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ORIGINAL PAPER

Factors affecting overwintering retreat-site selection in reptiles in an agricultural landscape

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Abstract
Context Understanding what characteristics influence retreat-site selection by fauna is critical for both habitat management and species conservation. Despite the documented ecological values of surface rocks, there is limited knowledge of the attributes of surface rock that contribute to their use in agricultural landscapes or during winter months when reptiles are brumating, activity patterns are reduced, and sheltering individuals are most vulnerable to disturbance.
Objectives We surveyed reptiles sheltering beneath surface rocks in grazing farms in south-eastern Australia to address two questions: (i) What landscape factors influence the occurrence of reptiles over austral winter? (ii) What physical and thermal factors influence retreat-site selection?
Methods We surveyed 14 sites, with three plots per site, stratified across a gradient of canopy cover. We measured landscape attributes of surveyed sites and thermal and physical characteristics of individual surface rocks to quantify relationships between the occurrence of reptiles in the landscape and the properties of retreats selected.
Results We found that relatively small patches of surface rock can support high reptile numbers, with density estimates up to of 208 individuals per hectare. Reptile abundance was positively associated with increased elevation and limited canopy cover. Reptiles selected smaller rocks with high surface area to volume ratio, were minimally embedded in the soil, and rocks supporting few invertebrates.
Conclusions Conserving cryptozoic reptiles in agricultural landscapes can be enhanced through the appropriate management and retention of surface rock. We discuss implications for reptile conservation and surface rock management in agricultural landscapes.

Keywords Cryptozoic fauna · Habitat use · Surface rock · Retreat-site selection · Overwintering

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Introduction

Over the past several decades, the range and size of populations of many reptile species have severely declined. Reptiles are consequently one of the most threatened taxonomic groups globally (Gibbons et al. 2000; Reading et al. 2010; Böhm et al. 2013;

Cox et al. 2022). The most prominent threat to reptiles is habitat loss and fragmentation (Ribeiro et al. 2009; Tingley et al. 2019). It is critical to understand the characteristics of habitat structures that support vulnerable reptile populations (Driscoll 2004; Martino et al. 2012; Driscoll et al. 2013; Vicenzi et al. 2021). Habitat structures such as rocky outcrops can support high reptile diversity (Michael and Lindenmayer 2018). Rocky outcrops provide species with diverse microhabitats, satisfying ecological, physiological, and behavioural needs, yet these features are often highly degraded, undervalued, and can be heavily impacted by agricultural activities (Michael et al. 2008, 2021; Vicenzi et al. 2021).

Retreat-sites are a key habitat element for fauna (Morrison et al. 2006). Surface rocks provide vital retreat habitat for a broad range of species, particularly ectotherms adapted to saxicoline environments (Goldsbrough et al. 2006; Chukwuka et al. 2021). Reptiles often use multiple criteria to select suitable retreat-sites (Downes and Shine 1998; Shah et al. 2004; Goldsbrough et al. 2006; Croak et al. 2012). At a landscape scale, reptile presence can be influenced by elevation (Fischer and Lindenmayer 2005; McCain 2010), canopy cover (Pringle et al. 2003; Goldsbrough et al. 2006; Pike et al. 2011b), aspect and slope (Pringle et al. 2003). At a rock level, thermal regimes (Huey et al. 1989; Webb and Shine 1998; Pringle et al. 2003; Shah et al. 2004), physical configuration (Croak et al. 2008; Penado et al. 2015; Cox et al. 2018), scent cues from other species (Head et al. 2002; Du et al. 2009; Webb et al. 2009) or colonisation of invertebrates (Head et al. 2002; Goldsbrough et al. 2006), can all influence selection of retreat-sites.

Understanding the factors influencing the selection of retreat-sites is critical for both habitat management and species conservation. Yet globally, few studies have examined overwintering retreat-site selection during which time reptiles are brumating, activity patterns are reduced, and sheltering individuals are most vulnerable to disturbance (Langkilde et al. 2003; Thienpont et al. 2004; Row and Blouin-Demers 2006; Filippi and Luiselli 2007; Cecchetto et al. 2019; Markle et al. 2020; Murphy et al. 2021). In addition, much of our knowledge about retreat-site selection in reptiles is based on laboratory experiments (Downes and Shine 1998; Shah et al. 2004; Cox et al. 2018), or from studies of saxicolous species that utilise rock-on-rock habitats (Schlesinger and Shine 1994a, b; Shah et al. 2004; Goldsbrough et al. 2006). As far as we are aware, no previous studies have quantified retreat-site selection for cryptozoic species in heavily modified agricultural landscapes. Approximately 16% of Australian terrestrial squamates utilise rocks for shelter (Michael et al. 2021), and this figure is likely to be equally high in other agricultural regions in the world (Ribeiro et al. 2009; Biaggini and Corti 2015; Rotem et al. 2020). A limited understanding of the ecological values of surface rock in agricultural landscapes impedes conservation and policy development.

Surface rocks are recognised as a retreat habitat for reptiles and are a common feature in agricultural landscapes that can support a diversity of reptile species (Garden et al. 2007; Michael et al. , 2008, 2018). In recent years there has been a major resurgence in rock clearing practices in agricultural landscapes (Michael et al. 2021). Advances in machinery have enabled widespread soil amelioration practices to crush and permanently destroy surface rock in the landscape (Michael et al. 2021), with the goal of improving agricultural efficiency. Unlike some biotic components of a species habitat, the formation of surface rock requires slow geomorphological change and erosion; lost surface rock is irreplaceable or can take many centuries to be replaced via natural processes (Schlesinger and Shine 1994a; Shine et al. 1998; Croak et al. 2013). Current legislative protection of surface rock habitat is inadequate and not in line with the rate of destruction or disturbance to this resource on private property, highlighting the need to quantify the factors affecting retreat-site selection in changing landscapes (Michael et al. 2021).

In this study, we surveyed reptiles sheltering beneath surface rocks on grazing farms in south-eastern Australia to address two questions: (i) What landscape factors influence the occurrence of reptiles over austral winter? (ii) What physical and thermal factors influence retreat-site selection? We measured landscape attributes of surveyed sites and canopy, thermal and physical characteristics of individual surface rocks to quantify relationships between the occurrence of reptiles in the landscape and the properties of retreats selected. We hypothesised that: (i) increasing canopy cover would negatively affect retreat-site selection (Row and Blouin-Demers 2006; Harvey and Weatherhead 2010; Pike et al. 2011b; Huang et al. 2014; Michael et al. 2018); (ii) aspect and elevation would influence occurrence (Fischer and

Lindenmayer 2005); (iii) there would be differences between occupied and unoccupied rocks in their thermal properties (Webb and Shine 1998; Langkilde et al. 2003; Pringle et al. 2003; Cox et al. 2018) and physical attributes such as volume and width (Goldsbrough et al. 2006; Croak et al. 2008; Cox et al. 2018). By quantifying what factors influence reptile occurrence and habitat selection, we aim to inform strategies to protect, manage and restore reptile populations in agricultural landscapes.

