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The importance of underground shelter resources for reptiles in dryland landscapes: a woma python case study

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Abstract

1 For effective fauna conservation and management, ecologists are required to identify
2 the resources that are critical for species to survive, and consider how these are distributed
3 across landscapes. The critical resources usually considered are food and water, but the
4 availability of appropriate shelter resources can be a key driver of habitat suitability for
5 terrestrial reptiles and amphibians. Reptiles are important components of dryland ecosystems,
6 yet we have little understanding about how anthropogenic disturbance affects the availability
7 of shelter resources and reptile survival in drylands. In this study, we used VHF radio-
8 tracking to assess the importance of shelter resources in determining the habitat use patterns
9 of a Near-Threatened reptile species, the woma (*Aspidites ramsayi*; Pythonidae), in modified
10 and intact dryland landscapes of Queensland, Australia. We compared the structural and
11 thermal attributes of locations that were used, with those that were available. Using an
12 information-theoretic approach, we found that the occurrence of womas was strongly
13 associated with the presence of ground burrows, which are excellent thermal insulators. No
14 other shelter type was capable of buffering our study species from sub-zero temperatures
15 during winter, although summer temperatures of $> 40^{\circ}\text{C}$ were buffered by hollow logs and
16 piles of woody debris. Habitat use patterns were influenced more by the occurrence of
17 underground shelters than by habitat type. Clearing status *per se* (cleared, regrowth or intact)
18 had minimal influence on occurrence. Thermally-buffered underground shelters are a vital
19 resource for our focal species, and the availability of this shelter resource drives habitat
20 suitability in modified dryland landscapes. Due to the key trophic role of reptiles in dryland
21 ecosystems, and the excellent thermal buffering capacity of underground shelters, we propose

22 that ground burrows be potentially considered as keystone structures in drylands, with a
23 similar level of protection to 'habitat' or 'legacy' trees in forested ecosystems.

24 **Key words:** Arid, *Aspidites ramsayi*, burrow, regrowth, vegetation clearing

25

Introduction

26 Successful fauna conservation hinges on the ability to identify threatening processes
27 and to predict current and future distributions of species (Franklin 2009). Predicting species
28 distributions requires a fundamental knowledge of the critical resources that drive habitat use
29 (Dennis et al. 2003), and an assessment of how the availability of these critical resources
30 varies across both intact and human-modified landscapes (Fischer et al. 2004, Manning et al.
31 2004, Dennis et al. 2006). The availability of water and food resources drives the landscape-
32 level habitat use patterns of many terrestrial species (e.g. Barton et al. 1992, Whitney and
33 Smith 1998, Nielson et al. 2010). However, the low-energy metabolic systems of reptiles and
34 amphibians suggest that the availability of shelter resources may be of primary importance in
35 determining habitat use in these taxa (Pough 1980, 1983). Studies by Seebacher and Alford
36 (2002), Beck and Jennings (2003), and Lagarde et al. (2012) support this hypothesis, and
37 demonstrate that the distribution of appropriate shelter resources for reptiles and amphibians
38 may be an important consideration in land management and conservation planning. However,
39 to date, few studies have empirically tested the importance of shelter resource availability in
40 driving the landscape-level habitat use patterns of ectotherms.

41 Dryland environments cover 40% of terrestrial earth, including grazing and irrigated
42 cropping lands used for the production of human food (Deichmann and Eklundh 1991,
43 Ffolliott et al. 2003). Savannas, woodlands, and dry open forests are dryland biomes that
44 provide multiple shelter opportunities for ectotherms (Simbotwe 1984, Williams et al. 1996,
45 de Castro and Kauffman 1998, McElhinny et al. 2006). However, extensive areas within
46 these vegetated dryland biomes have been cleared for pasture and irrigated crops (e.g. Accad
47 et al. 2008, Hoyos et al. 2012). Clearing of woody vegetation results in the loss of structural

48 heterogeneity, and cleared areas support fewer reptile species than adjacent, intact habitats
49 (Driscoll 2004, Schutz and Driscoll 2008, Pelegrin and Bucher 2012, Bruton et al. 2013).
50 Reptiles are efficient energy converters and provide a key trophic link between invertebrates
51 and predators in dryland ecosystems (Pough 1983, Blench 2004, Ayal 2007). Therefore, to
52 ensure ecosystem function is maintained in dryland ecosystems, we require a better
53 understanding about how the availability and distribution of shelter resources impacts reptile
54 occurrence, and how the distribution of shelter resources is affected by human interventions.

55 Reptiles are able to survive long periods of fasting (Pough 1983, McCue 2010). In
56 addition, they require very little food and water for day-to-day survival (Pough 1983), which
57 means they are well suited to dryland environments, where periods of limited food and water
58 resource availability are common (Ffolliott et al. 2003). However, this low-energy
59 metabolism comes at the cost of limited aerobic capacity, meaning reptiles are unable to use
60 sustained activity to escape hazardous situations (Pough 1983). These physiological
61 parameters suggest that the constant availability of shelter resources is more important for
62 reptile survivability than the constant availability of food and water resources, and therefore,
63 has a greater impact on patterns of reptile habitat use and distribution.

64 Dryland environments are thermally variable, experiencing extreme seasonal
65 temperatures, as well as large daily variations in temperature (Ffolliott et al. 2003). In these
66 systems, shelter resources can provide protection from both predators and thermal variability
67 (Anderson and Richardson 2005, Lagarde et al. 2012). Underground shelters, in particular,
68 are excellent thermal buffers (Williams et al. 1999, Whittington-Jones et al. 2011). However,
69 there has been little comparative research into the thermal buffering capacity of shelter

70 resources in dryland landscapes, and the role these thermal properties may play in driving the
71 landscape-level habitat use patterns of dryland reptiles.

