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Conserving reptiles within a multiple-use landscape: determining habitat affiliations of reptile communities in the northern Jarrah forest of south-western Australia

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RH: Reptile habitat affiliations in the Jarrah forest

Short Summary

Identifying species' habitat affiliations is important for their conservation so we completed reptile surveys in the Jarrah forest, aiming to identify habitat affiliations for all reptile species detected, including rare species. Exploratory analyses provided guidance for further research and informed habitat management for all species, including rare species, but maintaining habitat heterogeneity and complexity will likely conserve the greatest number of species.

Abstract: Disturbed landscapes can provide habitat for a variety of species; however, for fauna, a strong understanding of their habitat affiliations is critical both to detect species and develop management prescriptions to maintain their populations. We assessed habitat affiliations of common, uncommon and rare reptile species in a multiple-use landscape, the northern Jarrah forest of south-western Australia. To identify predictors of reptile occurrence, we related reptile presence/absence, or relative abundance, to habitat, climatic and seasonal variables. Because the reptiles studied have cryptic behaviours and low numbers of detections, we used a combination of analyses including non-metric Multi-Dimensional scaling, occupancy and regression models. We identified specific habitat affiliations for the most common species and potential linkages with vegetation structure for most uncommon species. There were insufficient detections to determine habitat affiliations accurately for most rare species. Often species were detected too infrequently to determine specific habitat variables that influence occupancy and detection, and altering survey time and scale may increase detections so that habitat affiliations can be determined. However, in highly speciose landscapes, like our study area, we may not be able to wait until we have enough detections to define the habitat affiliations of all reptiles before we make management decisions. Therefore management activities that maintain habitat heterogeneity and complexity is likely to be the best strategy to conserve the most reptile species.

Introduction

Biodiversity loss is increasing as humans clear and modify more of the earth’s surface (Pimm and Raven 2000; Sala *et al.* 2000). Thus, if society is to conserve biodiversity in the face of increasing habitat clearance and modification, it is increasingly important to understand species habitat affiliations (Koellner and Schmitz 2006; Lindenmayer *et al.* 2012). Understanding species’ habitat affiliations enables the identification of important habitat features to maintain species' persistence. This is especially important in multiple-use landscapes, where identifying and predicting fauna species’ habitat affiliations is critical for integrating conservation with competing extractive land uses (Morrison 2009), and in highly biodiverse communities, which occur primarily in tropical and southern temperate areas (Myers *et al.* 2000; [Böhm](#) *et al.* 2013) and contain many uncommon and rare species (Fisher *et al.* 1943; Magurran and Henderson 2003).

However, habitat affiliations are difficult to predict *a priori* in areas where the ecology of species is poorly known. Consequently, habitat affiliations of these elusive or rare species may, by necessity, be based on patterns of association from relatively few observations, increasing the probability of identifying spurious or incorrect habitat affiliations. Yet, because uncommon and rare species often form most of the biodiversity in hotspots, identifying their habitat affiliations significantly improves the ability to conserve biodiversity effectively. Furthermore, these uncommon and rare species may play an important role in maintaining ecosystem function during or after disturbances (Main 1982). Empirical (Hobbs *et al.* 2007) and theoretical studies (Yachi and Loreau 1999) support the importance of uncommon and rare species in the environment and suggest that they may become more critical as environments experience climate change.

The standard analysis for identifying habitat affiliations in community-wide studies is to model detectability with habitat variables, but this method can be data hungry and, hence is suitable only for the most common species unless the sampling effort is increased to adequately detect rare species (Fischer *et al.* 2004; Garden *et al.* 2007). Additionally, modelling detectability on sparse data from uncommon or rare species can often be worse than not accounting for detectability at all (Welsh *et al.* 2013). Therefore, different approaches need to be considered for identifying habitat affiliations of uncommon and rare species, and our goal here is to balance accurate data interpretation with useful analysis methods. Species specific habitat and behavioural information is often lacking for many Australian vertebrates and this is particularly true for reptiles (MacNally and Brown 2001). Part of the reason for this is that Australia has the world's most speciose reptile fauna (Groombridge 1992) and Australian reptile communities typically contains a high proportion of rare and uncommon species (Pianka 1986, 1989). Furthermore, reptiles may have specific habitat requirements that are not shared with other vertebrate groups because, unlike the best studied faunal groups, birds and mammals, habitat suitability for poikilothermic reptiles is heavily dependent on specific thermal conditions. This makes abiotic determinates such as climatic (thermal), seasonal variables and habitat structure critical in determining reptile habitat affiliations by influencing activity times, survival, reproduction, foraging and protection from predators (Heatwole and Taylor 1987; Adolph and Porter 1993; Spence-Bailey *et al.* 2010). This combination of high species richness, low abundance of many species and diverse habitat requirements means that elucidating the habitat affiliations and requirements of many reptile species will be critical for conserving biodiversity in Australia.

The northern Jarrah (*Eucalyptus marginata*) forest, a multiple-use forest in south-western Australia, lies within a biodiversity hotspot (Myers *et al.* 2000). The rich and unique biodiversity in the region is potentially threatened by habitat loss and alteration from multiple competing land uses (mining, logging, agriculture, fire management, water catchments and recreational use (Dell and Havel 1989; Gardner and Bell 2007)). Hence, it is essential to understand the habitat affiliations of the most species in the Jarrah forest to identify important habitats or features to help conserve its biodiversity (Yeatman *et al.* 2017). Specifically, the Jarrah forest has high reptile species richness (~45 species [Nichols and Muir 1989]), with the majority of species being small (<8 g) and rare, with patchy distributions or cryptic behaviours (Craig *et al.* 2009). These characteristics make Jarrah forest reptile species difficult to detect, and hence study and monitor (Williams and Mitchell 2001; Nichols and Grant 2007; Craig *et al.* 2009) and currently we know very little about many of the species' habitat affiliations. In this study we aimed to determine the habitat affiliations of as many reptiles as possible in the northern Jarrah forest based on vegetation structure, climatic or seasonal variables and, if required, assess common, uncommon and rare reptile species using different analyses to best predict their habitat affiliations.