Materials and methods

Study area and site selection

We conducted this study on five private grazing properties located in the South West Slopes bioregion, near the town of Jugiong, in New South Wales, Australia (34°58′S, 148°29′E) (Fig. 1). We completed surveys in August (austral winter) 2020. Annual precipitation across the study area ranges from 612 to 926 mm and is uniformly distributed throughout the year. The region experiences a temperate climate with mean daily minimum and maximum air temperatures for the month of August 3 and 15 °C, respectively (Bureau of Meteorology 2021). The elevation ranges from 267 to 560 m, and the landscape consists primarily of agricultural land with patches of remnant Western Slopes Grassy Woodland. The geology is dominated by Silurian transitional granites and volcanics (Colquhoun et al. 2018). Small insular rocky outcrops, expansive rocky slopes and scattered surface rocks dominate the landscape.

We selected grazing farms that had large areas of scattered surface rock located within patches of varying amounts of remnant vegetation. We established 14 sites across the five properties, with between one and four sites per farm, depending on the availability of suitable habitats (Fig. 1). Because canopy cover

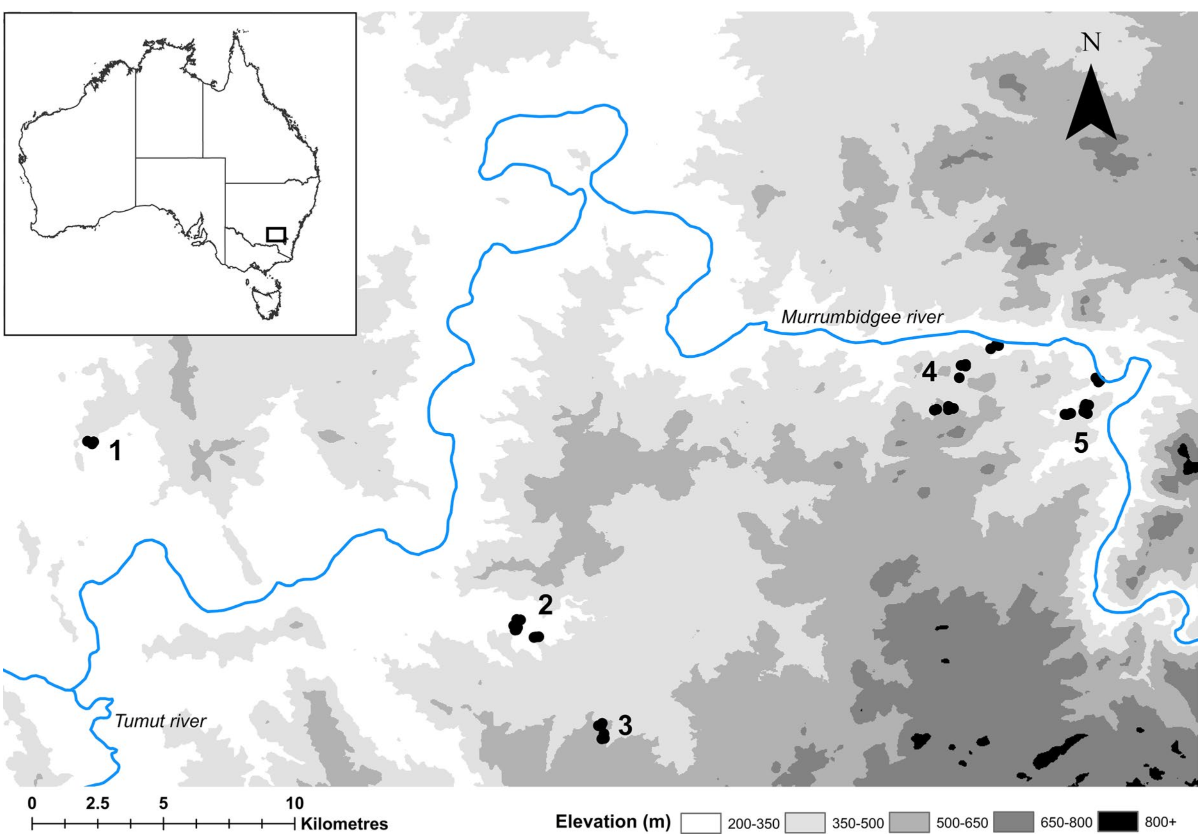

Fig. 1 The location of study sites in the South West Slopes bioregion of south-eastern Australia

can influence the thermal conditions of retreat-sites (Pringle et al. 2003), we stratified sampling units by canopy cover and established three 25 × 25 m plots per site; one each in open (0–30%), mid (30–60%) and closed (> 60%) canopy woodland remnants. Sites were located at least 500 m apart, and plots were established at least 50 m apart. We assumed that individuals did not move between plots or sites during the survey period as most species brumate or are inactive during this time of year (Greer 2022). We also assumed that individuals encountered had selected the sheltering site to overwinter and were therefore unlikely to occupy any other habitats while brumating. In total, we surveyed 42 plots across 14 sites.

Survey method

We conducted surveys in August of 2020 between 0800 and 1730 h on clear days with temperatures < 15 °C (mean = 11.2 °C ± 0.36 SE) and low wind speed (mean = 1.19 m/s ± 0.13 SE). We thoroughly searched all liftable surface rocks in a plot. Reptiles were hand captured from beneath the rocks within shallow burrow systems and processed. Only one observer (JLO) searched under rocks in each plot. Care was taken to replace all rocks to their original position to minimise disturbance to the microhabitat. After the rocks were replaced, all reptiles were placed back under their original rocks via burrow entrances. On all occasions, reptiles retreated under the rocks on their own accord. Large tors or sheathing rocks, or any other structural habitats were not surveyed. We extensively searched all shallowly embedded rocks found on the soil surface that could be safely lifted within the specified plot area.

Measurement of landscape and rock variables

We measured several covariates to quantify the landscape factors and rock attributes influencing reptile presence (Table 1). At a landscape level, we measured elevation, slope, and aspect (Table 1). We assessed canopy cover as a proxy for projected shade cover using a densitometer and measured at 10 random points within each plot. We took the average of the 10 measures to generate an overall canopy cover for each plot.

