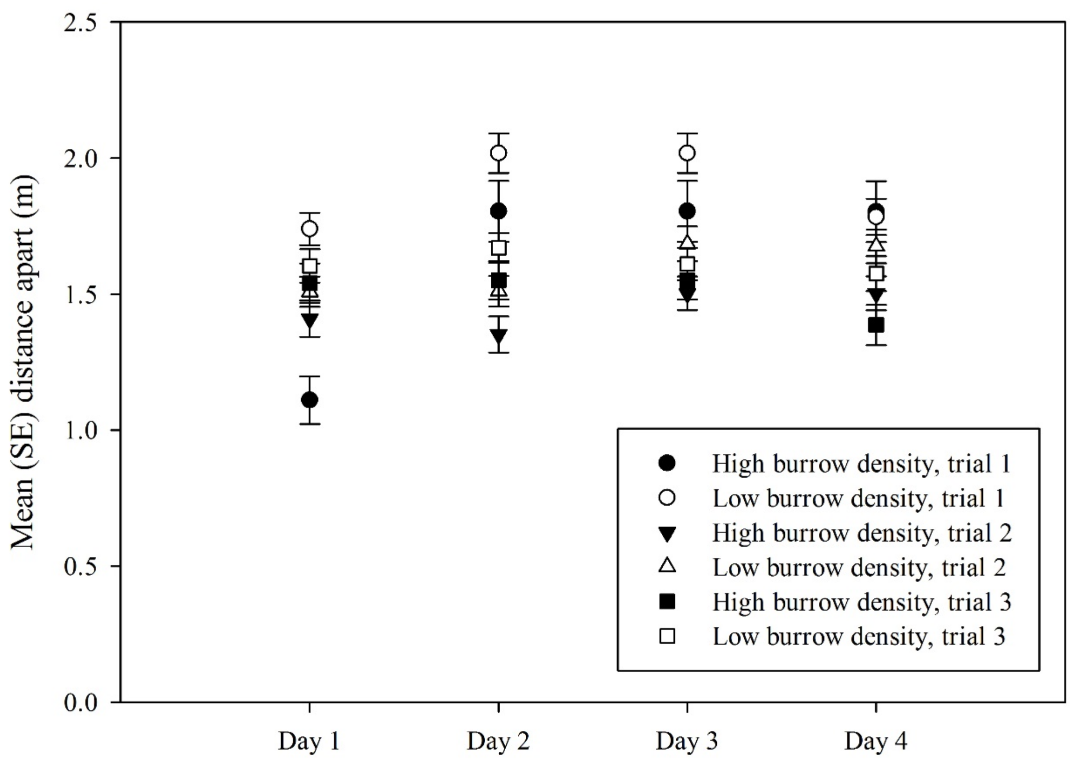
Mean (SE) distance apart (m)
0.0
0.5
1.0
1.5
2.0
2.5
Day 1
Day 2
Day 3
Day 4
High burrow density, trial 1
Low burrow density, trial 1
High burrow density, trial 2
Low burrow density, trial 2
High burrow density, trial 3
Low burrow density, trial 3

Fig 2. The mean distance apart of lizards at the end of each day of each trial in experiment 1

