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Craig, M.D, Grigg, A.H., Garkaklis, M.J., Hobbs, R.J., Grant, C.D., Fleming, P.A. and Hardy, G.E.St.J. (2009) Does habitat structure influence capture probabilities? A study of reptiles in a eucalypt forest. Wildlife Research, 36 (6). pp. 509-515.

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Does habitat structure influence capture probabilities? A study of reptiles in a eucalypt forest

Michael D. Craig ^{A G}, Andrew H. Grigg ^B, Mark J. Garkaklis ^C, Richard J. Hobbs ^{D F}, Carl D. Grant ^B, Patricia A. Fleming ^E and Giles E. St J. Hardy ^A

^A School of Biological Sciences and Biotechnology, Murdoch University, Murdoch, WA 6150, Australia.

^B Alcoa World Alumina Australia, Pinjarra, WA 6208, Australia.

^C Swan Regional Services, Department of Environment and Conservation, Kensington, WA 6151, Australia.

^D School of Environmental Sciences, Murdoch University, Murdoch, WA 6150, Australia.

^E School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch, WA 6150, Australia.

^F Present address: School of Plant Biology, University of Western Australia, Crawley, WA 6009, Australia

Abstract

Pitfall traps are commonly used to examine differences in reptile communities among habitat types and disturbance regimes that differ in structure. However, capture rates and probabilities may be influenced by habitat structure, which invalidates comparisons of relative abundance among habitat types. To assess whether pitfall traps provide accurate

reflections of density and whether habitat structure affects capture probabilities, we trapped at six sites in various jarrah-forest habitat types in south-western Australia, then intensively searched 150-m² total-removal plots around each pitfall grid to obtain absolute densities of reptiles. Pitfall captures were significantly correlated with numbers on total-removal plots for *Hemiergis initialis* and *Lerista distinguenda*, indicating that pitfall traps provided accurate reflections of density for these species. Capture probabilities of *H. initialis* and *L. distinguenda* and all reptiles combined showed no significant correlations with any structural variables, indicating that capture probabilities were consistent across sites. We conclude that trapping provided accurate estimates of relative abundance for some species and that capture probabilities were not influenced by vegetation structure. Because many studies use trapping to estimate abundances among habitat types, we encourage researchers to investigate how vegetation structure influences capture probabilities, so that general patterns can be determined; we also suggest improvements for any future studies.

Reptile communities are often sampled with pitfall traps (hereafter 'pitfalls') (e.g. Driscoll 2004; Kavanagh and Stanton 2005; Olsson *et al.* 2005) to estimate differences in abundance among habitats, habitat types (*sensu* Hall *et al.* 1997) or disturbance regimes within a habitat (Singh *et al.* 2002; James 2003; Leynaud and Bucher 2005). However, abundance estimates derived from pitfalls may not be comparable among habitats, habitat types or disturbance regimes, because of biases caused by differences in habitat structure (Melbourne 1999). The number of animals captured in any habitat is determined by both population density and capture probability, and capture probability is potentially affected by habitat structure (Luff 1975; Adis 1979; Schlesinger 2007). For example, capture probabilities of semi-arboreal or scansorial species may be greater in open, rather than closed, habitats because they spend more time moving around on the ground in open habitats. In this case, abundance estimates

would be biased upwards in open habitats, invalidating comparisons of relative abundance among habitats.

Despite potential differences in capture probabilities among habitats, habitat types or disturbance regimes, pitfalls continue to be used extensively in herpetological research to examine abundance and community differences among habitats (e.g. James 2003; Driscoll 2004; Thompson *et al.* 2005). This is probably because pitfalls are easy to use, require few prior skills and ensure that individuals can be identified and measured for demographic or genetic studies (Letnic and Fox 1997; How and Shine 1999). Only one study has examined variations in capture probabilities of reptiles between habitats and found no relationship between capture probabilities and habitat structure (Schlesinger 2007), although some studies conducted on invertebrate communities have found that capture probabilities do vary with habitat structure (Greenslade 1964; Halsall and Wratten 1988; Spence and Niemelä 1994; Melbourne 1999). One of the reasons for the dearth of studies is the difficulty in determining absolute densities against which to compare numbers of captures and, hence, capture probabilities. However, recently the total-removal technique has been developed, which allows absolute densities to be determined (Rodda *et al.* 2001a). Despite being incredibly labour intensive, the technique is currently the only way to determine absolute densities and provides an opportunity to address the critical question of the influence of habitat structure on capture probabilities.