72 Here, we address the question: how important is the availability of suitable shelter
73 resources for determining the habitat use patterns of dryland reptiles in human-modified
74 landscapes? To answer this question, we used an information-theoretic approach, with
75 generalised linear mixed-effects models, to examine the habitat use patterns of a large reptile
76 species in a subtropical woodland area partially modified by human interventions.

Methods

77 *Hypotheses*

78 Soil and water characteristics drive spatial heterogeneity in drylands, resulting in
79 structurally distinct ecosystems generally dominated by a few woody species (e.g. Swaine et
80 al. 1990, Prado 1993, Sattler and Williams 1999). Structural variation among dryland
81 ecosystems means they vary in the provision of shelter resources (e.g. Gonnet and Ojeda
82 1998, Edwards et al. 2002). Similarly, modified and intact ecosystems also differ in structure
83 and the shelter resources they provide. Therefore, in human-modified dryland landscapes, we
84 predicted that the occurrence of reptile species would vary among ecosystem types, as well as
85 among areas with different modification histories, due to differences in the availability of
86 shelter resources.

87 Underground burrows are excellent thermal buffers (Williams et al. 1999, Bulova
88 2002, Anderson and Richardson 2005, Whittington-Jones et al. 2011), whereas the capacity
89 for above-ground shelters to buffer fauna from thermal extremes is minimal (Bryant et al.
90 2012, Lagarde et al. 2012). Therefore, we predicted that underground burrows would have

91 the best thermal buffering capacity of all the potential shelter types available for reptiles, and
92 that the availability of underground burrows would drive differences in the occurrence of
93 reptile species among habitats in human-modified dryland landscapes.

94 Based on these ideas, we developed five alternative hypotheses that predict the
95 occurrence of a reptile species in relation to the availability of shelter resources in human-
96 modified dryland landscapes:

- 97 1. Null: The availability of shelter resources does not influence occurrence, and all
98 habitats are used equally.
- 99 2. Habitats discriminated: Occurrence varies among habitats, but the availability of
100 shelter resources does not influence this discrimination.
- 101 3. Single shelter: The availability of one shelter resource drives occurrence, and this
102 shelter type is a good thermal buffer.
- 103 4. Multiple shelters: Occurrence is driven by the availability of multiple shelter
104 resources (e.g. ground burrows and shrub cover).
- 105 5. Habitat + shelter: Variation in occurrence among habitats is primarily, but not
106 exclusively, driven by the availability of thermally-suitable shelter resources.

107 *Study area*

108 The study area is located at the interface of two dryland agricultural Bioregions; the
109 Brigalow Belt and Mulgalands of Queensland, Australia (Sattler and Williams 1999, Fig. 1).
110 The climate is subtropical semi-arid. Rainfall averages 530 mm/year, mostly during summer,
111 and air temperatures average 21-34°C in summer, and 6-20°C in winter (Bureau of
112 Meteorology 2013). The topology of the area is flat, with altitude varying between 220 m and

113 300 m above sea level. Rocky ironstone rises are dominated by bende *Acacia catenulata*
114 (Fabaceae) woodlands. These rises are interspersed with alluvial clay floodplains that are
115 dominated by poplar box *Eucalyptus populnea* (Myrtaceae) woodlands, with small stands of
116 brigalow *Acacia harpophylla* (Fabaceae). Intermediate slopes are dominated by mulga
117 *Acacia aneura* (Fabaceae) woodlands, with scattered stands of silver-leafed ironbark
118 *Eucalyptus melanophloia* (Myrtaceae).

119 The woodlands of the Brigalow Belt Bioregion have been extensively cleared for
120 pasture and irrigated crops, and parts of the Mulgalands Bioregion have also been subject to
121 broadscale clearing for pasture (Johnson 1997, Seabrook et al. 2006, Accad et al. 2008). Our
122 study area is a conservation reserve that is a recent amalgamation of former grazing
123 properties, which have all been partially cleared to create pastures for sheep and cattle.
124 Historical clearing patterns have resulted in a mosaic of intact, cleared and regrowth
125 woodlands in all three of the dominant woodland types at the reserve. At the time of this
126 study, regrowth vegetation at the reserve ranged in age from 12 to 25 years.

127 *Study species*

128 The woma (*Aspidites ramsayi*; Pythonidae) is a dryland specialist that has been
129 sighted in a wide variety of habitats, yet the ecology and natural history of this snake species
130 is poorly understood (Bruton 2013). Stomach content analyses revealed that the diet of
131 womas is broad (Shine and Slip 1990, Covacevich and Couper 1996). Womas are members
132 of the Pythonidae, which have low metabolic rates and can survive prolonged periods of
133 fasting (Bedford and Christian 1998, McCue et al. 2012). Pythons are solitary animals that
134 are tolerant of conspecifics (Slip and Shine 1988, Angelici et al. 2000, Wilson et al. 2006).
135 Therefore, it is unlikely that prey availability or social interactions have a large influence on

136 the habitat use patterns of womas. With current technology, womas are large enough to be
137 radio-tracked for approximately one year each, and their habitat and resource requirements
138 are not well known (Borsboom 2008). These factors make womas ideal candidates for
139 assessing the influence of shelter resources on the landscape-level habitat use patterns of
140 reptiles in human-modified dryland landscapes.

141 Womas are generally sighted in sand-plains and shrubby dune-fields (Pearson 1993,
142 Covacevich and Couper 1996). However, in the east of their range, this species inhabits
143 relatively fertile woodlands (Covacevich and Couper 1996), where there is concern that they
144 may be negatively impacted by woodland clearing for pasture and cropping (Borsboom 2008,
145 Richardson 2008, Queensland Government 2010). In these areas, womas have been sighted
146 adjacent to, and within, cleared paddocks (Borsboom 2008), suggesting that critical shelter
147 resources may be retained at these sites.