Materials and Methods

Study Area

This study was conducted within Alcoa of Australia's (hereafter, Alcoa) Huntly mine lease ~10 km N of Dwellingup in the northern Jarrah forest (32°36'S, 116°06'E). The Jarrah forest is a dry, open sclerophyll forest endemic to south-western Australia, where the canopy is dominated almost entirely by the two eucalypts Jarrah and Marri (*Corymbia calophylla*). Common midstorey species include Sheoak (*Allocasuarina fraseriana*), Bull Banksia (*Banksia grandis*) and Snottygobble (*Persoonia longifolia*) (Dell and Havel 1989). The area

has a Mediterranean climate (Dell and Havel 1989) with temperatures ranging from mean maxima and minima of 15.0 °C and 5.4 °C in July to 29.6 °C and 14.5 °C in February. Average annual rainfall is ~1236 mm at Dwellingup, the nearest weather station, with average rainfall peaking in July (208.7 mm; Bureau of Meteorology, <http://www.bom.gov.au/climate/data/>).

Study Design

We obtained data from 35 trapping arrays distributed randomly throughout reference areas at the Huntly mine lease (Fig. 1) which covers ~160 km². We defined reference areas as areas without current or previous mining which represent Alcoa's aim for current restoration practices. It is important to determine reptile habitat affiliations in these reference areas to later define an expectation and comparison for reptile occupancy in the successional stages of restoration. To best represent reference areas, survey sites were selected to minimize anthropogenic influences and therefore, we avoided forest infested with *Phytophthora cinnamomi* (an invasive plant pathogen), and areas burnt <5 years previously. To obtain a broad spatial spread across the mine lease while minimising potential edge effects (but see Craig et al. 2015) from cleared, mined and restored forest, all sites were located >70 m from current or past mining and post-mining restoration. To detect the greatest variety of species, and capture as much of the reptile community as possible, including uncommon and rare species, we employed pitfall, funnel, Elliott and cage traps. All surveys used the same trapping arrays (Fig. S1 consisting of a 29 m aluminium fly-wire drift fence (~30 cm tall) with 9 pitfall traps (three 41 cm high by 28 cm diameter 20L plastic buckets, four 11.3 cm high by 11.5 diameter 850 mL take-away containers, and two 40 cm long by 15cm diameter PVC tubes) located every 3 m along the fence, 4 funnel traps (two paired on each side of the drift fence) located 7 m from either end of the drift fence between the take-away containers

and the PVC tubing, 4 Elliott traps located 5m on either side of the end 20 L buckets, and 1 cage trap located 5 m from one of the end 20 L buckets. Elliott traps were baited with universal bait (peanut butter and rolled oats) and honey and contained shredded paper for warmth while pitfall traps were unbaited. Elliott traps were baited as data was also collected on mammals, but these mammal data are not presented here. Sites were surveyed between 2005 and 2012, although not every year, during the seasons when reptiles were active: 5 days/4 nights during October (early spring), December (early summer) and March (early autumn), with some sites additionally surveyed in November (late spring) (see Table S1). All individuals captured during surveys were identified to species and skinks (except *Egernia napolenois* and *Tiliqua rugosa* because of their large size and *Lerista microtis* as only one was detected) were individually marked by removing 1 or 2 toes (94.4% and 5.6% of the individuals marked, respectively), unless they had natural toe loss (~5.2%), and released at their capture site.

We completed structural assessments at each of the arrays after the completion of trapping to quantify habitat variables. There was some variation in the precise methodology between years (i.e. size of the survey area or number of estimates), but the majority of surveys were completed using the following method. Visual estimates of percent litter cover and bare ground and all vegetation in three strata (0-1 m, 1-2 m and 2-5 m) were made within twelve 0.25 m² plots at 5 and 10 m on either side of all 20 L bucket pitfalls. Understorey (<3 m in height) and overstorey (>3 m in height) plant densities were determined by measuring the distance from the centre of 0.25 m² plots to the closest understorey or overstorey plant and averaging distances to get density estimates using the formula from Barbour *et al.* (1987). Canopy cover was recorded by taking vertical digital images above the centre of 0.25 m² plots and classifying crown cover from the images (Pekin and Macfarlane 2009). Earlier

surveys (pre-2011) used a densiometer to measure canopy cover and estimates from those years were calibrated with canopy photograph estimates before analysis. Canopy height was estimated from the height of the 5 tallest trees within 40 m of the trapping grid, measured using a tree vertex, and coarse woody debris (CWD: >5 cm in diameter at one end) was estimated by measuring the diameter and length of all debris within 5 m of the drift-fence. In addition we included the fuel age (determined from GIS data at the Western Australia Department of Parks and Wildlife) and the proportion of restored area within 100 m of the array to assess additional anthropogenic landscape influences (see below). The climatic variables calculated were the maximum and minimum temperature for each trapping day (averaging the day before and the day of checking) and the precipitation within two weeks preceding the day of the trapping session (<http://www.bom.gov.au/climate/data/>; summary of all habitat variables in Table S2). Information on the month and year of surveys (seasonal variables) were recorded to determine the influence of these categorical variables on reptile detectability and occupancy.