Alcoa World Alumina Australia has restored bauxite mines in the northern jarrah forest since 1966. Succession at older restored sites has now progressed to the stage where active management of sites is being investigated to satisfy multiple land-use objectives (Grant

2006). Management objectives being explored include thinning and burning, which result in marked changes to habitat structure (Grant and Norman 2006). To assess how these management practices affect reptile communities, it is critical to know whether relative abundances derived from pitfalls accurately reflect differences in the abundance of reptile communities among habitat types. To achieve this, we used the total-removal technique to estimate absolute densities around pitfall grids and compared these results with pitfall captures to determine whether capture probabilities varied significantly with habitat structure. We conducted total removal and reptile trapping at six jarrah-forest sites with a range of vegetation structures to test the following hypotheses:

1. numbers of reptiles trapped are an accurate reflection of the absolute density of animals present around each pitfall grid; and
2. capture probabilities of the reptile community, or individual species, do not vary with habitat structure.

Materials and methods

Study area

The study was conducted east of Banksiadale Dam (32°37'49"S, 116°05'15"E), on Alcoa's Huntly mine, 10 km north of Dwellingup in south-western Australia. The climate at Dwellingup is Mediterranean, with cool, wet winters and warm, dry summers. Rainfall averages 1258 mm year⁻¹, with more than 75% falling between May and September. The study area consisted of pits, mined in the 1980s and restored between 1988 and 1992, interspersed with unmined jarrah forest. All pits were restored with overstorey mixes (80 : 20) of jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*), mimicking the

abundance of these species in unmined forest, and understorey mixes of 60–100 jarrah-forest species (Koch 2007). For details of restoration procedures see Grant and Koch (2007) and Koch (2007).

Methods

Six pitfall grids were used for the study in jarrah forest, covering a range of vegetation structures. Unmined areas were examined as well as restored mine-pits. We sampled reptiles at all sites with pitfall grids, consisting of nine pitfalls (four 850-mL plastic take-away containers, three 20-L white plastic buckets and two 40-cm-long 15-cm-diameter PVC tubing) located every 3 m along 29-m aluminium fly-wire drift fences (Fig. 1). Reptiles were sampled for four nights in each of winter (22–26 August 2005), spring (10–14 October 2005), summer (28 November–2 December 2005) and autumn (13–17 March 2006). We chose four sampling sessions in one year because many reptile studies use a similar trapping intensity over a similar period (e.g. Anderson and Burgin 2002; James 2003; Letnic *et al.* 2004; Olsson *et al.* 2005). All animals captured were toe-clipped for individual identification and released at their site of capture.

To derive absolute densities of reptiles, we used the total-removal technique (Rodda *et al.* 2001a) on 30×5 m plots around each trapping grid, running the length of the drift fence and extending 2.5 m either side (Fig. 1). The total-removal technique involved raking through all leaf litter and soil to a depth of 10 cm, turning over all logs and rocks, taking apart all logs and stumps with suitable microhabitats, removing all decorticating bark and searching all other potential microhabitats up to a height of 2 m. Each total-removal plot took ~18 person

hours to search thoroughly. The total-removal technique typically requires the construction of fences to prevent reptiles from escaping. However, we managed to avoid this problem by conducting the total-removal sessions from 6 to 11 July 2006, in the middle of winter, when reptiles were inactive and unable to move rapidly enough to escape. All reptiles we encountered moved slowly, because of low temperatures (mean daily maxima \pm s.e. were $16.7 \pm 1.9^{\circ}\text{C}$), and we easily captured all reptiles encountered. Further, to ensure that reptiles did not escape, we commenced searching around perimeters of plots and worked inwards towards drift fences. All animals captured on total-removal plots were checked to see whether they had been previously trapped and perpendicular distances from drift fences to their capture sites were recorded.