148 Known woma shelters include hollow logs, animal burrows, and thick ground
149 vegetation (Wilson and Knowles 1988, Ehmann 1992, Pearson 1993). Therefore, we
150 identified hollow logs and other fallen timber (woody debris), ground vegetation, and
151 underground burrows, as shelter resources that could potentially drive patterns of woma
152 occurrence among habitats. Other terrestrial python and boa species are known to shelter in
153 shrubs and thick vegetation (Pearson et al. 2003, Alexander 2007); as are terrestrial vipers
154 (Beck 1995, Warner 2009), which have similar ecology, morphology and behavioural habits
155 to pythons and boas (Vitt and Vangilder 1983, Guyer and Donnelly 1990, França et al.
156 2008). Therefore, we included shrub cover as a shelter resource that could also potentially
157 influence the habitat use patterns of womas.

158 *Radio-tracking*

159 Seven adult male and five adult female womas were found over nine months, using
160 two search methods: i) spotlighting night and day, during warmer months, and ii) diurnal
161 searches at known and suspected shelter sites during cooler months. Access tracks for
162 spotlighting were not biased towards woodland types or clearing states. Captured womas
163 were implanted with temperature sensitive Holohil SI-2T (11g) VHF transmitters using the
164 procedures recommended by Bryant et al. (2010). Minor modifications include: i) anaesthesia
165 was induced by intravenous or subcutaneous injections of alfaxalone prior to intubation, and
166 ii) to prevent contamination, the surgical wound was sealed with tissue adhesive post-
167 implantation (Bruns and Worthington 2000). External absorbable sutures often remained *in*
168 *situ* for up to six months post-implantation, requiring manual removal to reduce the risk of
169 injury.

170 After a minimum of 12 hours post-surgical recovery, the womas were released at their
171 capture locations during suitable weather. Each individual was located approximately every
172 55 hours (mean = 55.04 +/- 4.08 hrs) for one year (mean = 362 days, range = 191-480 days,
173 Appendix A), between Oct 2010 and May 2012. Being a predominately — but not
174 exclusively — nocturnal species (Borsboom 2008), this schedule allowed shelter and habitat
175 use to be assessed during every hour of the daily cycle. The radio-tracking interval increased
176 to 79 hours when: i) the womas were immobile during winter, and ii) record flooding
177 occurred in February 2012. The womas were not radio-tracked for three weeks during winter
178 2011; however, they were all in the same locations upon return. Once located, all care was
179 taken to avoid disturbing the womas with vibrations, sudden movements and scent; unless
180 they were due to have their external sutures removed.

181 *Habitat assessments*

182 Location and a series of habitat variables (Table 1) were recorded by a single observer
183 (M.B.) at each of 416 unique radio-tracked woma locations, and 291 random locations.
184 Movements within shelters did not contribute to defining unique locations. Random locations
185 were evenly located at 500 m grid intervals across the study site, and within 1 km of any
186 woma location (Fig. 2). A 1 km buffer was arbitrarily chosen as a relevant outer margin for
187 the potential area that each radio-tracked woma could use, because they had core areas of
188 activity and generally travelled less than 1km between radio-tracking locations (M.B.
189 unpublished data). Habitat variables were assessed at: i) each new woma location at the time
190 of the radio-tracking event, and ii) random locations progressively between January 2011 and
191 June 2012.

192 To gain insight into the potential drivers of shelter use by this dryland reptile species,
193 we measured the thermal attributes of woma-sized terrestrial shelter resources that were
194 available across our study area, and three non-shelter microhabitats. The five shelter locations
195 measured were: 50 cm into the entries (approximately 5 cm diameter) of two previously used
196 underground burrow systems (1x shaded, 1x exposed); the centre of two fallen hollow logs
197 (1x shaded, 1x exposed); and the base of a large pile of woody debris (approximately 1.5 m
198 high x 3 m wide x 8 m long). The underground burrow systems at the study site were
199 multiple-entry (up to 20 discrete entries) tunnel systems of unknown origin. Surface features
200 suggest the tunnel systems ranged from approximately 4 – 50m diameter. Collapsed areas
201 suggest the horizontal sections of the tunnels ranged from approximately 30-60cm depth.

202 The three non-shelter microhabitats measured were: i) at the base of a clump of grass;
203 ii) on shaded bare soil; and iii) on exposed bare soil. The eight microhabitats measured were

204 selected to measure the thermal buffering capacity (Dyck and MacArthur 1993) of the
205 microhabitats used by, and available to, the terrestrial womas. Plastic-coated thermal data
206 loggers (DS 1921G, Maxim, Dallas, USA) recorded the hourly temperature between Feb
207 2011 and May 2012 within each of the eight microhabitats.

208 We quantified the thermal buffering capacity of each shelter by identifying the
209 minimum and maximum temperatures recorded at each site, and comparing these to
210 minimum and maximum air and woma body temperatures. Air temperatures were recorded
211 every 10 minutes for 21 months, using a portable Kestrel weather meter that was permanently
212 established in the centre of the area used by the woma pythons. Woma body temperatures
213 were recorded during every radio-tracking event (n = 1 645; all seasons) using the calibrated
214 pulse-interval of the temperature-sensitive transmitters.

215 *Analyses*

216 Using an information-theoretic model selection approach (Anderson 2008), we
217 simultaneously compared the influence of habitat type and the availability of shelter
218 resources, on woma occurrence in human-modified landscapes. We used binomial
219 generalised mixed effects models to account for variation in habitat use among individual
220 womas. The mixed effects models were developed using the ‘lme4’ package (Bates et al.
221 2013) in the statistical program R (R Core Team 2013). The random covariate was the
222 individual womas, and the fixed covariates were woodland type, clearing status, and the four
223 shelter resources (Table 1). The shelter variables had low levels of correlation ($r < 0.4$,
224 Spearman), and were all retained in the model analyses.