Overall, our study was designed to gain information on reference areas and avoid the impacts of anthropogenic disturbances; however, we acknowledge that reptile relationships with disturbances are well documented and the impacts of fire (Schmidt and Mason 1973, Penn *et al.* 2003, Kavanagh and Stanton 2005, Driscoll and Henderson 2008), logging (Goldingay *et al.* 1996, Kavanagh and Stanton 2005) and mining (Taylor and Foxx 2001) likely exist in our study area. As these disturbances may alter the composition of the reptile species for many years (Taylor and Fox 2001), we assessed time since fire and the proportion of mined and restored area; however, the influence of logging was not addressed as it is rarely possible to quantify the intensity of logging and, even with years of trapping data, it is challenging, if not

impossible, to assess the influence of logging on small vertebrate species of the Jarrah forest (Wayne et al. 2001).

Statistical Analyses

Trapping data were converted into presence/absence detection histories (0 = absent, 1 = present) for each species by site (with recapture events being removed prior to analysis, ~3.7% of individuals were recaptured) or, for less common species (<10% of detections), left as the count of individuals captured. These abundance classifications were based on the ability to analyse the data; rare species (<1.5% of detections) relationships were potentially spurious and no individual analyses could be completed on them, uncommon species (between 1.5 and 10% of detections) did not contain adequate detections for occupancy modelling, but did for Poisson regressions, and common species (>10% of detections) were regularly detected and did not have any analysis restrictions. To assess the sampling regime and survey effort, we completed species accumulation curves on the number of detections per day for each species after correcting for the number of sites surveyed each day.

We removed habitat and climatic variables that were highly correlated ($r_{33} > 0.60$), which resulted in the removal of bare ground (correlated with litter cover $r_{33} = 0.65$) and understorey density (correlated with cover from 1 to 2 m, $r_{33} = 0.73$) from analyses. To define community groupings, we performed non-metric multidimensional scaling (nMDS) on the relative abundance (i.e. individual counts) of each species at each site (common, uncommon and rare) detected, with singletons removed to avoid errors in the analysis (*L. microtis* only). The rank order correlation of the data by site was explored, along with the fitted habitat variables relationship with the nMDS ordination, using the function Bioenv which compares the dissimilarity matrices of the species and habitat variables to determine a best subset of habitat

variables (Clarke and Ainsworth 1993). This subset of habitat variables was then assessed through permutation tests to determine the significance using Procrustes analyses.

Single species multi-season occupancy models (also referred to as dynamic occupancy models (MacKenzie *et al.* 2003; Kéry *et al.* 2013)) were only ran for the 5 common species (*Acritoscincus trilineatus*, *Hemiergis initialis*, *Lerista distinguenda*, *Menetia greyii*, and *Morethia obscura*) as these analyses were unable to be conducted on species with fewer detections. Occupancy was predicted using maximum likelihood estimation (MacKenzie 2006) and we assessed the impact of habitat, climatic and seasonal variables on probability of detection (p) and occupancy (ψ). First, the best models for detection probability were determined based on climatic and seasonal variables (e.g. $p(\text{MaxT}) \psi(.) = \text{detection probability is influenced by maximum temperature and occupancy is constant}$). Next combined models (p and ψ), which used the best models for detection probability, were added to occupancy with different habitat variables (e.g. $p(\text{MaxT}) \psi(0-1 \text{ m})$; where detection probability is influenced by maximum temperature and occupancy by the percent cover from 0 to 1 m). The Akaike information criterion (AIC; Burnham and Anderson 2002) was used to determine top models with associated variables. All well-supported models, which we define as those with $\Delta\text{AIC} \leq 2$ from the top model, were retained (Burnham and Anderson 2002) and if models that had $\omega < 0.9$, multiple models were considered plausible (Burnham and Anderson 2002). Parametric bootstrapping ($n = 1000$) of the models determined the fit of the models (Kéry *et al.*, 2005; Kéry *et al.* 2013) by generating a fit statistic (SSE, or Chi-square) for the top AIC model of each species, with large P -values indicating no evidence of lack of fit of the top model.

We determined potential habitat affiliations of uncommon species (*Christinus marmoratus*, *Cryptoblepharus buchananii*, *Ctenotus labillardieri*, *Diplodactylus lateroides* and *E. napoleonis*), using Poisson regression models in which the outcome (relative abundance) was modelled as a linear combination of the predictor variables (habitat covariates). Model averaging was completed to define significance of the habitat covariates quantified by summing the weights of a subset of models with $\Delta AICc < 2$, and consideration was taken (i.e. variables removed, under/over dispersion evaluated) to reduce issues arising from collinearity in model averaging (Cade 2015). Additionally, we report the relative importance of variables, as outlined in Cade (2015), as the absolute value of the z-values weighted by the maximum value. This weights the most important variable as 1.00 and all other variables in relation to it, to incorporate effect size and variance instead of focusing on the number of times a variable is present in the model subset. Relative importance values >0.5 were considered to be important.

All analyses were completed in R 2.14.1 (R Core Development Team 2016). The nMDS was completed using function Bioenv in package “Vegan” (Oksanen *et al.* 2015), occupancy models were generated using package “unmarked” (Fiske and Chandler 2011) and Poisson regression (glm) models were available within the core application of R, with model averaging completed with package “MuMIn” (Barton 2013).

Results

Across all surveys, we captured 706 individuals of 17 reptile species. The number of detections, excluding recaptures, for each species, over 8,840 trap nights, ranged from 171 for *M. obscura* to 1 for *L. microtis* (Table 1). The 5 most common skink species comprised >80% of all individuals captured, uncommon species accounted for ~17% of detections and

3 rare species the remaining 3% (see Table 1 for a species list and categories and Fig. S2 for
4 photos of the most common species detected). Additionally, species accumulation curves
5 verified that the sampling regime and number of surveys were adequate to document the
6 reptile biodiversity identified as occurring in the study area by Nichols and Nichols (2003),
7 with any other reptiles potentially occurring either extremely rare or requiring specific
8 sampling methods to detect (Fig. S3).