We conducted vegetation assessments on 3 November 2006 to quantify structural characteristics around each trapping site. Canopy cover was measured by taking four densitometer readings, in the four compass directions, at each of 12 points located 5 and 10 m either side of the 20-L bucket pitfalls. Understorey (plants <3 m in height) and overstorey (plants >3 m in height) plant densities were estimated by the nearest-neighbour methods (Barbour *et al.* 1987). First, we located the understorey or overstorey plant nearest to each 20-L bucket pitfall, on both sides of the drift fence, and then measured the distance from this plant to its nearest neighbour. We also measured the heights of all overstorey plants by using tree vertexes, and estimated canopy heights as averages of the five tallest plants. The volume of coarse woody debris (CWD: any debris >5 cm diameter at the thickest end) was calculated from lengths and end diameters of all CWD located on four 5×5 m plots that extended out from the middle of trapping grids and whose corners were located 5 m either side of the two 20-L bucket pitfalls at each end of the trapping grid. Percentage cover of leaf litter, bare

ground and all vegetation in three strata (0–1, 1–2 and 2–5 m) was visually estimated on 0.25-m² areas centred on points located 5 and 10 m either side of the 20-L bucket pitfalls.

Statistical analyses

Capture probabilities were calculated as numbers of individuals caught in pitfalls (recaptures were excluded), divided by absolute density (individuals recorded in total-removal plots). We used correlations and linear regressions to examine relationships between numbers of individuals trapped and absolute density for all reptiles and individual species. We used *t*-tests to determine whether regression line intercepts and slopes differed significantly from zero and restricted analyses to individual species that were trapped and found on total-removal plots at three or more sites. We used perpendicular distance from capture sites to drift fences to determine absolute densities we would have obtained if the total-removal plots had been smaller (60, 90 and 120 m²) and then correlated these absolute densities against the numbers of animals trapped. We restricted this analysis to *H. initialis* because it was the only species showing a significant correlation at the 150-m² scale that was abundant enough to obtain absolute densities at smaller scales.

We examined relationships between capture probabilities and vegetation structure by using correlations and linear regressions with capture probabilities of all reptiles, and individual species, as dependent variables. For regressions, we used *t*-tests to determine whether intercepts and slopes differed significantly from zero. We restricted these analyses to those species that were trapped or found on total-removal plots at three or more sites. All analyses were conducted with JMP 3.2.5. (SAS 1999) and an α value of 0.05 was used for all analyses.

Results

We trapped 57 individuals of 12 reptile species, and on total-removal plots we recorded 47 individuals of eight reptile species. As expected, we trapped the greatest number of reptiles in summer (27), with smaller numbers trapped in spring (14) and autumn (15) and only one reptile trapped in winter. The pattern of greatest captures in summer was the same for the five most common species. Combined numbers from all total-removal plots provided an estimate of reptile density for the jarrah forest of 522 ± 115 individuals ha^{-1} , with *H. initialis* being the most abundant species (Table 1).

Are numbers of animals trapped an accurate reflection of absolute density?

Although there was a trend for more individuals to be trapped at sites with higher absolute densities, there was no significant correlation between the number of reptiles trapped and the absolute density ($r_4 = 0.64$, $P = 0.169$) (Fig. 2). However, of the five individual species that were both trapped and found on total-removal plots at three or more sites, two showed significant correlations between the numbers of individuals trapped and the absolute density (Table 2). For *H. initialis*, the area of total-removal plots influenced the correlation between the numbers trapped and the absolute density. Correlations would have been non-significant if our total-removal plots had been only 60 m^2 ($r_4 = 0.33$, $P = 0.528$), 90 m^2 ($r_4 = 0.39$, $P = 0.443$) or 120 m^2 ($r_4 = 0.70$, $P = 0.120$) around trapping grids.

Do capture probabilities vary with habitat structure?

Structural variables varied greatly among sites and sites chosen covered most of the range present in the jarrah forest (Table 3); however, there were no significant correlations between

capture probabilities of all reptiles and any structural variable measured (Table 4). Because of the low numbers of reptiles caught on total-removal plots, it was possible to analyse only the two most common species individually. Capture probabilities of *H. initialis* and *L. distinguenda* were not significantly correlated with any of the structural variables measured (Table 4).

Discussion

Are numbers of animals trapped an accurate reflection of absolute density?