225 The inclusion of the categorical variables ‘woodland type’ and ‘clearing status’ in the
226 one model resulted in an overfit and non-convergent model (Bolker et al. 2009). Therefore,
227 we combined these variables to create a new variable with eight categories called ‘habitat’.
228 Within this variable, the positive effects of regrowth mulga (*A. aneura*) and regrowth poplar
229 box (*E. populnea*) woodlands on woma occurrence were highly correlated (> 0.6 ,
230 Spearman), as were the effects of intact mulga and intact poplar box woodlands. Therefore,
231 we combined these groups so the final categories for the variable ‘habitat’ were: i) cleared, ii)
232 regrowth bendee (*A. catenulata*), iii) intact bendee, iv) regrowth mulga & poplar box, v) intact
233 mulga & poplar box, and vi) other. We used ‘cleared’ as the baseline standard for comparing
234 the effects of habitat type on woma occurrence. To evaluate the additive influence of
235 woodland type and clearing status, we compared the fit of models that included the ‘habitat’
236 variable to the fit of equivalent models with only the factors ‘woodland type’ or ‘woodland
237 status’.

238 We used a two-stage model selection approach to identify the hypothesis that was best
239 supported by our data. In the first stage, we created a candidate model set by identifying the
240 best fit model or models for each of our five alternative hypotheses (Appendix B). If model
241 uncertainty existed for a hypothesis, then the top 95% of models (i.e. $\Sigma_{\omega} = 0.95$) were
242 selected to represent the relevant hypothesis in the final candidate model set and comparison
243 (Appendix B). In the second stage of model selection, we compared the relative fits of the
244 models in the final candidate model set to identify the model and hypothesis that was best
245 supported by our data (Table 2).

246 We assessed the fit of the most parsimonious model using quantile-quantile plots with
247 95% confidence intervals (Appendix C), by simulating model residuals one thousand times

248 and plotting them against the fitted residuals (Landwehr et al. 1984). Straight-line
249 relationships close to the 1:1 line within the confidence intervals indicate a good model fit
250 with no major departures from the underlying model assumptions (Landwehr et al. 1984,
251 Rhodes et al. 2009). We tested for spatial autocorrelation among the model residuals for our
252 best model using a spline correlogram in the ‘ncf’ package in R (Bjørnstad and Falck 2001).
253 Spline correlograms use a smoothed spline and 95% bootstrap confidence intervals to display
254 the amount of spatial structure. A correlogram displaying a flat spline within the 95%
255 confidence intervals encapsulating the zero line represents spatial randomness (Bjørnstad and
256 Falck 2001).

Results

257 The radio-tracked womas were located 1 645 times at 416 unique locations within an
258 area of approximately 10 000 ha (Fig. 2). The number of unique locations for each woma
259 ranged from 19 to 59. Summary statistics are provided in Appendix A.

260 *Habitat use patterns*

261 The radio-tracked womas were located in cleared, regrowth and intact woodlands
262 (Fig. 2), and in all three of the dominant woodland types. The womas were also located in the
263 less abundant woodlands such as silver-leafed ironbark (*E. melanophloia*) and brigalow (*A.*
264 *harpophylla*). Clearing status had a weaker influence on the occurrence of womas than
265 woodland type; however, occurrence was better explained by a combination of both
266 woodland type and clearing status (‘habitat’), than by woodland type alone (Appendix B).

267 Based on Akaike weights, a single model, representing hypothesis five, was clearly
268 the best-fit model from our candidate model set (Table 2). According to this model, the radio-

269 tracked womas were more likely to occur in mulga & poplar box woodlands than cleared
270 paddocks (Fig. 3), and they were also more likely to use regrowth than intact mulga & poplar
271 box woodlands ($\beta = 0.748$, CI = 0.39 to 1.106). Bendee woodlands were generally avoided,
272 with womas more likely to occur in cleared paddocks than in regrowth or intact bendee
273 (Fig. 3). The likelihood of womas using cleared paddocks did not differ from other habitats
274 (Fig. 3).

275 *Shelter use*

276 The radio-tracked womas sheltered in underground burrows during 69% of the radio-
277 tracking events, and were exposed on only 8% of occasions. The use of above-ground
278 shelters was minimal: fallen hollow logs were used most frequently (16%), followed by
279 woody debris (4%) and pushed-over tree root balls (2%). Vegetation was rarely used for
280 shelter (1%), and shrub cover did not influence woma occurrence (Table 2, Appendix B).

281 The best-fit model, with parameters ‘habitat’, ‘burrow’, ‘debris’, and ‘groundveg’
282 (m21), was 63 times more likely to represent reality than the same model without ‘habitat’
283 (m14, Table 2). Therefore shelter availability did not explain all of the variation in woma
284 occurrence among habitats in our study. However, the model containing only the three
285 influential shelter variables (m14) was 172 times more likely to explain woma occurrence in
286 human-modified landscapes than the model that contained only habitat (m4, Table 2).
287 Therefore, variation in woma occurrence in human-modified landscapes is better explained
288 by the availability of shelter resources than by a combination of woodland type and clearing
289 status.

290 Ground burrows were present at 47% of the unique woma locations, compared with
291 9% of random locations. Consequently, the best fit model identified the occurrence of ground
292 burrows as the most influential shelter variable affecting the occurrence of womas in human-
293 modified woodland landscapes (Table 2, Fig. 3). The direction of this influence was positive,
294 with the occurrence of ground burrows considerably increasing the likelihood of woma
295 occurrence (Fig. 3). In the best-fit model, ground cover and woody debris were also
296 positively associated with the likelihood of woma occurrence, although the magnitude of
297 influence was minimal in comparison to the influence of ground burrow shelters (Fig. 3,
298 Appendix B).