After searching all liftable rocks in each plot, we measured the attributes of all occupied rocks and three randomly selected unoccupied rocks. We measured the attributes of three unoccupied rocks per plot instead of using a matched case design so that reptile abundance did not confound the rock attributes measured. In areas of high reptile abundance, it is likely that most rocks are suitable, and an individual animal has chosen a rock at random. Hence, if an equal number of occupied and unoccupied rocks were measured at each site, unoccupied rock sampling would be biased towards favourable rocks/sites (Goldsbrough et al. 2006). For each rock, we recorded: (i) rock length (longest axis), (ii) width (longest axis perpendicular to length), and (iii) height (longest axis perpendicular to plane defined by length and width). An Optris MS Infrared Thermometer was used to take

Table 1 Landscape, canopy, and rock attribute covariates taken

Explanatory variable	Description	Mean, range
Elevation (metres above sea level)	The highest point in the plot obtained from a Global Positioning System	400, 267—560
Slope (degrees)	Measured using a clinometer	19, 4—42
Aspect	Grouping value of aspect—northeast, northwest, southeast, southwest	NA
Canopy cover	Mean canopy cover (proportion out of 1) across the plot measured using a GRS densitometer at 10 random points. A proxy for projected shade cover	0.36, 0—0.8
Rock volume (m^3)	length x width x height	0.014, 0.001—0.11
Surface area to volume ratio	(length x width)/volume. A proxy for rock flatness	0.09, 0.02—0.5
Embeddedness (cm)	Depth of rock buried below the surface level	5.9, 0—30
Δ T°C (surface temperature °C—adjacent temperature °C)	Difference in temperature between the underside of the rock and the ground adjacent to the rock	0.31, -8.7—6.1
Time since sunrise (hours)	Hours since sunrise at the time of survey commencement	7.1, 2.0—10.8
Invertebrate cover	Proportion (out of 1) of invertebrate colonisation of surface under rock	0.29, 0—1

temperature measures beneath each rock and on the ground surface adjacent to each rock (Table 1). We assessed invertebrate cover visually by estimating the colonisation of the surface under a rock to the nearest 0.05 proportion.

Statistical analyses

We performed our statistical analyses in two stages. First, we examined which landscape factors influenced reptile abundance at the plot level, and second, we examined retreat-site selection within occupied plots by testing whether rock properties differed between occupied and unoccupied rocks. We conducted all analyses in R version 4.1.0 (R Core Team 2022).

To test which landscape factors influenced the occurrence of reptiles over winter, we used data from all sites to model the effect of landscape factors on plot-level reptile abundance. We used generalised linear mixed models (GLMM) using Laplace approximation in the package "glmmTMB" (Brooks et al. 2017). To allow for possible over-dispersion or zero-inflation in the count data, we modelled the abundance of reptiles at a plot using five different distributional assumptions for the response variable. We tested whether (i) Poisson, (ii) zero-inflated Poisson, (iii) Conway-Maxwell Poisson (Huang 2017), (iv) negative binomial with quadratic parameterisation, or (v) hurdle negative binomial, fit our data best as ranked by the Akaike Information Criterion with correction for small sample sizes calculated for each model with all covariates included (AICc, Burnham and Anderson 2002). The fitted model in each case was: abundance ~ slope + canopy cover + aspect + elevation + (1|site). We found that the Poisson distribution fit our data best according to AICc (Supplementary Table S2).

To test whether rock attributes differed between occupied and unoccupied rocks in multivariate space, we performed a permutational analysis of variance (PERMANOVA) (Anderson 2001), using the 'adonis' function in the "vegan" R package (Oksanen et al. 2013). We then further tested what rock and thermal factors influenced retreat-site selection when reptiles occur by testing for differences in the characteristics of occupied and unoccupied rocks, fitting an individual GLMM for each rock attribute, with attribute as the response, and rock occupancy as the predictor. Plots including no occupied rocks were excluded from the analysis. We fit a Gaussian distribution for the continuous response variables of rock volume, embeddedness and Δ T°C, and a beta distribution for proportional response variables (Damgaard and Irvine 2019) including surface area to volume ratio, rock shading and invertebrate cover. We included site as a random-intercept in each model to account for site-level effects. The model for Δ T°C (surface temperature °C—adjacent temperature °C) was fitted with an interaction effect of occupancy and time since sunrise to account for time-of-day effects on air and surface temperatures.

We used the "DHARMa" package to conduct goodness-of-fit tests on the scaled residuals (Hartig 2022) of all linear models. We tested for multicollinearity using the package "olsrr'" (Hebbali 2018) among potential explanatory variables and found no evidence for strong effects (the highest Variance Inflation Factor value among variables was 1.30). Finally, we conducted post hoc calculations of the marginal effects of predicted values for specific model terms using the R package "ggpredict" (Lüdecke 2018). For predictions, all variables other than the variable of interest were held at their mean value.

Results

The abundance of reptiles varied from zero to 25 individuals per site (mean = 3.7, SD = 6.6). No reptiles were found at four out of 14 sites. At the plot level, reptile abundance ranged from zero to 13 individuals per plot (mean = 1.2, SD = 2.6), equivalent to mean and maximum densities of 19 and 208 individuals per hectare, respectively. *Ctenotus robustus* (63.5% of individuals captured) was the most frequently captured species, followed by *Carlia tetradactyla* (9.6% of individuals captured) and *Morethia boulengeri* (9.6% of individuals captured). All species captured were native taxa. Medium-bodied species (mean snout-vent-length > 5 cm) comprised the majority of captures (73.1% of captures) compared to small-bodied species (mean snout-vent-length < 5 cm; see Table S1).

Landscape factors

Elevation significantly influenced the abundance of reptiles per plot (Table 2; Fig. 2). Canopy cover also significantly influenced the abundance of reptiles (Table 2; Fig. 2). Our analyses revealed that reptile abundance increased with increasing elevation and decreasing canopy cover (Fig. 2).

Retreat-site attributes

At occupied plots, we measured the attributes of 100 rocks, of which 46 were occupied by reptiles and 54 were unoccupied. Of rocks occupied by reptiles, there were four instances of more than one individual sheltering under the same rock. Permutational analysis of variance provided evidence for multivariate differences in rock traits between occupied and unoccupied rocks (Fig. 3; $F = 10.07$ 5, $P = 0.001$). Multivariate dispersion was significantly lower for occupied than for unoccupied rocks (Fig. 3; $F = 5.911$ $P = 0.017$).

Table 2 The abundance of reptiles per plot and landscape variables: aspect (northeast, northwest, southeast, southwest), slope, canopy cover and elevation

Predictors	Est	SE	*Z*	*P*
Intercept (Northeast)	– 0.510	0.425	– 1.199	0.231
Northwest	– 0.271	0.477	– 0.568	0.570
Southeast	– 0.387	0.527	– 0.736	0.462
Southwest	– 0.851	0.894	– 0.952	0.341
Slope	0.157	0.307	0.511	0.610
Canopy cover	**– 0.443**	**0.200**	**– 2.212**	**0.027**
Elevation	**0.984**	**0.321**	**3.063**	**0.002**

Site was included as a random-intercept. Values in bold indicate statistical significance of variables ($P < 0.05$)

We found that occupied rocks had significantly smaller volume, were less embedded, had a higher surface area to volume ratio, had less shading, and supported fewer invertebrates compared to unoccupied rocks (Table 3; Fig. 4).