We trapped more reptiles during warm periods, as expected, and this was consistent for the five most common species. This indicates that the increased capture rates during warm weather were due to increased reptile activity, rather than migration or seasonal movements. Because there is no evidence that any reptile in south-western Australia shows seasonal migration or movements (Bush *et al.* 1995; Wilson and Swan 2003; Gilmore *et al.* 2007), we can reasonably assume that the numbers of reptiles found on total-removal plots in winter are indicative of the numbers present year round and, therefore, comparable to trapping data.

Our study demonstrated that the numbers of animals trapped were an accurate reflection of the absolute density, although only for some species. Significant correlations between the number of individuals trapped and absolute densities were found only in the two reptiles with reduced limbs (*H. initialis*, *L. distinguenda*) (Bush *et al.* 1995). Although home range and movement data are lacking for these species, the limb reduction in the reptiles suggests that their home ranges may be small. These were the two most abundant species in the total-removal plots and, for *H. initialis*, we trapped far fewer individuals than we found on these

plots, indicating that home ranges of individuals within total-removal plots may not have been large enough to intersect trapping grids. If these species have small home ranges, as the data suggest, then the small area of total-removal plots was likely to be sufficiently large to provide accurate estimates of absolute density in the source areas for trapping grids for these species. The significant correlations indicate that the numbers of individuals trapped were an accurate reflection of absolute density.

In contrast, our study did not show that the numbers of individuals trapped were an accurate reflection of the absolute densities of *Acritoscincus trilineatum*, *Menetia greyii* or *Morethia obscura*. The lack of significant correlations for these species suggests that either trapping is a poor estimator of relative abundance (i.e. capture probabilities differ among sites) or that total-removal plots were too small to provide accurate estimates of absolute density for these species in the source areas for trapping grids. Although our study cannot distinguish between these two explanations, we believe that the latter explanation is most likely. These three species are all active foragers (actively search for and run down prey) that show no indication of limb reduction (Bush *et al.* 1995). Again there is no information on the home ranges or movements of these species; however, it is likely that their home ranges are larger than those of the two species discussed previously. In comparison with *H. initialis* and *L. distinguenda*, we found fewer individuals of *A. trilineatum*, *M. greyii* or *M. obscura* on total-removal plots. We also trapped over three times more individuals of *A. trilineatum*, *M. greyii* or *M. obscura* than we found on total-removal plots, indicating that the home ranges of individuals outside these plots were large enough to intersect trapping grids. We also found no trapped individuals of these species on total-removal plots (although we found two trapped *H. initialis*), further indicating that individuals of these species had large home ranges that extended outside the total-removal plots. If these species do have large home ranges then it is

likely that the total-removal plots were too small to estimate densities accurately over the source areas for trapping grids. Further supporting this hypothesis, the correlation between the numbers of *H. initialis* trapped and those found on total-removal plots would have been non-significant if the total-removal plots had been smaller than 150 m².

When all species were combined, we also found no correlation between the total numbers of reptiles trapped and those found on total-removal plots. Although this would appear to indicate that trapping does not reflect variations in absolute abundance and that capture probabilities, therefore, differ among sites, we propose, that the total-removal plots were too small to provide accurate estimates of overall reptile density over the source areas for trapping grids. Given that numbers of active foragers trapped at the six sites varied from 2 to 12 individuals and these numbers, as a percentage of reptiles trapped, varied from 43 to 86%, it is not surprising that the correlation was non-significant for all reptiles. This is especially true when we consider that no active foragers were found in total-removal plots at three sites (and more than two were found at only one site). Therefore, it is more likely that the lack of correlation reflects total-removal plots being too small to estimate densities of all reptiles accurately over source areas for trapping grids, rather than capture probabilities varying across sites.

Do capture probabilities vary with habitat structure?

Given the limited replication in our study, and the low density of reptiles in the jarrah forest, it is not possible to answer this question with certainty. However, our study found no evidence that capture probabilities of reptiles varied with vegetation structure in the jarrah

forest, because there was no significant relationship between capture probabilities and any structural variable measured. Although we measured only a selection of structural variables, we chose those, such as leaf litter, canopy cover, CWD and understorey cover, that have been shown to be important in structuring reptile communities elsewhere (e.g. Trainor and Woinarski 1994; Smith *et al.* 1996; Urbina-Cardona *et al.* 2006; Hodgkison *et al.* 2007). If capture probabilities were to vary because of habitat structure, we would expect the variables we measured to be those most likely to influence capture probabilities, although it is possible that capture probabilities varied in response to structural variables we did not measure.