0 Three habitat variables, percent cover from 0 to 1 m, overstorey density and leaf litter, were
1 most correlated (0.20) with overall reptile community composition. Based on visual
2 assessments of the nMDS and habitat variables there appear to be three potential groupings of
3 species based on abundances and habitat affiliations (Fig. 2). One potential group, comprising
4 five skinks (*M. greyii*, *M. obscura*, *L. distinguenda*, *C. buchananii*, and *T. rugosa*), one gecko
5 (*D. lateroides*) and one elapid (*Parasuta nigriceps*), occurred in sites with low understorey
6 density and more open forest structure. Another potential group, consisting of two skinks (*E.*
7 *napoleonis* and *A. trilineatus*) and one dragon (*Pogona*- *minor*) was associated with increased
8 ground (0-1 m) cover and overstorey density, representing sites with a denser forest structure.
9 The last potential group was associated with increased leaf litter and included two skinks (*H.*
0 *initialis* and *C. labillardieri*) one pygopodid (*Aprasia pulchella*) one blind snake
1 (*Ramphotyphlops australis*) and one gecko (*C. marmoratus*). *Varanus rosenbergi*
2 [Varanidae] did not separate obviously into any group and no habitat affiliations were
3 identified for this species.

4
5 For occupancy models, in step one, species detection probabilities were influenced by
6 climatic ($n = 4$) and seasonal ($n = 1$) variables (Table 2 and Fig. S4). Maximum temperature
7 (mean $\pm$ SE: 24.9 ± 0.20 , range: 15.5 - 36.3 °C) influenced detection probabilities for *M.*

obscura, *M. greyii*, *L. distinguenda* and *A. trilineatus*. Two species displayed quadratic trends with temperature whereby their detection increased to an optimal temperature and then decreased (optimal temperatures, detection probability $\pm$ SE: *M. obscura* 31.2 °C, $p = 0.49 \pm 0.05$; *L. distinguenda*, 33.0 °C, $p = 0.44 \pm 0.08$). *M. greyii* and *A. trilineatus* detection probabilities both increased linearly as temperature increased. *H. initialis* detectability was influenced by month (March $p = 0.04$, October $p = 0.29$, November $p = 0.16$, December, $p = 0.35$).

The well-supported models for *A. trilineatus* suggested that occupancy increased with vegetation cover from 2 to 5 m. *H. initialis* had four well-supported models, and showed preferences for decreased CWD and increased cover from 0 to 1 and 1 to 2 m and overstorey density. In the well-supported models for *L. distinguenda*, occupancy increased with decreased cover from 0 to 1 m and overstorey density. *M. greyii* occupancy increased as cover from 1 to 2 and 2 to 5 m decreased. *M. obscura* occupancy increased as overstorey density decreased, being present only when densities were < 3220 stems ha^{-1} . Overall the models suggest that *A. trilineatus* and *H. initialis* prefer dense understorey and overstorey and *L. distinguenda*, *M. greyii*, and *M. obscura* prefer open areas with low cover. None of the goodness of fitness tests were significant indicating that models represented the data well.

Interestingly, the models also matched the outputs from the nMDS community grouping results as well.

Poisson models showed potential links between uncommon species and multiple habitat covariates (Table 3). Significant relationships between species relative abundances and habitat covariates were identified for *D. lateroides* and *C. marmoratus* with relative importance indicating strong positive relationships between *D. lateroides* and CWD and a

strong negative relationship between *C. marmoratus* and cover from 0 to 1 m (Table 3). Relative importance also indicated well-supported, positive relationships between *E. napoleonis* and cover from 0 to 1 and 2 to 5 m and a negative relationship with fuel age (Table 3). *Ctenotus labillardieri* also displayed a well-supported negative relationship with fuel age (Table 3). Additionally, *C. buehneri* had well-supported positive relationship with fuel age and a negative relationship with cover from 0 to 1 m (Table 3). Again, the results from these preliminary analyses matched the outputs from the community groupings well.

Discussion

We generated species specific models for 10 of the 17 detected reptiles (only the 5 most common included probability of detection), showing it is possible to define habitat affiliations for common and uncommon species using standard plot-based survey methods. However, cryptic and rare species' habitat affiliations were more difficult to determine with these methods, as they needed to be based on community level analyses. Our results suggested the community level analyses may identify habitat relationships for some rare and cryptic species but that it would be unlikely to identify potential relationships for those rare and cryptic species that were detected using general trapping methods.

Common reptiles

The habitat affiliations identified from the majority of our models for common species agreed with habitat affiliations observed in the limited previous studies present on reptiles in the Jarrah forest. *M. obscura*, *M. greyii* and *L. distinguenda* occupied forest areas that had low overstorey density and/or cover and overall a more open forest (Smith *et al.*, 1996; Nichols and Muir 1989; Bush *et al.* 2007; Craig *et al.* 2010; Craig *et al.* 2012). Increased leaf litter, which is important for *L. distinguenda* and *M. greyii* (Pianka 2011a) specifically, may

provide preferred foraging habitat if associated with highest abundance of preferred invertebrate prey (Simmonds *et al.* 1994; Cuccovia and Kinnear 1999; Majer *et al.* 2007). Decreased overstorey density likely provides an increased abundance of basking sites for all three species (Blouin-Demers and Weatherhead 2001). *Hemiergis* *initialis* was associated with multiple habitat covariates, which all suggest a link to increased habitat cover and complexity. Similarly, Craig *et al.* (2012) found that this species was related to increasing canopy height and CWD, which are likely proxies for sites that have greater productivity and habitat complexity. *Acritoscincus* *trilineatus* preferred dense habitats with increased low cover (<5 m), which was expected as they are often associated with stream zone vegetation with dense understorey (Nichols and Bamford 1985; Nichols and Muir 1989; Craig *et al.* 2012). Overall, the five most common species partitioned into two groups, with three preferring open forest and two associated with dense forest, suggesting that a heterogeneous landscape would help maintain populations of these species. Importantly, these preferences for open or dense forests were congruent between the community and individual species analyses and matched the few previous studies conducted on our common species.