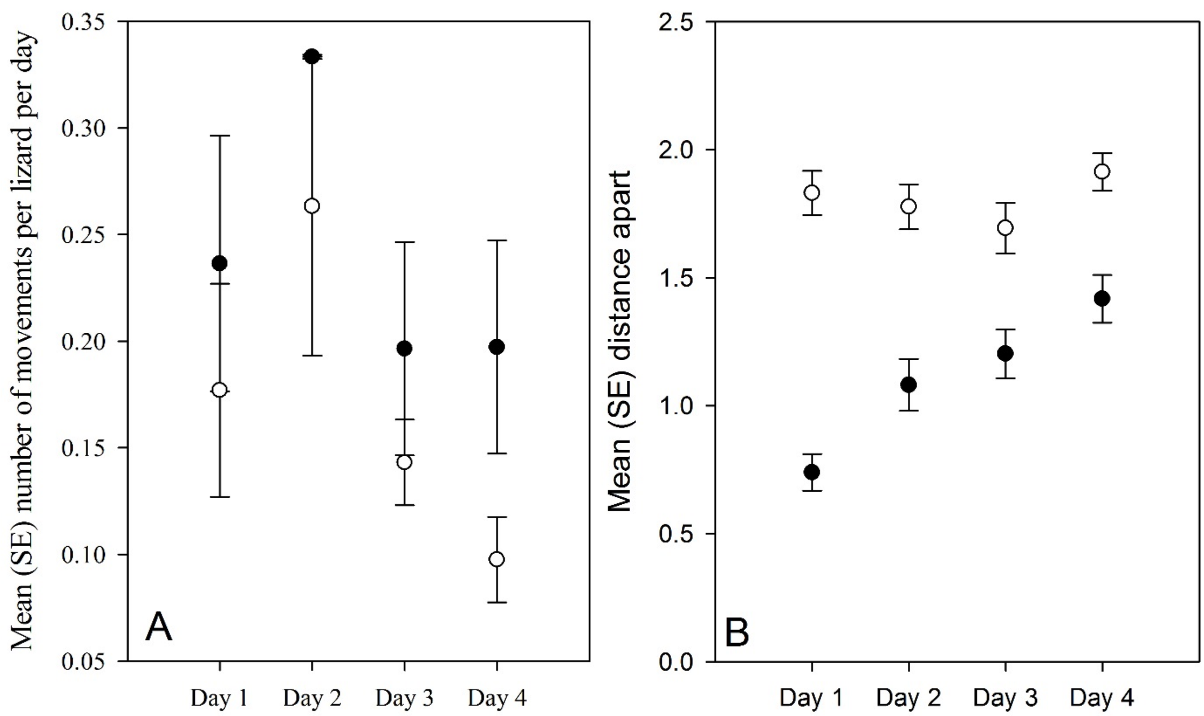

Fig 3. (A) Mean number of movements per lizard per day, and (B) mean distance apart at the end of each day when lizards were released close to each other (filled circles) or further apart (open circles) in experiment 2.

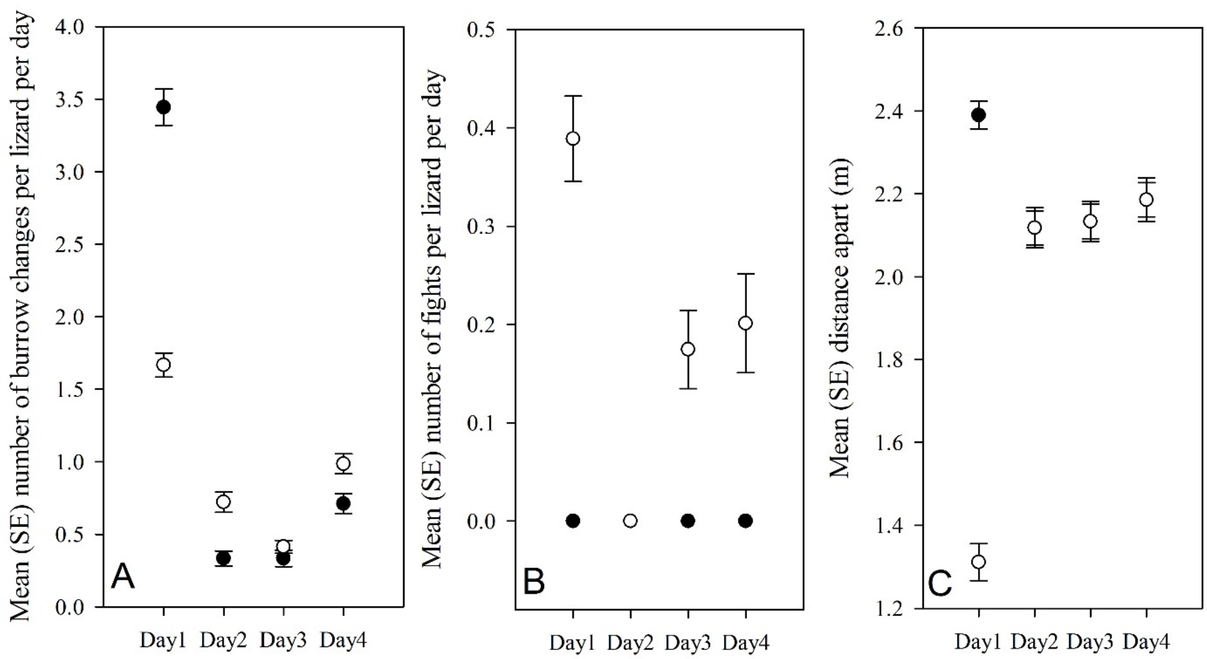

Fig 4. (A) Mean number of burrow changes, (B) mean number of fights, and (C) mean distance apart at the end of each day, for lizards released 150 cm apart in evenly spaced burrows (open symbols) or 250 cm apart in clustered burrows (filled circles) in experiment 3. (Where mean values coincide only the open symbol is shown).