Discussion

Quantifying the factors that influence retreat-site selection by fauna is critical for habitat and species management and identifying areas for protection. We found that landscape factors, elevation, and canopy cover influenced the occurrence of reptiles over winter and physical factors influenced the selection of retreat-sites. Our analyses revealed a higher abundance of reptiles on high elevation sites with little to no canopy cover. At the rock level, smaller rocks with a greater surface area, minimally embedded in the soil, with little invertebrate colonisation of the ground surface under a rock, were preferred by reptiles as retreat-sites. We discuss our key findings in the remainder of this section and conclude with some commentary on implications for reptile conservation and surface rock management, where further research is needed, and outline ways surface rocks might be

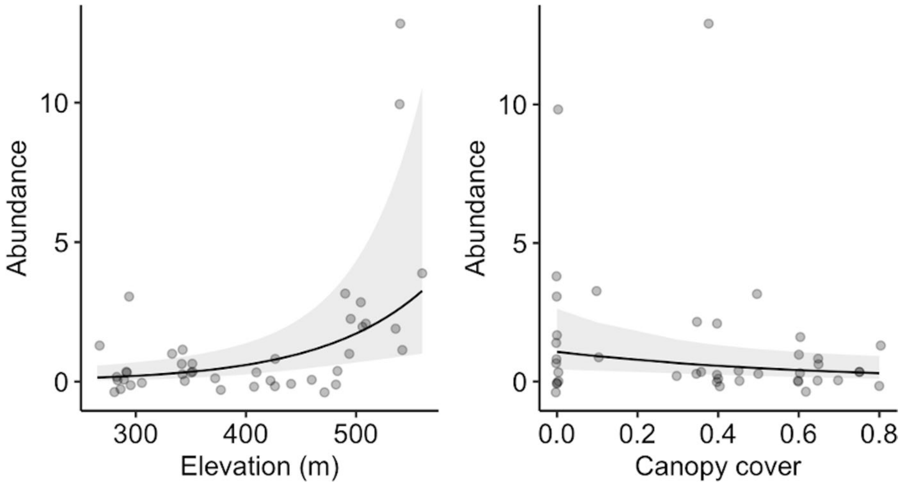

Fig. 2 Predicted effects of plot-scale factors influencing the abundance of reptiles. Graphs were constructed from predictions calculated from the Poisson model, with other covariates being held at their mean value to predict reptile abundance. 95% credible intervals are indicated by the grey shaded areas

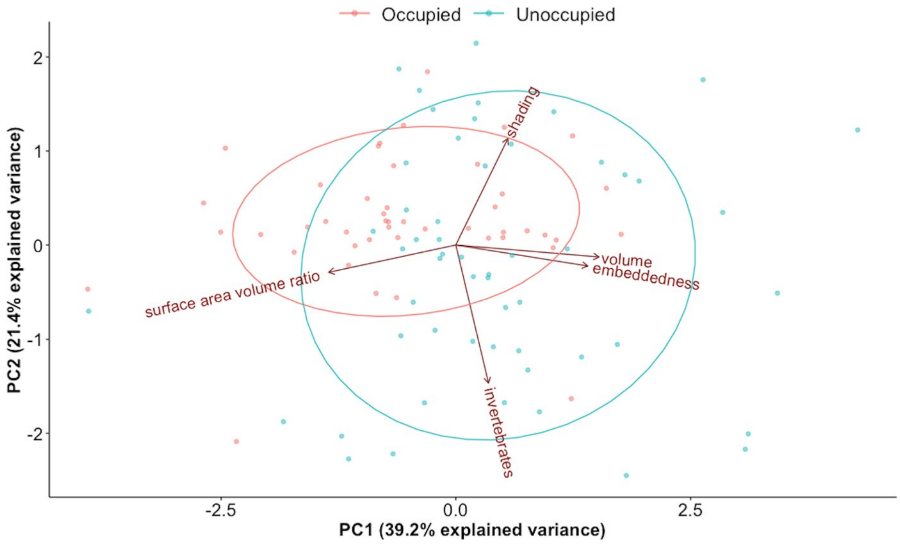

Fig. 3 Principal components analysis of rock attributes by occupancy

Table 3 Results of GLMM of rock attributes by occupancy at present sites

Attribute	Distribution	Est		SE		*Z*		*P*	
		Occ	Unc	Occ	Unc	Occ	Unc	Occ	Unc
Rock volume (m^3)	Gaussian	0.0102	0.004	0.0208	0.0211	4.927	1.869	**< 0.001**	0.062
Surface area to volume ratio	Beta	− 2.086	− 0.209	0.092	0.125	− 22.576	− 1.666	**< 0.001**	0.096
Embeddedness	Gaussian	2.785	3.624	0.794	0.914	3.509	3.966	**< 0.001**	**< 0.001**
Rock shading	Beta	− 1.429	0.300	0.202	0.237	-7.083	1.265	**< 0.001**	0.206
Invertebrate cover	Beta	− 1.808	1.118	0.206	0.248	-8.766	4.513	**< 0.001**	**< 0.001**
*Δ T°C	Gaussian	0.478	0.057	0.233	0.317	2.051	0.179	**0.040**	0.858

A Gaussian distribution was fit for the following continuous response variables: rock volume, embeddedness, and Δ T°C, and a beta distribution for the proportional response variables: surface area to volume ratio, rock shading and invertebrate cover. Site was included as a random-intercept in each model. *Model Δ T°C (surface temperature °C—adjacent temperature °C) includes occupancy fitted with an interaction effect of time since sunrise; this interaction was not significant ($P = 0.870$). Values in bold indicate statistical significance of variables ($P < 0.05$)

used as a management tool to improve biodiversity outcomes in agricultural landscapes.

Landscape factors

Aspect preferences are associated with warming and basking physiological requirements in reptiles (Langkilde et al. 2003; Shah et al. 2004). However, we did not find significant preferences for aspect in this study. In contrast, elevation was positively related to reptile abundance. Reptiles can be sensitive to small changes in elevation (Fischer and Lindenmayer 2005). Species composition, particularly of oviparous and viviparous reptiles can change with elevation, with intermediate elevations supporting diverse reptile populations (Shine et al. 2003; Fischer and Lindenmayer 2005; McCain 2010). The elevation range assessed in our study is reflective of an intermediate range (267 to 560 m) when compared with other studies from this region (see Fischer and Lindenmayer 2005) and to dry mountains globally (McCain 2010). In addition, increased abundance at higher elevation sites in our study could be driven by greater availability of suitable surface rock habitat as weathering and erosion processes are more pronounced on peaks and ridges than on lower slopes where silt deposits can bury rocks. This could increase local scale carrying capacity and potentially cause a concentration effect in higher elevation areas if there is limited overwintering habitat in the surrounding landscape.