Our results concur with Schlesinger (2007), who found no effect of ground-cover density on capture probabilities of reptiles in mulga shrublands in Australia; however, a broad generalisation that capture probabilities of reptiles generally do not differ among habitats cannot be made from the two studies. Instead, we propose that capture probabilities are less likely to differ among habitat types, or disturbance regimes, where herpetofaunas consists primarily of terrestrial species, such as the jarrah forest (Nichols and Muir 1989) and mulga shrublands. Differences in capture probabilities among habitats are more likely to occur where arboreal or scansorial species spend differing amounts of time on the ground, because it is logical to assume that capture rates in pitfalls will be reduced if animals spend less time on the ground. We are unaware of any studies that have examined whether reptiles spend differing amounts of time on the ground in different habitats. However, a study on eastern pygmy-possums (*Cercartetus nanus*) (a species commonly caught in pitfalls) showed that these animals spend more time on the ground in burnt heathland than in unburnt woodland (Tulloch and Dickman 2006). Therefore, we would expect capture probabilities for this species to be greater in burnt heathlands and similar patterns to be shown in arboreal or scansorial reptiles, where time spent on the ground varies among habitats. For this reason, we

suspect that habitats with a greater proportion of arboreal or scansorial reptile species, such as rainforests, would be more likely to show differences in capture probabilities among habitat types and disturbance regimes than is the case for jarrah forests or mulga shrublands.

Limitations of the study

Our study should be considered a preliminary examination of the questions asked because we sampled only six sites and our total-removal plots were probably too small, relative to source areas, for some species. In addition, the density of reptiles in the jarrah forest appeared low which meant that we found low numbers of reptiles on total-removal plots. We had no *a priori* information on home-range sizes or source areas for any reptiles in jarrah forest, so our original design, with six 150-m² removal plots, was largely based on logistical constraints. These plots were the largest areas we could sample with the personnel and time available, given the incredibly time-intensive nature of conducting searches in total-removal plots (two person days per 100 m²). If the study was to be repeated, in the jarrah forest or elsewhere, we recommend making total-removal plots much larger, at least 1000 m², and preferably ~2000 m². Given the effort involved, it would take a team of 10 people ~20 days to conduct a search in 10 total-removal plots of 1000 m² in a similar forest, assuming that the searching of the plots were conducted in winter, precluding the need for constructing fences around plots (constructing fences would likely add about five person days per plot). We suspect it would take less time in structurally simpler habitats (heaths, grasslands) and more time in more complex habitats (rainforest). The use of undergraduate groups of students is one potential method of conducting searches in large total-removal plots, considering the person days required to search these plots within a short time period. Given the destructive nature of total-removal plots, they should be sampled in areas that are scheduled for clearing, where

possible. Some consideration should also be given to alternative ways of answering the key questions in the present paper, that are less time and labour intensive.

Another reason for our inconclusive results was the low density of reptiles in the jarrah forest, which meant that we trapped low numbers of reptiles and also low numbers on total-removal plots. Although there are few studies with which to compare, the reptile density we estimated (522 individuals ha^{-1}) appeared low, with densities of some island reptile communities reaching 55 100 individuals ha^{-1} (Genet *et al.* 2001; Rodda *et al.* 2001*b*; Rodda and Dean-Bradley 2006). Although we consider our study to be preliminary, we did record significant correlations between the numbers of animals trapped and the density for some species, which shows that trapping did provide an accurate assessment of abundance for these species. In contrast, we recorded no significant correlations between capture probabilities and vegetation structure, which suggests that, if there was a relationship, it was relatively weak for the structural variables we measured.