299 *Thermal buffering capacity of shelters*

300 During this study, air temperature at the field site ranged from -5.2°C to 40.7°C (Fig.
301 4). Of the five shelter resources assessed, the ground burrow system located in a sunny
302 position was the only shelter that was capable of buffering womas against cold winter
303 temperatures (Fig. 4). The temperature of this burrow system did not exceed the minimum or
304 maximum body temperatures experienced by any of the radio-tracked womas. The thermal
305 buffering capacity of the shaded ground burrow system was comparable to that of the sunny
306 ground burrow system (Fig. 4); however, the minimum temperature of 7°C fell below the
307 minimum woma body temperature recorded during this study (Fig. 4).

308 In addition to ground burrow systems, the pile of woody debris and the hollow logs
309 were also capable of buffering womas against hot summer temperatures, with maximum
310 temperature records of 31°C and 37.5°C respectively (Fig. 4). However, these shelter
311 resources were unable to buffer womas against cool winter temperatures, with minimum
312 temperatures of less than 0.5°C (Fig. 4). Grass clumps were poor thermal insulators, with the

313 maximum and minimum temperatures far exceeding the range of woma body temperatures
314 recorded during this study. The temperature of both the sunny and the shaded bare soil were
315 extreme, with records of greater than 55°C in summer, and less than 0°C in winter (Fig. 4).

316 *Seasonal use of ground burrows*

317 The frequency of ground burrow use varied among months ($\chi^2 = 72.6$, $df = 11$, $p <$
318 0.001), with the radio-tracked womas using ground burrows exclusively during the cold
319 months of July, August and September (Fig. 5). The individuals that were radio-tracked pre-
320 and post-winter, remained in the same burrow for between 101 and 194 days ($\bar{x} = 134$ days, n
321 $= 10$); however, they remained mobile within their winter burrows, regularly moving several
322 metres underground between radio-tracking events. Six out of seven radio-tracked womas
323 used different winter burrows in 2011 and 2012.

Discussion

324 This is the first published study to comprehensively assess the habitat use patterns and
325 ecology of wild womas. Our study revealed that the availability of thermally-buffered
326 underground shelters is a strong driver of the landscape-level habitat use patterns of this
327 dryland reptile species. All areas of the landscape that contained ground burrow shelters,
328 including cleared areas and regrowth woodlands, were used by the womas, although bendee
329 woodlands on rocky ridges were generally avoided. Human-modified ecosystems were not
330 avoided in favour of intact woodlands, suggesting that modified areas can be suitable habitat
331 for dryland reptile species when critical shelter resources are retained. Ground burrows were
332 thermally stable, and were the only shelter resource capable of buffering our study species

333 against sub-zero winter temperatures. Consequently, the availability of ground burrows is
334 vital to the persistence of this reptile species in human-modified dryland landscapes.

335 Ground burrows effectively buffer reptiles from both high and low lethal temperatures
336 (Figure 4, Appendix D). However, it has been suggested that the lower lethal limit has greater
337 relevance to the distribution and ecology of reptile species than the upper lethal limit
338 (Spellerberg 1972, Azocar et al. 2012), possibly due to the diminishing capacity of reptiles to
339 detect and escape hazardous situations as temperatures decrease (Andry et al. 1971, Peterson
340 et al. 1993). During sub-zero temperatures at our study site, the exposed ground burrow
341 system remained above 12°C, and the shaded ground burrow system remained above 7°C. In
342 contrast, temperatures dropped to below 0.5°C in all of the above-ground shelters that were
343 monitored. The lower lethal limit (CTMin) of reptile species throughout the world is known
344 to range from 1.9 to 14.6°C (Appendix D). Therefore, we suggest that only below ground
345 shelter resources are capable of effectively buffering dryland reptiles from cold overnight
346 winter temperatures in the subtropical and temperate zones, and the availability of
347 underground shelters in these areas is of critical importance to species persistence.

348 There is a tendency in conservation planning to disregard cleared and regrowth
349 ecosystems as habitat for threatened wildlife (Franklin and Lindenmayer 2009, Prevedello
350 and Vieira 2010), despite ongoing recognition that reserves alone cannot conserve
351 biodiversity (Franklin and Lindenmayer 2009). Our study has demonstrated that when critical
352 resources are retained, human-modified ecosystems can be considered valuable habitat, and
353 can contribute considerably to the amount of habitat available for wildlife (Franklin and
354 Lindenmayer 2009). In the case of womas, the exclusion of hard-hoofed stock protected
355 ground burrow systems from being trampled and allowed this species to inhabit cleared

356 paddocks, despite an absence of above-ground shelters. Our study species was not
357 disadvantaged by above-ground disturbances to woodland ecosystems, and may have derived
358 a small benefit from the increased amounts of woody debris in regrowth areas.

359 Ground burrows are important resources for many dryland taxa (Kinlaw 1999, Read
360 et al. 2008), with an additional 13 species of reptiles and two species of frogs incidentally
361 observed sheltering in, or retreating into, ground burrows during this study. The excellent
362 thermal buffering capacity of ground burrows revealed during this study suggests that the
363 availability of underground shelter resources is of critical importance for the persistence of
364 reptile diversity in human-modified landscapes. As such, we propose that burrows could
365 potentially be considered as keystone structures in dryland environments (Tews et al. 2004),
366 playing a similar role in maintaining fauna diversity to hollow-bearing trees in forested
367 landscapes (Abbott and Whitford 2002, Gibbons and Lindenmayer 2002, Mazurek and
368 Zielinski 2004). Consequently, a similar level of protection may be required to maintain
369 ecosystem function. A greater investment in research is needed to identify the importance of
370 ground burrows for the persistence of a range of dryland fauna.