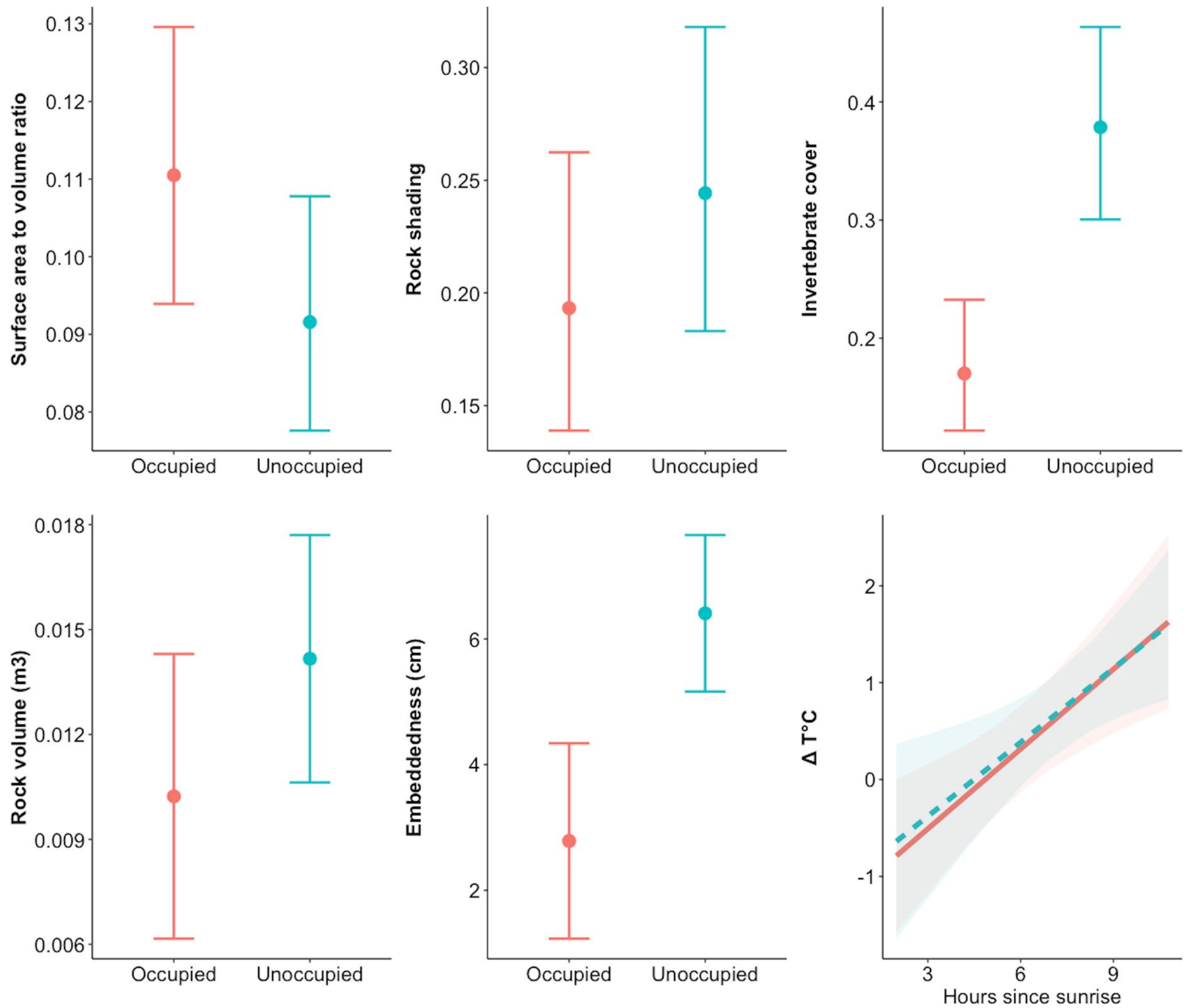

Fig. 4 Predicted values of rock traits influencing reptile occupancy at present sites. Values represent mean ± 95% confidence interval. Site is fitted as a random-intercept effect in all models. Model Δ T°C (surface temperature °C—adjacent temperature °C) includes occupancy fitted with an interaction effect of time since sunrise

The negative association with canopy cover found in our study corroborates other evidence that rock-dependent reptiles actively avoid shaded areas (Langkilde et al. 2003; Pringle et al. 2003; Goldsbrough et al. 2006; Row and Blouin-Demers 2006; Harvey and Weatherhead 2010; Croak et al. 2012; Huang et al. 2014). Increased canopy cover reduces the quality of thermally suitable basking and retreat-sites for reptiles and other ectotherms (Pringle et al. 2003; Goldsbrough et al. 2006; Row and Blouin-Demers 2006; Harvey and Weatherhead 2010). This correlation has implications for vegetation management and the rehabilitation of rocky environments in production landscapes. In agricultural areas, the primary conservation strategy is to fence off native remnant areas and introduce dense tree and shrub plantings, typically in areas that landholders perceive as low productivity. Often these areas of perceived low productivity contain rock habitat. Tree and shrub plantings result in a high density of stems, canopy cover and shade levels. This could have a perverse effect on the diversity of rock-dependent reptile species occupying these areas. In addition, rocky areas are less likely to burn, and prescribed fire is often ineffective for thinning eucalypts in rocky habitats, leading to areas becoming overgrown (Clarke 2002).

The conservation conundrum of improving vegetation cover in the landscape while maintaining structurally open habitats, highlights the need to consider the effects of conservation actions on all taxa and manage areas appropriately to ensure both structural and vegetative aspects are maintained.

Rock factors

We found evidence that reptile retreat-site selection was associated with the physical characteristics of the habitat, consistent with previous work (Shah et al. 2004; Goldsbrough et al. 2006; Chukwuka et al. 2021). As the majority of the species captured in our study were medium-bodied skinks, our results would most closely reflect the preferences of this group rather than other size classes. Occupied rocks were smaller and had a greater surface area to volume ratio than unoccupied rocks. By contrast, retreat-site selection was positively related to greater rock size in New Zealand (Chukwuka et al. 2021), but the results are mixed for other reptiles in Australia (Shah et al. 2004; Goldsbrough et al. 2006; Croak et al. 2008; Dennison et al. 2012), although these studies examined only rock-on-rock habitat. However, our results are consistent with other research that saxicolous reptiles select thinner rocks, suggesting that larger surface area to volume ratios may explain the mixed results of rock size and the prevailing preference for thinner rocks (Schlesinger and Shine 1994a; Webb et al. 2004; Croak et al. 2008). Flatter rocks have a greater surface area and thus receive more solar radiation across the rock resulting in a broader thermal gradient within or underneath it (Huey et al. 1989). A significant difference in thermal properties of occupied and unoccupied rocks was not found in this study, most likely due to the single time point of rock temperature measurements, and measurement of displaced rocks, rather than a series of continuous under-rock measurements (Pike et al. 2010). Including individual size data or species size classes (small-bodied compared with medium-large bodied species) may help to further explain thermal refugia preferences due to differences in cooling and heating rates among reptiles and individuals. Nevertheless, the physical rock traits selected by reptiles in this study are likely explained by their favourable thermal properties, which is consistent with other research that thermal regimes profoundly influence retreat-site selection of rocks by reptiles (Huey et al. 1989; Kearney 2002; Sabo 2003; Webb and Pringle 2004; Row and Blouin-Demers 2006; Harvey and Weatherhead 2010; Cox et al. 2018; Chukwuka et al. 2021). Traits of occupied rocks can help to inform management and restoration efforts, particularly in agricultural areas.