Conclusions and recommendations

In conclusion, the present study found no evidence that reptile-capture probabilities differed with vegetation structure in the jarrah forest and we demonstrated that trapping provided an accurate estimate of abundance for some species. Although our study sampled few plots and had relatively small total-removal plots, we believe that our study is a useful preliminary investigation of an important, although neglected, topic. Given the number of studies, and management decisions, that are based on differences in pitfall capture rates among habitats, habitat types and disturbance regimes (e.g. Owens *et al.* 2008), it is concerning that only one

study (Schlesinger 2007) has previously examined how capture probabilities differ with vegetation structure. We strongly encourage researchers to investigate how vegetation structure influences capture probabilities and would recommend that future studies include a minimum of 10 total-removal plots that are 1000 m² in area, unless less labour-intensive methods of examining capture-probability issues can be identified. Only when general patterns emerge can we be confident that trapping provides an unbiased estimate of abundance across a range of habitat types and disturbance regimes.

Acknowledgements

We thank Rod Armistead, Finlay Bender, Kaitlyn Height and Angela Mercier who assisted with the total-removal plots and Anna Whitfield, Dion Trevithick-Harney, Alicia Sparnon, Adam Peck, Angela Mercier, Kaitlyn Height, Finlay Bender and Jane Adcroft who helped install trapping grids. We also thank Christine Schlesinger who provided constructive comments on an earlier version of this manuscript. This project was conducted with Department of Environment and Conservation Permit No. SF005179 and Murdoch University Animal Ethics Committee Approval No. W1152/05. Financial support was provided by Alcoa World Alumina Australia and Australian Research Council Linkage Grant No. LP0455309.

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Fig. 1. Layout of trapping grids used for the study in relation to total-removal plots around each grid. The approximate position of the pitfall traps along the aluminium drift fence are also shown.