371 *Persistence of ground burrows*

372 Shallow ground burrows do not persist where soil is tilled and ploughed for annual
373 crops. The persistence of ground burrows in human-modified dryland landscapes may also be
374 threatened by grazing, particularly in wet conditions (Greenwood and McKenzie 2001). The
375 radiotracked womas in this study readily used cleared areas that were free of stock; however,
376 they were rarely located in the central cleared area (Fig. 2), which is still used for light cattle
377 grazing. Excluding cropping and livestock grazing from dryland areas of high ground burrow
378 density, particularly during wet conditions, may benefit reptiles and other dryland taxa.

379 In dryland Australia, a major threat to ground burrows is the control of introduced
380 rabbits *Oryctolagus cuniculus* (Linnaeus). This pest species is predominately managed by
381 ‘ripping’ burrows (Williams and Moore 1995, Moseby et al. 2005), with all ground burrows
382 in the area destroyed (Parer and Parker 1986). Ground burrows are used by many vertebrate
383 and invertebrate species in dryland Australia (Read et al. 2008); however, most of
384 Australia’s native dryland burrowing mammals have declined or become extinct (James and
385 Eldridge 2007). Burrowing mammals were major ecosystem engineers in dryland Australia
386 prior to the invasion by rabbits (James and Eldridge 2007). Consequently, the extensive loss
387 of underground shelters caused by rabbit management in dryland areas is likely to affect the
388 persistence of fauna that now rely on these burrows for protection from thermal extremes and
389 predators (Read et al. 2008). The ecological impacts of current rabbit management practices
390 in dryland areas need to be given greater consideration. Research into developing and
391 implementing more sustainable control methods or programs to re-introduce native
392 burrowing mammals to rabbit-exterminated areas are required (Moseby et al. 2005, Read et
393 al. 2008, Cooke 2012).

394 *Conservation implications for womas*

395 Snakes are ill-equipped to dig their own burrows, and rely on the creation of
396 appropriate burrow shelters by other sources (Woodbury 1954). Research into the genesis of
397 the ground burrow systems is of prime importance to the conservation of womas, as is the
398 protection of ground burrow systems in areas where this species is known to occur. At our
399 study site, the genesis of the burrow systems is not clear. With few exceptions, the ground
400 burrow systems used by the radio-tracked womas were extensive complexes of
401 interconnected underground tunnels with several entries (approximately 5 cm diameter or

402 less) over flat, grassy areas, with no signs of rabbit or hare faecal pellets. Although rabbits are
403 present at the study site, this description does not fit published descriptions of rabbit warrens
404 (Parker et al. 1976, Eldridge and Myers 2001, Barrio et al. 2011) and most of the burrow
405 systems entries were too small for rabbits to access. Other potential generators include: i)
406 small burrowing mammals (Ehmann 1992, Covacevich and Couper 1996), ii) local burrowing
407 reptiles (Wilson and Knowles 1988), and iii) tunnel erosion (Covacevich and Couper 1996).
408 The womas in this study relied heavily on these pre-existing burrows for shelter. Therefore,
409 research into the generator/s of these burrow systems is needed to assess if they are a
410 regenerating resource, and if their availability is sustainable.

411 *Conclusion*

412 Information about the resource needs of a species or taxon can be used to understand
413 the mechanisms driving landscape-level patterns of habitat use. The availability of shelters
414 that protect reptiles from both predators and extreme temperatures may be pivotal to ensuring
415 that this functionally important fauna group persists in human-modified dryland ecosystems.
416 Consequently, the protection or provision of thermally suitable shelter resources may need to
417 be considered a priority for ensuring reptile persistence and ecosystem function in modified
418 dryland landscapes.

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References:

- 430 Abbott, I. and K. Whitford. 2002. Conservation of vertebrate fauna using hollows in forests of south-
431 west Western Australia: strategic risk assessment in relation to ecology, policy, planning, and
432 operations management. *Pacific Conservation Biology* **7**:240-255.
- 433 Accad, A., V. J. Neldner, B. A. Wilson, and R. E. Niehus. 2008. Remnant Vegetation in Queensland.
434 Analysis of remnant vegetation 1997-1999-2000-2001-2003-2005, including regional
435 ecosystem information. Queensland Herbarium, Environmental Protection Agency, Brisbane,
436 Queensland.
- 437 Alexander, G. 2007. Thermal biology of the Southern African Python (*Python natalensis*): does
438 temperature limit its distribution? Pages 50-75 in R. W. Henderson and R. Powell, editors.
439 *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Utah.
- 440 Anderson, D. R. 2008. *Model Based Inference in the Life Sciences: a Primer on Evidence*. Springer,
441 New York.
- 442 Anderson, M. D. and P. R. K. Richardson. 2005. The physical and thermal characteristics of aardwolf
443 dens. *South African Journal of Wildlife Research* **35**:147-153.
- 444 Andry, M. L., M. W. Luttges, and R. I. Bamow. 1971. Temperature effects on spontaneous and
445 evoked neural activity in the garter snake *Experimental neurology* **31**:32-44.
- 446 Angelici, F. M., M. A. Inyang, C. Effah, and L. Luiselli. 2000. Analysis of activity patterns and habitat
447 use of radiotracked african burrowing pythons, *Calabaria reinhardtii*. *Israel Journal of*
448 *Zoology* **46**:131-141.
- 449 Ayal, Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. *Journal*
450 *of Arid Environments* **68**:171-187.
- 451 Azocar, D. L. M., B. Vanhooydonck, M. F. Bonino, M. G. Perotti, C. S. Abdala, J. A. Schulte, and F. B.
452 Cruz. 2012. Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards.
453 *Physiological Ecology* **171**:773-788.
- 454 Barrio, I. C., R. Villafuerte, and F. S. Tortosa. 2011. Harboured pests: rabbit warrens in agricultural
455 landscapes. *Wildlife Research* **38**:756-761.
- 456 Barton, R. A., A. Whiten, S. C. Strum, R. W. Byrne, and A. J. Simpson. 1992. Habitat use and resource
457 availability in baboons. *Animal Behaviour* **43**:831-844.
- 458 Bates, D., M. Maechler, and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes
459 <http://lme4.r-forge.r-project.org/>.