We found that reptiles selected rocks that were shallowly-embedded in the soil. Minimal embeddedness is likely to provide easy access under rocks, particularly for species that construct burrows underneath rocks for nocturnal retreats (Goldsbrough et al. 2006). Further, the small depressions between a rock and soil substrate provides an opportunity for thermoregulation, allowing reptiles to position themselves to maximise heat conduction (Huey et al. 1989; Croak et al. 2008; Chukwuka et al. 2021). We also found that reptiles avoided rocks that had high colonisation by invertebrates of the substrate surface. Our results were broadly consistent with laboratory trials indicating avoidance behaviours by similar reptiles such as the copper-tailed skink *Ctenotus taeniolatus* (Goldsbrough et al. 2006) and juveniles of the yellow-bellied water-skink *Eulamprus heatwolei* (Head et al. 2002) when exposed to chemosensory cues of predatory invertebrates such as ants and spiders. Understanding additional features of the three-dimensional space available under rocks, including colonisation patterns by other species, may assist in management and refining restoration efforts (Croak et al. 2008).

Conservation implications and further research

Our analyses revealed that surface rocks support abundant reptile populations at small spatial scales in temperate agricultural landscapes. Yet there is a paucity of information concerning the properties of surface rock that provide optimal habitat, how to best manage this habitat or the importance of surface rock for conservation globally. For example, surface rocks can provide a refuge against the effects of fire and extreme temperatures (Clarke 2002; Atkins et al. 2015), yet protection from fire may lead to outcrops becoming overgrown (Clarke 2002). There is a need to protect critical surface rock from clearing (Shine et al. 1998; Michael et al. 2021), overgrowth (Pike et al. 2011a, b), invasive plants and animals (Michael et al. 2008) and potentially from inappropriate grazing regimes (Michael et al. 2008, 2010). However, further research is needed to quantify appropriate grazing and fire regimes in landscapes dominated by scattered surface rocks. Based on our results, we suggest canopy openness is maintained in surface rock habitats, particularly those supporting high densities of smaller, flat rocks. There is evidence that targeted canopy removal can increase the availability of sun-exposed habitat patches for specialist reptiles and restore reptile assemblages (Pike et al. 2011a, b). Further, vegetation restoration should occur adjacent to, not within areas of high densities of surface rock. Actively managing and monitoring changes in vegetation structure to maintain thermally suitable environments is critical for reptile persistence.

While there are numerous studies documenting the surface rock preferences of reptiles (Schlesinger and Shine 1994a; Langkilde et al. 2003; Shah et al. 2004; Goldsbrough et al. 2006; Croak et al. 2012), these studies focus on rock sheaths and crevices (rock-on-rock). Studies of surface rocks on soil substrates are limited, and in some ecosystems, the study of these retreat-sites is actively avoided (Kearney 2002; Croak et al. 2012). However, it is important that surface rock on soil is recognised as being important for conservation, given the ecological values documented in this study and threats faced by this habitat (Michael et al. 2021). The relatively small size of surface rocks in agricultural landscapes enables vast areas to be picked, crushed, and destroyed with little time or effort. Concerningly, the scale and rate of current and past rock removal from farming regions are unknown as there are no reporting or offsetting requirements as part of routine agricultural activities anywhere in the world. The occurrence of surface rocks in the landscape is also not easily detected by satellite imagery, so remote methods are currently unsuitable for mapping this habitat at small spatial scales. By contrast, large outcrops are rarely targeted for agriculture, although they do face their own threats such as bush-rock collection (Schlesinger and Shine 1994a; Pike et al. 2010), quarrying, heavy shading by vegetation, and the impacts of pest species (Michael et al. 2010).

The loss and degradation of surface rocks in agricultural landscapes has broad implications for maintaining populations of cryptozoic species. For example, many cryptozoic species that depend on surface rocks rarely occupy alternative overwintering habitats (e.g., logs or vegetation), such as the nationally vulnerable pink-tailed worm-lizard *Aprasia parapulchella* (*Environment Protection and Biodiversity Conservation Act 1999*). Grass tussocks and logs can provide some surrogate habitat in the absence of rocks during warmer months when species are active, yet they do not provide the same protection and thermal properties, particularly for burrowing species (Atkins et al. 2015). Therefore, declines in vulnerable reptile populations in agricultural regions will go undetected without on-ground monitoring or policy changes pertaining to the clearing of rock habitats as part of routine agricultural activities (Michael et al. 2021).

Current global estimates are that one in five reptiles are threatened with extinction (Cox et al. 2022) with agricultural expansion and intensification the most prominent threat to reptiles (Ribeiro et al. 2009; Tingley et al. 2019; Cox et al. 2022). There is an urgent need to protect and manage habitats that support reptile populations, particularly in agricultural areas where extinction threats are greatest. In Australia, approximately 16% of terrestrial squamates utilise surface rocks for shelter (Michael et al. 2021) and this is likely to be equally high in other regions of the world (Ribeiro et al. 2009; Biaggini and Corti 2015; Rotem et al. 2016; Chukwuka et al. 2021). To combat potential population extinctions, we recommend greater protection for current surface rock habitat and suggest that incorporating surface rock in restoration programs (see McDougall et al. 2016; Alvarez and Guida-Johnson 2019; Palmer et al. 2022) can improve biodiversity outcomes in agricultural landscapes.

Conclusion

We found that surface rocks are utilized as overwintering retreat-sites by many reptiles in a temperate agricultural landscape. Because many temperate zone reptiles brumate or have reduced activity during cool seasons, prolonged use of surface rocks makes these species vulnerable to disturbance. Our study highlights that relatively small patches of surface rock can support high reptile numbers, with maximum density estimates up to 208 individuals per hectare. Our analyses highlight that multiple factors at multiple spatial scales have an important influence on site and retreat-site selection in surface rock habitats. Our results suggest that, in the study region, focusing conservation and restoration efforts on areas at intermediate elevations, with minimal canopy cover and smaller, flatter rocks is likely to be of most benefit to reptiles in this landscape. To date, restoration on farms has focused primarily on improving and maintaining native vegetation attributes and related functions. The negative association with canopy cover found in our study corroborates other evidence suggesting that native vegetation restoration may not always lead to beneficial conservation outcomes for reptiles (Cunningham et al. 2007; Craig et al. 2010; Michael et al. 2011; Pike et al. 2011a, b). Maintaining and restoring abiotic habitats is just as important as their living counterparts.