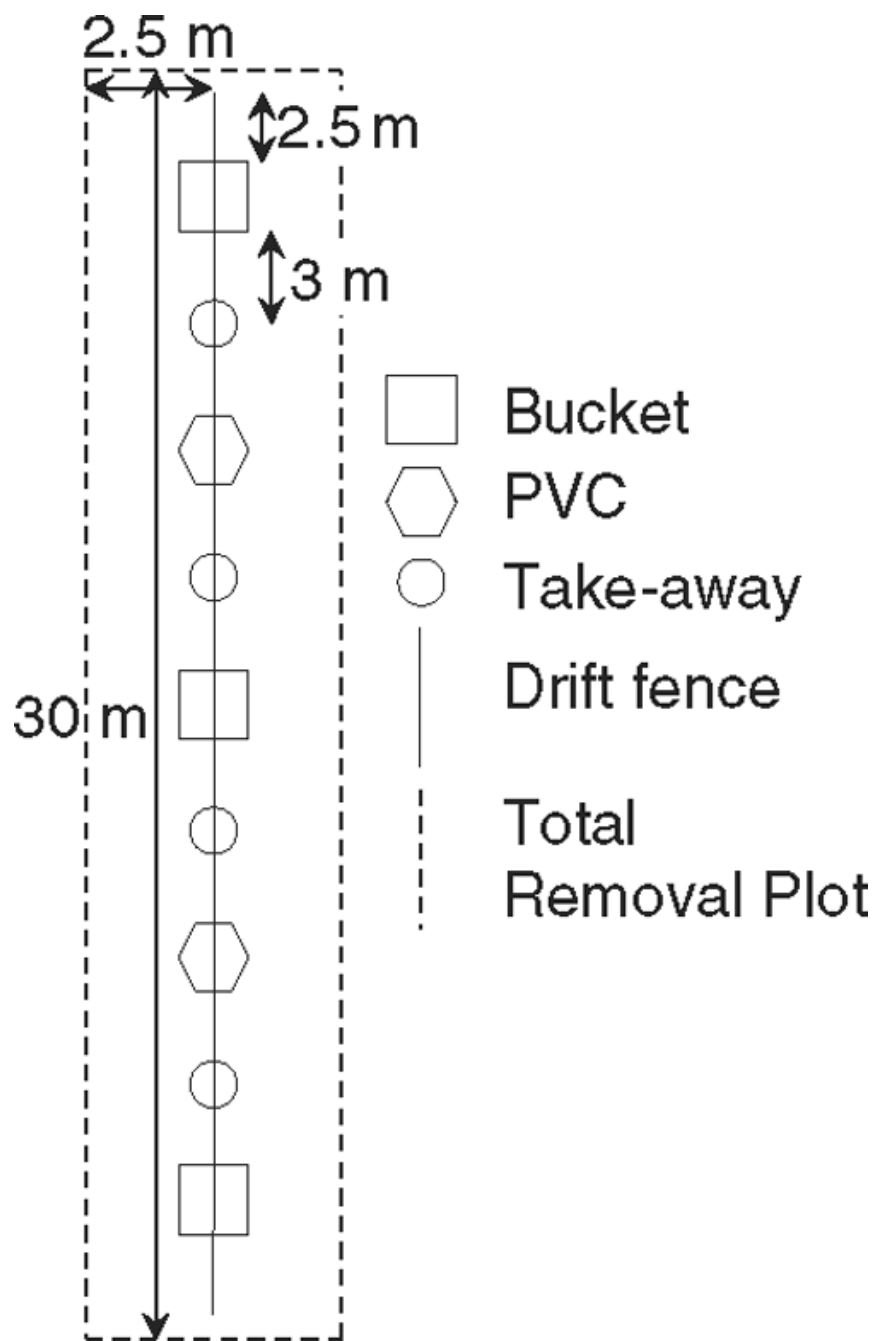


Fig. 2. Relationship between reptile pitfall captures and absolute densities. Scattergram of reptile densities and the numbers trapped at each of six sites. Line is the regression line of the best fit; however, there is no significant relationship between the two variables.

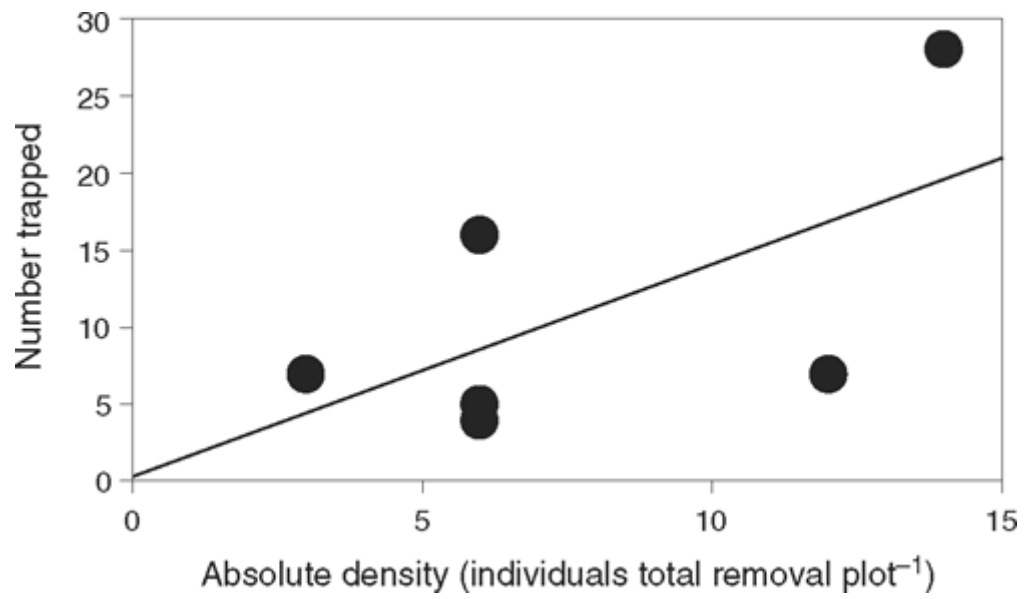


Table 1. Total number of individuals of each reptile species recorded during trapping and on total-removal plots as well as estimated densities derived from total-removal plots

Also shown are the corresponding values for all reptiles combined. Estimated densities were calculated by dividing the total number of reptiles caught on total-removal plots by the total area of those plots (0.09 ha)