- 460 Beck, D. D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran
461 Desert. *Journal of Herpetology* **29**:211-223.
- 462 Beck, D. D. and R. D. Jennings. 2003. Habitat use by gila monsters: the importance of shelters.
463 *Herpetological Monographs* **17**:111-129.
- 464 Bedford, G. S. and K. A. Christian. 1998. Standard metabolic rate and preferred body temperatures in
465 some Australian pythons. *Australian Journal of Zoology* **46**:317-328.
- 466 Bjørnstad, O. N. and W. Falck. 2001. Nonparametric spatial covariance functions: estimation and
467 testing. *Environmental and Ecological Statistics* **8**:53-70.
- 468 Blench, R. 2004. Biodiversity in arid lands: an overview. *Annals of Arid Zone* **43**:229-254.
- 469 Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S.
470 White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution.
471 *Trends in Ecology and Evolution* **24**:127-135.
- 472 Borsboom, A. 2008. Nomination to re-classify the 'rare' *Aspidites ramsayi* to 'near threatened' under
473 the *Nature Conservation Act 1992*. Environmental Protection Agency, Brisbane, Queensland.
- 474 Bruns, T. B. and J. M. Worthington. 2000. Using tissue adhesive for wound repair: a practical guide to
475 dermabond. *American Family Physician* **61**:1383-1388.
- 476 Bruton, M. J. 2013. Arboreality, excavation, and active foraging: novel observations of radiotracked
477 woma pythons *Aspidites ramsayi*. *Memoirs of the Queensland Museum* **56**:313-329.
- 478 Bruton, M. J., C. A. McAlpine, and M. Maron. 2013. Regrowth woodlands are valuable habitat for
479 reptile communities. *Biological Conservation* **165**:95-103.
- 480 Bryant, G. L., S. J. Dundas, and P. A. Fleming. 2012. Tree hollows are of conservation importance for a
481 Near-Threatened python species. *Journal of Zoology* **286**:81-92.
- 482 Bryant, G. L., P. Eden, P. de Tores, and K. Warren. 2010. Improved procedure for implanting
483 radiotransmitters in the coelomic cavity of snakes. *Australian Veterinary Journal* **88**:443-448.
- 484 Bulova, S. J. 2002. How temperature, humidity, and burrow selection affect evaporative water loss in
485 desert tortoises. *Journal of Thermal Biology* **27**:175-189.
- 486 Bureau of Meteorology. 2013. Climate Data Online. Australian Government
487 <http://www.bom.gov.au/climate/data/>.
- 488 Cooke, B. D. 2012. Rabbits: manageable environmental pests or participants in new Australian
489 ecosystems? *Wildlife Research* **39**:279-289.
- 490 Covacevich, J. A. and P. J. Couper. 1996. *Aspidites ramsayi* (Boidae) in the Brigalow Biogeographic
491 Region of Queensland: occurrence, conservation status and possible bilby associations.
492 *Memoirs of the Queensland Museum* **39**:243-246.
- 493 de Castro, E. A. and J. B. Kauffman. 1998. Ecosystem structure in the Brazilian Cerrado: a vegetation
494 gradient of aboveground biomass, root mass and consumption by fire. *Journal of Tropical
495 Ecology* **14**:263-283.
- 496 Deichmann, U. and L. Eklundh. 1991. *Global Digital Datasets for Land Degradation Studies: A GIS
497 Approach*. UNEP/GEMS, Nairobi, Kenya.
- 498 Dennis, R. L. H., T. G. Shreeve, and H. Van Dyck. 2003. Towards a functional resource-based concept
499 for habitat: a butterfly biology viewpoint. *Oikos* **102**:417-426.
- 500 Dennis, R. L. H., T. G. Shreeve, and H. Van Dyck. 2006. Habitats and resources: the need for a
501 resource-based definition to conserve butterflies. *Biodiversity and Conservation* **15**:1943-
502 1966.
- 503 Driscoll, D. A. 2004. Extinction and outbreaks accompany fragmentation of a reptile community.
504 *Ecological Applications* **14**:220-240.
- 505 Dyck, A. P. and R. A. MacArthur. 1993. Seasonal variation in the microclimate and gas composition of
506 beaver lodges in a boreal environment. *Journal of Mammalogy* **74**:180-188.

507 Edwards, G. P., N. de Preu, I. V. Crealy, and B. J. Shakeshaft. 2002. Habitat selection by feral cats and
508 dingoes in a semi-arid woodland environment in central Australia. *Austral Ecology* **27**:26-31.

509 Ehmann, H. 1992. *Encyclopedia of Australian Animals: Reptiles*. Angus & Robertson, Pymble NSW.

510 Eldridge, D. J. and C. A. Myers. 2001. The impact of warrens of the European rabbit (*Oryctolagus*
511 *cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. *Journal of*
512 *Arid Environments* **47**:325-337.