Uncommon reptiles

Uncommon species' habitat affiliations, with the exception of *E. napoleonis*, were more difficult to substantiate due to a lack of species-specific studies. *Egernia* *napoleonis* appeared to prefer sites with low cover, which matches other studies that found this species preferred more open sites (Craig *et al.* 2011). *Egernia napoleonis* also displayed a link to decreased fuel age, which likely relates to cover as a study on *E. napoleonis* in restored sites suggested that they do not have a preference for burn age of logs (Christie *et al.* 2013). The presence and status of logs is important to *E. napoleonis* and they often display links with CWD when comparing restored and reference forest (Craig *et al.* 2012). This study focuses

only on reference forest, and it is likely that most reference forest areas at Huntly have sufficient CWD for *E. napoleonis*, as forests in our study area, have on average, 121 logs ha⁻¹ (Whitford *et al.* 2008) and *E. napoleonis* typically requires ~50 logs ha⁻¹ (Christie *et al.* 2013). Additionally, *D. lateroides* preferred areas with more CWD and the species is known to shelter under logs (Bush *et al.* 1995). However, other studies have suggested a preference for open rocky areas (Nichols and Bamford 1985; Bush *et al.* 2007) or areas with low litter cover (Craig *et al.* 2012) suggesting this species' habitat preferences may be more complex than our study identified, although the preference for areas with greater CWD volumes may be real. We determined that *C. labillardieri* preferred areas with younger fuel ages which matches well with anecdotal observations that the species prefers areas of dense cover (Nichols and Bamford 1985). The species also inhabits wet sclerophyll Karri (*E. diversicolor*) forests (Bush *et al.* 1995), again suggesting a preference for areas with high cover. The strongest relationship for *C. buehmanni* was a strong positive relationship with fuel age and, to a lesser extent cover from 0 to 1 m. A study in the Banksia woodlands also found that they prefer long unburnt areas within the Banksia woodlands (Valentine *et al.* 2012); however other studies in the Jarrah forest found that this arboreal species favours tree trunks (Pianka and Harp 2011) and shelters in crevices in dead wood (Nichols and Bamford 1985) and hence may prefer low cover. The strongest relationship for *C. marmoratus* was a negative relationship with cover from 0 to 1m and the few previous studies on this arboreal species have indicated it preferred areas with high densities of large trees and also sheltered under logs (Claridge *et al.* 2003; Cunningham *et al.* 2007). The Jarrah forest tends to have an open understorey when trees are over 30m (Ashton and Attiwill 1994); hence, it is likely that, in the Jarrah forest, *C. marmoratus* has a preference for an open understorey. Thus, for four of our uncommon species (*D. lateroides*, *C. labillardieri*, *C. buehmanni* and *C. marmoratus*), our results matched well with previous studies, although, for one species (*E. napoleonis*), our

study may not have identified all the habitat affiliations. Like our common species, though, there was good congruence between relationships identified from community and individual species analyses.

Rare reptiles

Our community analyses suggested that, although habitat affiliations could not be identified for *V. rosenbergi*, most rare and cryptic species seemed either to be associated with open or closed forests. The difficulty with these rare and cryptic species is that they are typically unknown ecologically and so it is not possible to determine whether these broad habitat affiliations are accurate. Our community analyses suggested that *P. minor* was associated with closed forests and this matches well with the few studies published on this species. Craig *et al.* (2007) reported that *P. minor* preferred sites with greater cover of dead plants between 0 and 1 m than random samples, while Craig *et al.* (2012) found that *P. minor* abundance increased with increasing understorey density. Results from these two studies are consistent with *P. minor* preferring closed forests and suggests that our community analyses accurately identified broad habitat preferences for this species. Two rare or cryptic species (*R. australis* and *A. pulchella*) were associated with dense leaf litter. Although the dearth of ecological information on these species make it impossible to evaluate the likelihood this association is true, anecdotal observations are that *R. australis* favours damp conditions (Bush *et al.* 1995) and shelters beneath leaf litter (Bush *et al.* 2007) while *A. pulchella* both forages (Bush *et al.* 1995) and shelters beneath leaf litter (Bush *et al.* 2007). These qualitative observations suggest that a preference for areas with high litter cover might be accurate reflection of true habitat affiliations. Our community analyses suggested that *T. rugosa* and *P. nigriceps* prefer open forests. Little is known about *P. nigriceps* to support the likelihood of this habitat association being true, but studies of *T. rugosa* outside the Jarrah forest have typically shown

a preference for areas that have low dense bushes (Fergusson [and](#) Algar 1986; Kerr *et al.* 2003; Kerr [and](#) Bull 2004) but these habitats were more open than the Jarrah forest although one study from the Jarrah suggested a preference for closed forest due to a positive relationship between *T. rugosa* and overstorey density (Craig *et al.* 2012). We believe these contrary results likely arise due to the mismatch between the spatial scale of the sampling arrays and the spatial scale of *T. rugosa* home ranges which results in detections [leading to the identification of spurious relationships due to](#) inaccurate measures of the distribution and abundance of *T. rugosa*. *Tiliqua rugosa* can have home ranges >5ha (Bull [and](#) Freake 1999; Kerr [and](#) Bull 2006) and we believe that the inability of the community analyses to identify habitat affiliations for *V. rosenbergi* [and unverifiable predictions for P. nigriceps](#) also result from the same issue. *Varanus rosenbergi* can have home ranges >40ha (Green [and](#) King 1978) and [it is likely that P. nigriceps, whose home range is unknown, is likely to have a home range size similar to another elapid Hoplocephalus stephensii, which](#) can have home ranges >20ha (Fitzgerald *et al.* 2002). It is well known that sampling plots most effectively detect the distribution and abundance of species if they are the around the same size, or larger, than the home ranges of individual species (Craig [and](#) Roberts 2005; Fischer *et al.* 2004; Morrison *et al.* 2006). Thus, the community analyses appeared to correctly identify habitat affiliations for one rare species (*P. minor*) and likely correctly identified affiliations for two further species (*R. australis* and *A. pulchella*). However, community analyses did not accurately identify habitat affiliations for the remaining three rare species (*T. rugosa*, *P. nigriceps* and *V. rosenbergi*), probably because these species had large home ranges.