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Author contributions JLO and DRM originally formulated the idea. JLO, CNF, DRM, WB., DBL conceived and designed the methodology. JLO conducted fieldwork. JLO, CNF, WB analysed the data. JLO wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated during the study are available from the corresponding author on request.

Declarations

Conflict of interest The authors do not have conflicts of interest to declare.

References

Alvarez LM, Guida-Johnson B (2019) Habitat restoration for endemic lizards in an oilfield in payunia Argentina. Ecol Restor 37(4):217–221

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26(1):32–46

Atkins Z, Clemann N, Robert KA (2015) Does shelter site selection aid persistence of a threatened alpine lizard? assessing *Liopholis guthega* populations a decade after severe fire in southeastern Australia. J Herpetol 49(2):222–229

Biaggini M, Corti C (2015) Reptile assemblages across agricultural landscapes: where does biodiversity hide? Anim Biodivers Conserv 38(2):163–174

Böhm M, Collen B, Baillie JEM et al (2013) The conservation status of the world's reptiles. Biol Cons 157:372–385

Brooks ME, Kristensen K, Van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R Journal 9(2):378–400

Bureau of Meteorology (2021) Climate statistics for Australian locations. Monthly climate statistics. https://www.bom.gov.au/climate/averages/tables/cw_073141.shtml. Accessed 27 June 2022

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, Germany

Cecchetto NR, Medina SM, Taussig S, Ibargüengoytía NR (2019) The lizard abides: cold hardiness and winter refuges of *Liolaemus pictus* argentinus in patagonia Argentina. Can J Zool 97(9):773–782

Chukwuka CO, Mello RSR, Cree A, Monks JM (2021) Thermal heterogeneity of selected retreats in cool-temperate viviparous lizards suggests a potential benefit of future climate warming. J Therm Biol 97:102869

Clarke PJ (2002) Habitat islands in fire-prone vegetation: do landscape features influence community composition? J Biogeogr 29(5–6):677–684

Colquhoun G, Hughes K, Deyssing L et al (2018) New South Wales Seamless Geology dataset, version 1 [Digital Dataset]. Geological Survey of New South Wales, NSW Department of Planning and Environment, Maitland. https://datasets.seed.nsw.gov.au/dataset/nsw-seamless-geology. Accessed 27 June 2022

Cox CL, Logan ML, Bryan O et al (2018) Do ring-necked snakes choose retreat sites based upon thermal preferences? J Therm Biol 71:232–236

Cox N, Young BE, Bowles P et al (2022) A global reptile assessment highlights shared conservation needs of tetrapods. Nature 605:285–290

Craig MD, Hobbs RJ, Grigg AH et al (2010) Do thinning and burning sites revegetated after bauxite mining improve habitat for terrestrial vertebrates? Restor Ecol 18(3):300–310

Croak BM, Pike DA, Webb JK, Shine R (2008) Three-dimensional crevice structure affects retreat site selection by reptiles. Anim Behav 76(6):1875–1884

Croak BM, Pike DA, Webb JK, Shine R (2012) Habitat selection in a rocky landscape: experimentally decoupling the influence of retreat site attributes from that of landscape features. PLoS One 7(6):e37982

Croak BM, Webb JK, Shine R (2013) The benefits of habitat restoration for rock-dwelling velvet geckos *Oedura lesueurii*. J Appl Ecol 50(2):432–439

Cunningham RB, Lindenmayer DB, Crane M, Michael D, MacGregor C (2007) Reptile and arboreal marsupial response to replanted vegetation in agricultural landscapes. Ecol Appl 17(2):609–619

Damgaard CF, Irvine KM (2019) Using the beta distribution to analyse plant cover data. J Ecol 107(6):2747–2759

Dennison S, Smith S, Stow A (2012) Long-distance geneflow and habitat specificity of the rock-dwelling coppertail skink *Ctenotus Taeniolatus*. Austral Ecol 37(2):258–267

Downes S, Shine R (1998) Heat, safety or solitude? using habitat selection experiments to identify a lizard's priorities. Anim Behav 55(5):1387–1396

Driscoll DA (2004) Extinction and outbreaks accompany fragmentation of a reptile community. Ecol Appl 14(1):220–240

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. Trends Ecol Evol 28(10):605–613

Du W, Webb J, Shine R (2009) Heat, sight and scent: multiple cues influence foraging site selection by an ambush-foraging snake *Hoplocephalus bungaroides* (Elapidae). Curr Zool 55(4):266–271

Filippi E, Luiselli L (2007) Non-random seasonal variation in the structure of a Mediterranean snake community. Web Ecol 7(1):40–46

Fischer J, Lindenmayer DB (2005) The sensitivity of lizards to elevation: a case study from south-eastern Australia. Divers Distrib 11(3):225–233

Garden JG, McAlpine CA, Possingham HP, Jones DN (2007) Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: a case study from Brisbane Australia. Austral Ecol 32(6):669–685

Gibbons JW, Scott DE, Ryan TJ et al (2000) The global decline of reptiles, déjà vu amphibians: reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. BioScience 50(8):653–666

Goldsbrough C, Shine R, Hochuli DF (2006) Factors affecting retreat-site selection by coppertail skinks (*Ctenotus taeniolatus*) from sandstone outcrops in eastern Australia. Austral Ecol 31(3):326–336

Greer A (2022) Encyclopedia of Australian Reptiles. Australian Museum, Sydney

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4. http://florianhartig.github.io/DHARMa/

Harvey DS, Weatherhead PJ (2010) Habitat selection as the mechanism for thermoregulation in a northern population of massasauga rattlesnakes (*Sistrurus catenatus*). Écoscience 17(4):411–419

Head ML, Keogh JS, Doughty P (2002) Experimental evidence of an age-specific shift in chemical detection of predators in a lizard. J Chem Ecol 28(3):541–554

Hebbali A (2018) olsrr: Tools for Building OLS Regression Models. R package version 0.5. 2.