Family	Species	Trapping	Total-removal plots	Estimated density (individuals ha ⁻¹)
Scincidae	<i>Acritoscincus trilineatum</i>	7	2	22
	<i>Cryptoblepharus plagiocephalus</i>	1	0	0
	<i>Ctenotus labillardieri</i>	1	0	0
	<i>Egernia napoleonis</i>	1	0	0
	<i>Hemiernis initialis</i>	7	29	322
	<i>Lerista distinguenda</i>	15	5	56
	<i>Menetia greyii</i>	19	3	33
	<i>Morethia obscura</i>	14	4	44
Gekkonidae	<i>Christinus marmoratus</i>	1	1	11
	<i>Diplodactylus polyophthalmus</i>	3	0	0
Pygopodidae	<i>Aprasia pulchella</i>	2	1	11
Agamidae	<i>Pogona minor</i>	1	0	0
Typhlopidae	<i>Ramphotyphlops australis</i>	0	2	22
All reptiles		72	47	522

Table 2. Correlations between numbers of animals trapped and absolute density

Results are shown for all five species recorded during both trapping and on total-removal plots on at least three plots. The intercept and slope of the regression line, as well as the probability that either was significantly different from zero, is shown for those species with a significant correlation

Species	r	P	Intercept	P	Slope	P
<i>Acritoscincus trilineatum</i>	0.32	0.541				
<i>Hemiergis initialis</i>	0.96	0.003	-0.38	0.496	4.81×10^{-3}	0.028
<i>Lerista distinguenda</i>	0.94	0.005	-0.15	0.882	4.46×10^{-2}	0.012
<i>Menetia greyii</i>	0.00	1.000				
<i>Morethia obscura</i>	0.56	0.246				

Table 3. Values for the 10 structural variables measured on each of the six trapping sites

Each site was located either in unmined forest or in restored mine-pits

Structural variable	Site 1 (Forest)	Site 2 (Forest)	Site 3 (Restoration)	Site 4 (Restoration)	Site 5 (Restoration)	Site 6 (Restoration)
Bare ground cover (%)	24.67	0.75	15.17	15.58	32.17	24.33
Leaf litter cover (%)	73.58	99.25	84.33	84.42	66.17	75.42
Cover 0–1 m (%)	43.25	21.08	31	58.58	65.42	71.42
Cover 1–2 m (%)	2.08	4.58	21.58	45.33	23.08	12.92
Cover 2–5 m (%)	1.25	0.58	34.75	27.58	17.5	5
Canopy cover (%)	85.48	87.1	86.71	89.19	79	72.73
Canopy height (m)	25	18.18	10.72	9.96	11.66	15.64
Understorey plant density (stems ha ⁻¹)	6151	3360	17 300	4717	19 209	20 037
Overstorey plant density (stems ha ⁻¹)	1169	921	5134	3608	1040	1003
Coarse wood-debris density (m ³ ha ⁻¹)	41.68	72.12	0	0	0.15	0.4

Table 4. Correlations between capture rates and vegetation structure

Results are shown for all reptiles, *Hemiergis initialis* and *Lerista distinguenda*. There were no significant correlations. Sample sizes differ because capture rates could be calculated only if individuals were found on total-removal plots and *H. initialis* and *L. distinguenda* were not found on one and three plots respectively

Structural variable	All reptiles		Hemiergis initialis		Lerista distinguenda	
	<i>r</i> (<i>n</i> = 6)	<i>P</i>	<i>r</i> (<i>n</i> = 5)	<i>P</i>	<i>r</i> (<i>n</i> = 3)	<i>P</i>
Bare ground cover (%)	0.18	0.736	-0.54	0.334	0.13	0.919
Leaf litter cover (%)	-0.22	0.682	0.54	0.351	-0.16	0.899
Cover 0–1 m (%)	-0.12	0.817	-0.30	0.619	-0.22	0.857
Cover 1–2 m (%)	-0.46	0.362	-0.47	0.428	0.45	0.704
Cover 2–5 m (%)	-0.56	0.246	-0.82	0.091	0.63	0.569
Canopy cover (%)	0.04	0.936	0.1	0.873	0.54	0.64
Canopy height (m)	0.53	0.283	0.79	0.114	-0.51	0.659
Understorey plant density (stems ha ⁻¹)	-0.28	0.592	-0.64	0.246	-0.16	0.899
Overstorey plant density (stems ha ⁻¹)	-0.69	0.128	-0.71	0.177	0.19	0.879
Coarse wood debris density (m ³ ha ⁻¹)	0.5	0.255	0.88	0.051	0.11	0.929