Management outcomes

The results of our study highlighted issues that are likely to be typical of studies investigating habitat affiliations of reptiles in Australia, which has the world's richest reptile fauna

(Groombridge 1992). Namely, that most species will be recorded very infrequently (Pianka 1989; Thompson *et al.* 2003; Pianka 2011b), due to either rarity or crypsis, and that habitat affiliations will be difficult to identify for these rarely caught species. The standard trapping arrays used were designed to maximise captures rates across all species and therefore have lower capture rates for large, rare and cryptic reptiles and we were unable to identify their habitat associations with any confidence. Additionally, even with our extensive trapping effort we failed to capture some species (e.g. carpet python) that occur in the study area. For these species target survey methods including the use of active searches, coverboards and motion-sensitive cameras (e.g. Ryan *et al.* 2002; Kanowski *et al.* 2006; Welbourne *et al.* 2015), might obtain sufficient detections that combined with innovative methods of analysing the data collected (e.g. Sutherland *et al.* 2016), might correctly identify their habitat affiliations. Alternatively, using adaptive sampling methods, which expand trapping and habitat surveys based the location of detections of focal species to adjacent areas around these detections (Thompson and Seber 1996; Morrison *et al.* 2008), or using niche-based models (Guisan *et al.* 2006) to better target areas for sampling, may also improve detection rates for rare species although the number of detections is still likely to remain too small to identify habitat associations for many rare species. Radio-tracking is often an effective method of identifying habitat affiliations and resource requirements for rare species and has been widely used (e.g. Green and King 1978; Fitzgerald *et al.* 2002) but it is labour intensive, meaning only a few rare species could be studied contemporaneously using this method. Radio-tracking is appropriate for large species, but its use may be limited for rare species as they can only be placed on species with a body mass >4g and harmonic radar enables the tracking of species >2g in predominantly open areas only (Gourret et al. 2011). The issues identified with these methods, combined with the scarcity of long-term studies, the high richness of Australian reptile communities and the remoteness of much of the Australian landmass

means, however, that short-term plot based studies are likely to remain the primary method of identifying habitat affiliations for most rare species in Australia. This means that identifying habitat associations for many rare species in highly speciose communities will remain impossible, even with extensive surveys and suggests that we cannot wait until we have identified habitat affiliations for all reptiles in order to implement effective conservation plans. Our study suggests that implementing management activities that maintain habitat heterogeneity and complexity will be the most effective strategy for conserving the most reptile species. This was exemplified in our study by the fact that the important habitat variables for various species related to the ground, understorey, overstorey and no single habitat variable was identified as ‘most important’, even at the community level.

Conclusion

Our study suggests that, for species with small home ranges, community analyses of data from plot based studies likely identifies habitat affiliations for many common and uncommon species. However, given the uncertainty surrounding which affiliations were correctly identified, and the dearth of information to verify any postulated affiliations, it would be prudent to treat affiliations for rare species as hypotheses to be tested by further study (Doak *et al.* 2005). Our study also suggested that, while different reptile species can have similar habitat affiliations, there was a wide variety of affiliations among different species. Together these results suggest that, until habitat affiliations are identified for many uncommon and rare reptile species, it would be prudent to retain as much habitat heterogeneity and complexity as possible across landscapes. Habitat heterogeneity is typically associated with increased species richness (Schoener 1974) and is known to be important in maintaining speciose reptile communities (Brown and Nelson 1993; Nichols and Nichols 2003; Fischer *et al.* 2004; Driscoll *et al.* 2012). Habitat heterogeneity in Australia will typically involve appropriate

prescriptions to manage disturbance, such as fire (Driscoll et al. 2012; Pianka and Goodyear 2012) and thinning (Kutt et al. 2012; Eyre et al. 2015), to maintain sufficient patches of different post-disturbance ages at an appropriate spatial scale. This is likely to prove increasingly challenging as more landscapes are affected by anthropogenic activities, but will be necessary to effectively conserve our rich herpetofauna with limited ecological knowledge.

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Table 1. Reptile species detected

The total number of detections (No. detections) summed over all sites and all years and the number of sites occupied by each species (No. sites occupied; $n = 35$). Five skink species make up $\geq 80\%$ of the total number of detections. Species were grouped into common (C), uncommon (U) and rare (R) categories for analysis; with rare species containing too few detections for any individual analysis.