Huang A (2017) Mean-parametrized Conway–Maxwell–Poisson regression models for dispersed counts. Stat Model 17(6):359–380

Huang S-P, Porter WP, Tu M-C, Chiou C-R (2014) Forest cover reduces thermally suitable habitats and affects responses to a warmer climate predicted in a high-elevation lizard. Oecologia 175(1):25–35

Huey RB, Peterson CR, Arnold SJ, Porter WP (1989) Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology 70(4):931–944

Kearney M (2002) Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. J Therm Biol 27(3):205–218

Langkilde T, O'Connor D, Shine R (2003) Shelter-site use by five species of montane scincid lizards in south-eastern Australia. Aust J Zool 51(2):175–186

Lüdecke D (2018) ggeffects: tidy data frames of marginal effects from regression models. J Open Source Soft 3(26):772

Markle CE, Moore PA, Waddington JM (2020) Temporal variability of overwintering conditions for a species-at-risk snake: Implications for climate change and habitat management. Glob Ecol Conserv 22:e00923

Martino JA, Poulin RG, Parker DL, Somers CM (2012) Habitat selection by grassland snakes at northern range limits: Implications for conservation. J Wildl Manag 76(4):759–767

McCain CM (2010) Global analysis of reptile elevational diversity. Glob Ecol Biogeogr 19(4):541–553

McDougall A, Milner RN, Driscoll DA, Smith AL (2016) Restoration rocks: integrating abiotic and biotic habitat restoration to conserve threatened species and reduce fire fuel load. Biodivers Conserv 25(8):1529–1542

Michael D, Lindenmayer D (2018) Rocky outcrops in Australia: ecology conservation and management. CSIRO Publishing Collingwood, Australia

Michael DR, Cunningham RB, Lindenmayer DB (2008) A forgotten habitat? granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. J Appl Ecol 45(6):1742–1752

Michael DR, Lindenmayer DB, Cunningham RB (2010) Managing rock outcrops to improve biodiversity conservation in Australian agricultural landscapes. Ecol Manag Restor 11(1):43–50

Michael DR, Cunningham RB, Lindenmayer DB (2011) Regrowth and revegetation in temperate Australia presents a conservation challenge for reptile fauna in agricultural landscapes. Biol Cons 144(1):407–415

Michael DR, Crane M, Florance D, Lindenmayer DB (2018) Revegetation, restoration and reptiles in rural landscapes: insights from long-term monitoring programmes in the temperate eucalypt woodlands of south-eastern Australia. Ecol Manag Restor 19(1):32–38

Michael DR, Moore H, Wassens S et al (2021) Rock removal associated with agricultural intensification will exacerbate the loss of reptile diversity. J Appl Ecol 58(7):1557–1565

Morrison ML, G. MB, William MR, (2006) Wildlife-habitat relationships : concepts and applications. Island Press, Washington

Murphy CM, Smith LL, O'Brian JJ, Castleberry SB (2021) Overwintering habitat selection of the eastern diamond-back rattlesnake (*Crotalus adamanteus*) in the Longleaf Pine ecosystem. Herpetol Conserv Biol 16(1):203–210

Oksanen J, Blanchet FG, Kindt R et al (2013) R Package 'vegan': Community Ecology Package 2.3–3 edn

Palmer A, Milner RNC, Howland B, Gibbons P, Kay GM, Sato CF (2022) Rock supplementation as an ecological restoration strategy for temperate grassland reptiles. Austral Ecol 47(7):1402–1414

Penado A, Rocha R, Sampaio M, Gil V, Carreira B, Rebelo R (2015) Where to "rock"? choice of retreat sites by a gecko in a semi-arid habitat. Acta Herpetol 10(1):47–54

Pike DA, Croak BM, Webb JK, Shine R (2010) Subtle—but easily reversible—anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. Anim Conserv 13(4):411–418

Pike DA, Webb JK, Shine R (2011a) Chainsawing for conservation: ecologically informed tree removal for habitat management. Ecol Manag Restor 12(2):110–118

Pike DA, Webb JK, Shine R (2011b) Removing forest canopy cover restores a reptile assemblage. Ecol Appl 21(1):274–280

Pringle RM, Webb JK, Shine R (2003) Canopy structure, microclimate, and habitat selection by a nocturnal snake. *Hoplocephalus Bungaroides* Ecol 84(10):2668–2679

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Austria

Reading CJ, Luiselli LM, Akani GC et al (2010) Are snake populations in widespread decline? Biol Let 6(6):777–780

Ribeiro R, Santos X, Sillero N, Carretero MA, Llorente GA (2009) Biodiversity and land uses at a regional scale: Is agriculture the biggest threat for reptile assemblages? Acta Oecol 35(2):327–334

Rotem G, Gavish Y, Shacham B, Giladi I, Bouskila A, Ziv Y (2016) Combined effects of climatic gradient and domestic livestock grazing on reptile community structure in a heterogeneous agroecosystem. Oecologia 180(1):231–242

Rotem G, Giladi I, Bouskila A, Ziv Y (2020) Scale-dependent correlates of reptile communities in natural patches within a fragmented agroecosystem. Landscape Ecol 35(10):2339–2355

Row JR, Blouin-Demers G (2006) Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Écoscience 13(4):443–450

Sabo JL (2003) Hot rocks or no hot rocks: overnight retreat availability and selection by a diurnal lizard. Oecologia 136(3):329–335

Schlesinger CA, Shine R (1994a) Choosing a rock: Perspectives of a bush-rock collector and a saxicolous lizard. Biol Cons 67(1):49–56

Schlesinger CA, Shine R (1994b) Selection of diurnal retreat sites by the nocturnal gekkonid lizard *Oedura Lesueurii*. Herpetologica 50(2):156–163

Shah B, Shine R, Hudson S, Kearney M (2004) Experimental analysis of retreat-site selection by thick-tailed geckos *Nephrurus milii*. Austral Ecol 29(5):547–552

Shine R, Webb JK, Fitzgerald M, Sumner J (1998) The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides* (Serpentes : Elapidae). Wildl Res 25(3):285–295

Shine R, Elphick MJ, Barrott EG (2003) Sunny side up: lethally high, not low, nest temperatures may prevent oviparous reptiles from reproducing at high elevations. Biol J Lin Soc 78(3):325–334

Thienpont S, Cadi A, Quesada R, Cheylan M (2004) Overwintering habits of the European pond turtle (*Emys orbicularis*) in the Isere department (France). Biologia, Bratislava 59(14):143–147

Tingley R, Macdonald SL, Mitchell NJ et al (2019) Geographic and taxonomic patterns of extinction risk in Australian squamates. Biol Cons 238:108203

Vicenzi N, Massarelli R, Ibargüengoytía N, Corbalán V (2021) Basking and retreat site selection of *Phymaturus palluma*, a rock-dwelling lizard in the Highlands of Aconcagua. An Acad Bras Ciênc 93(2):e20190662

Webb JK, Shine R (1998) Using thermal ecology to predict retreat-site selection by an endangered snake species. Biol Cons 86(2):233–242

Webb JK, Pringle RM, Shine R (2004) How do nocturnal snakes select diurnal retreat sites? Copeia 4:919–925

Webb JK, Pike DA, Shine R (2009) Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. Behav Ecol 21(1):72–77