Species	No. Detections (%)	No. sites occupied (%)	Group
<i>Morethia obscura</i> (Scincidae)	171 (24.22)	33 (94.29)	C
<i>Menetia greyii</i> (Scincidae)	113 (16.01)	25 (71.42)	C
<i>Hemiergis initialis</i> (Scincidae)	107 (15.16)	31 (88.57)	C
<i>Lerista distinguenda</i> (Scincidae)	105 (14.87)	22 (57.14)	C
<i>Acritoscincus trilineatus</i> (Scincidae)	77 (10.91)	28 (80.00)	C
<i>Egernia napoleonis</i> (Scincidae)	38 (5.38)	23 (65.71)	U
<i>Ctenotus labillardieri</i> (Scincidae)	25 (3.54)	14 (40.00)	U
<i>Cryptoblepharus buchananii</i> (Scincidae)	17 (2.41)	10 (28.57)	U
<i>Diplodactylus lateroides</i> (Gekkonidae)	15 (2.12)	10 (28.57)	U
<i>Christinus marmoratus</i> (Gekkonidae)	13 (1.84)	8 (22.86)	U
<i>Aprasia pulchella</i> (Pygopodidae)	9 (1.27)	6 (17.14)	R
<i>Ramphotyphlops australis</i> (Typhlopidae)	4 (0.57)	2 (5.71)	R
<i>Tiliqua rugosa</i> (Scincidae)	4 (0.28)	2 (5.71)	R
<i>Varanus rosenbergi</i> (Varanidae)	3 (0.42)	3 (8.57)	R
<i>Parasuta nigriceps</i> (Elapidae)	2 (0.28)	2 (5.71)	R
<i>Pogona minor</i> (Agamidae)	2 (0.28)	2 (5.71)	R
<i>Lerista microtis</i> (Scincidae)	1 (0.14)	1 (2.86)	R
Total	706		

Table 2. Occupancy model output for common reptile species

Summary of well-supported ($\Delta\text{AIC} < 2$ from top model) occupancy models for the 5 most common species. The table includes ΔAIC values, Akaike weights (ω), the number of parameters (nP), the trend of detection probability (p) and occupancy (Ψ) indicating changes associated habitat or seasonal variables ($\cap$ = optimal value; $\uparrow$ = increasing; $\downarrow$ = decreasing; $\leftrightarrow$ = no influence). Models with weights ≥ 0.5 are bold. Additionally, it includes goodness of fit (GoF) results for each species from the top model with a non-significant p-value indicating model fit.

Species	Model ^a	ΔAIC	ω	nP	p trend	Ψ trend	GoF (p)
<i>M. obscura</i>	p(MaxT ²), $\Psi(\text{OD})$	<u>0.00</u>	<u>0.46</u>	<u>7</u>	$\cap$	$\downarrow$	0.28
	p(MaxT ²), $\Psi(.)$	<u>2.25</u>	<u>0.15</u>	<u>6</u>	$\cap$	$\leftrightarrow$	
<i>L. distinguenda</i>	p(MaxT ²), $\Psi(0\text{-}1\text{m})$	<u>0.00</u>	<u>0.47</u>	<u>7</u>	$\cap$	$\downarrow$	0.42
	p(MaxT ²), $\Psi(\text{OD})$	<u>1.59</u>	<u>0.22</u>	<u>7</u>	$\cap$	$\downarrow$	
<i>H. initialis</i>	p(Month), $\Psi(1\text{-}2\text{m})$	<u>0.00</u>	<u>0.23</u>	<u>8</u>	$\uparrow\downarrow$	$\uparrow$	0.53
	p(Month), $\Psi(\text{OD})$	<u>0.81</u>	0.16	<u>8</u>	$\uparrow\downarrow$	$\uparrow$	
	p(Month), $\Psi(\text{CWD})$	<u>0.86</u>	<u>0.15</u>	<u>8</u>	$\uparrow\downarrow$	$\downarrow$	
	p(Month), $\Psi(0\text{-}1\text{m})$	<u>1.46</u>	0.11	<u>8</u>	$\uparrow\downarrow$	$\uparrow$	
<i>M. greyii</i>	p(MaxT), $\Psi(1\text{-}2\text{m})$	<u>0.00</u>	<u>0.37</u>	<u>6</u>	$\uparrow$	$\downarrow$	0.19
	p(MaxT), $\Psi(.)$	<u>1.96</u>	<u>0.15</u>	<u>6</u>	$\uparrow$	$\downarrow$	
<i>A. trilineatus</i>	p(MaxT), $\Psi(2\text{-}5\text{m})$	<u>0.00</u>	<u>0.67</u>	<u>6</u>	$\uparrow$	$\uparrow$	0.55
	p(MaxT), $\Psi(0\text{-}1\text{m})$		0.07		$\uparrow$	$\uparrow$	

^aModel descriptors: MaxT²=maximum temperature squared, MaxT=maximum temperature, OD=overstorey density, 0-1m=0-1m cover, CWD= coarse woody debris, Month=month surveyed, LL=leaf litter, 2-5m=2-5m cover, and 1-2m=1-2m cover, and (.) indicates a null model.

Table 3. Poisson regression output for uncommon reptile species

	0-1m	1-2m	2-5m	OD	CC	LL	CWD	FuelAge	PropRest
<i>E. napoleonis</i>									
estimate	0.015	-0.002	0.019	0.000	0.001	0.016	0.000	-0.020	-0.015
SE	0.015	0.007	0.018	0.000	0.006	0.027	0.000	0.022	0.025
z-value	1.032	0.280	0.998	0.256	0.221	0.574	0.068	0.888	0.566
p-value	0.302	0.779	0.318	0.798	0.825	0.566	0.946	0.374	0.572
relative importance	1.000	0.271	0.967	0.248	0.214	0.556	0.066	0.860	0.548
<i>C. labillardieri</i>									
estimate	-0.001	0.000	0.008	0.000	0.013	0.023	0.000	-0.076	-0.017
SE	0.007	0.006	0.016	0.000	0.020	0.039	0.001	0.030	0.038
z-value	0.212	0.003	0.500	0.112	0.628	0.582	0.326	2.488	0.422
p-value	0.832	0.998	0.617	0.911	0.530	0.561	0.744	0.013	0.673
relative importance	0.085	0.001	0.201	0.045	0.252	0.234	0.131	1.000	0.170
<i>D. lateroides</i>									
estimate	-0.002	0.008	-0.011	0.000	0.005	-0.004	0.003	0.016	0.000
SE	0.010	0.016	0.024	0.000	0.014	0.025	0.002	0.031	0.014
z-value	0.173	0.464	0.428	0.374	0.321	0.161	1.656	0.510	0.033
p-value	0.863	0.643	0.669	0.709	0.748	0.873	0.098	0.610	0.974
relative Importance	0.104	0.280	0.258	0.226	0.194	0.097	1.000	0.308	0.020
<i>C. marmoratus</i>									
estimate	-0.084	0.026	-0.025	0.000	-0.002	0.002	0.000	0.000	0.000
SE	0.029	0.037	0.042	0.000	0.009	0.022	0.001	0.013	0.010
z-value	2.860	0.681	0.597	0.082	0.192	0.075	0.142	0.025	0.046
p-value	0.004	0.496	0.551	0.935	0.848	0.940	0.887	0.980	0.963
relative importance	1.000	0.238	0.209	0.029	0.067	0.026	0.050	0.009	0.016
<i>C. buehnanii</i>									
estimate	-0.045	0.021	-0.010	0.000	0.013	0.000	0.000	0.099	0.000
SE	0.031	0.032	0.023	0.000	0.020	0.018	0.001	0.046	0.007
z-value	1.421	0.632	0.435	0.370	0.635	0.004	0.123	2.057	0.000
p-value	0.155	0.528	0.664	0.711	0.526	0.997	0.902	0.040	1.000
relative importance	0.691	0.307	0.211	0.180	0.309	0.002	0.060	1.000	0.000

Poisson regression top models and model-average estimates. The table includes habitat covariates and their influence: decreasing (-), or increasing (+), standard errors (SE), z-values, p-values and relative importance.

- 4 ^aModel descriptors 0-1m=0-1m cover, 1-2m=1-2m cover, , 2-5m=2-5m cover, OD=overstorey density,
5 CC=canopy cover LL=leaf litter , CWD=coarse woody debris, FuelAge=time since the last fire, and
6 PropRest=the proportion of restored area within 100m.

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Map of Huntly minesite showing the mosaic of unmined and restored forest across the landscape. All trapping arrays were located in unmined forest.

Fig. 1

Procrustes analysis of reptile abundance data obtained at 35 sites in the Jarrah forest, with lines indicating species (black arrows) and grey text indicating the location of habitat covariate correlations at sites (+) with the arrows and text location indicating the direction of the relationship and the length of the line indicating the strength of the correlation between the ordination and the variable. Only significant habitat variables are shown (OD = overstorey density; 0-1m = percent cover from 0 to 1 m; LL = percent leaf litter).

1 **Table S1.** Variations in yearly sampling
2 Sites were surveyed for reptiles between 2005 and 2013, but not in all years as displayed
3 below. The number of trapping arrays includes the number of reference forest sites that were
4 surveyed.

Year	Month								
2005	Oct	x	x						
	Dec	x	x						
2006	Mar	x	x						
	May	x	x						
	Oct				x				
	Dec				x				
2007	Mar				x				
	May				x				
2009	Oct					x			
	Nov					x			
	Dec					x			
2010	Mar					x			
	Oct						x		
	Nov						x		
	Dec						x		
2011	Mar					x			
	Oct							x	x
	Nov							x	x
	Dec							x	x
2012	Mar						x	x	
	Oct								x
	Nov								x
	Dec								x
2013	Mar								x
No. arrays		4	4	4	4	2	10	2	5

5

6

7

Table S2. Summary of habitat variables

Descriptive statistics of the habitat variables measured at all reference forest sites (minus correlated variables). Habitat variables are: percent cover in the three strata 0-1, 1-2 and 2-5m; percent cover of leaf litter (LL); percent canopy cover (CC); overstorey density (OD; stems ha⁻¹); log volume of coarse woody debris (CWD; m³ ha⁻¹); maximum temperature (MaxT; ° C); minimum temperature (MinT; ° C); precipitation in the last 2 weeks (Precip2; mm); and the number of days since rainfall (RainD).

	0-1m	1-2m	2-5m	LL	CC	OD	CWD
Max	67.70	65.08	44.03	100.00	62.75	18647.83	520.93
Min	4.42	0.30	0.00	68.33	0.00	416.72	0.67
Mean	43.61	15.23	12.79	92.76	41.81	3221.17	144.27
SE	2.68	2.34	1.85	1.23	2.89	608.66	25.24

	MaxT	MinT	Precip2	RainD
Max	36.30	25.34	106.55	51.50
Min	15.50	3.50	0.00	0.00
Mean	24.85	11.67	35.39	8.95
SE	0.20	0.54	6.02	1.78

19

20 **Fig. S1.**

21 The layout of trapping arrays and vegetation surveys used to detect reptiles in the Jarrah
22 forest. The pitfall traps included three 20 L plastic buckets (Bucket), four 850 mL plastic,
23 take-away containers (Take-away), and two 40 cm long by 15 cm diameter PVC tubing
24 located every 3 m along a 29 m aluminium fly-wire drift fence, and two paired funnel traps
25 located on both sides of the drift fence between take-aways and PVC tubes. Four Elliot traps
26 were located 5 m on both sides of the end buckets and one cage trap was placed in line with
27 the drift fence ~5 m from one of the end buckets.

28

29

Fig. S2.

The five most commonly detected reptiles in the Jarrah forest during surveys from 2005-2012; a) *Acritoscincus trilineatus*, b) *Hemiergis initialis*, c) *Lerista distinguenda*, d) *Menetia greyii* and e) *Morethia obscura*.

50

51 **Fig. S3.**

52 Species accumulation curve of the number of species detected by the number of days
53 surveyed; with each day weighted by the number of sites that were open that day. The
54 number of species detected increased rapidly until ~80 days after which time few new species
55 were detected.

56

57

58 **Fig. S4.** Examples of detection probability for the best fit models for common reptile species
 59 detected in the Jarrah forest.