513 Ffolliott, P. F., J. O. Dawson, J. T. Fisher, I. Moshe, T. E. Fulbright, A. Al Musa, W. C. Johnson, and P.
514 Verburg. 2003. Dryland environments. Pages 3-18 *Proceedings of the IALC conference &*
515 *workshop, assessing capabilities of soil and water resources in drylands: The role of*
516 *information retrieval and dissemination technologies*, Tucson, Arizona.

517 Fischer, J., D. Lindenmayer, and I. Fazey. 2004. Appreciating ecological complexity: habitat contours
518 as a conceptual landscape model. *Conservation Biology* **18**:1245-1253.

519 França, G. R., D. O. Mesquita, C. C. Nogueira, and F. B. Araújo. 2008. Phylogeny and ecology
520 determine morphological structure in a snake assemblage in the central Brazilian cerrado.
521 *Copeia* **2008**:23-38.

522 Franklin, J. 2009. *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge
523 University Press, New York.

524 Franklin, J. F. and D. B. Lindenmayer. 2009. Importance of matrix habitats in maintaining biological
525 diversity. *PNAS* **106**:349-350.

526 Gibbons, P. and D. Lindenmayer. 2002. The hollow-using fauna of Australia. Pages 4-19 *in* P. Gibbons
527 and D. Lindenmayer, editors. *Tree Hollows and Wildlife Conservation in Australia*. CSIRO
528 Publishing, Collingwood, Victoria.

529 Gonnet, J. M. and R. A. Ojeda. 1998. Habitat use by small mammals in the arid Andean foothills of
530 the Monte Desert of Mendoza, Argentina. *Journal of Arid Environments* **38**:349-357.

531 Greenwood, K. L. and B. M. McKenzie. 2001. Grazing effects on soil physical properties and the
532 consequences for pastures: a review. *Australian Journal of Experimental Agriculture*
533 **41**:1231-1250.

534 Guyer, C. and M. A. Donnelly. 1990. Length-mass relationships among an assemblage of tropical
535 snakes in Costa Rica. *Journal of Tropical Ecology* **6**:65-76.

536 Hoyos, L. E., A. M. Cingolani, M. R. Zak, M. V. Vaieretti, D. E. Gorla, and M. R. Cabido. 2012.
537 Deforestation and precipitation patterns in the arid Chaco forests of central Argentina.
538 *Applied Vegetation Science* **16**:260-271.

539 James, A. I. and D. J. Eldridge. 2007. Reintroduction of fossorial native mammals and potential
540 impacts on ecosystem processes in an Australian desert landscape. *Biological Conservation*
541 **138**:351-359.

542 Johnson, R. W. 1997. The impact of clearing on brigalow communities and consequences for
543 conservation. Pages 359-363 *in* P. Hale and D. Lamb, editors. *Conservation Outside Nature*
544 *Reserves*. Centre for Conservation Biology, the University of Queensland, Brisbane.

545 Kinlaw, A. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of*
546 *Arid Environments* **41**:127-145.

547 Lagarde, F., T. Louzizi, T. Slimani, H. El Mouden, K. Ben Kaddour, S. Moulherat, and X. Bonnet. 2012.
548 Bushes protect tortoises from lethal overheating in arid areas of Morocco. *Environmental*
549 *Conservation* **39**:172-182.

550 Landwehr, J. M., D. Pregibon, and A. C. Shoemaker. 1984. Graphical methods for assessing logistic
551 regression models. *Journal of the American Statistical Association* **79**:61-71.

552 Manning, A. D., D. B. Lindenmayer, and H. A. Nix. 2004. Continua and Umwelt: novel perspectives on
553 viewing landscapes. *Oikos* **104**:621-628.

- 554 Mazurek, M. J. and W. J. Zielinski. 2004. Individual legacy trees influence vertebrate wildlife diversity
555 in commercial forests. *Forest Ecology and Management* **193**:321-334.
- 556 McCue, M. D. 2010. Starvation physiology: reviewing the different strategies animals use to survive a
557 common challenge. *Comparative biochemistry and physiology Part A* **156**:1-18.
- 558 McCue, M. D., H. B. Lillywhite, and S. J. Beaupre. 2012. Physiological Responses to Starvation in
559 Snakes: Low Energy Specialists. Pages 103-131 in M. D. McCue, editor. *Comparative*
560 *Physiology of Fasting, Starvation, and Food Limitation*. Springer-Verlag, Berlin.
- 561 McElhinny, C., J. W. Gibbons, C. Brack, and J. Bauhus. 2006. Fauna-habitat relationships: a basis for
562 identifying key stand structural attributes in temperate Australian eucalypt forests and
563 woodlands. *Pacific Conservation Biology* **12**:89-110.
- 564 Moseby, K. E., S. De Jong, N. Munro, and A. Pieck. 2005. Home range, activity and habitat use of
565 European rabbits (*Oryctolagus cuniculus*) in arid Australia: implications for control. *Wildlife*
566 *Research* **32**:305-311.
- 567 Nielson, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat
568 models: seasonal foods and mortality risk predict occupancy-abundance and habitat
569 selection in grizzly bears. *Biological Conservation* **143**:1623-1634.
- 570 Parer, I. and B. S. Parker. 1986. Recolonisation by rabbits (*Oryctolagus cuniculus*) after warren
571 destruction in western New South Wales. *Australian Rangeland Journal* **8**:150-152.
- 572 Parker, B. S., L. S. Hall, K. Myers, and P. J. Fullagar. 1976. The distribution of rabbit warrens at
573 Mitchell, Queensland, in relation to soil and vegetation characteristics. *Australian Wildlife*
574 *Research* **3**:129-148.
- 575 Pearson, D. 1993. Distribution, status and conservation of pythons in Western Australia. Pages 383-
576 395 in D. Lunney and D. Ayers, editors. *Herpetology in Australia: A Diverse Discipline*. Royal
577 Zoological Society of NSW, Mosman, New South Wales.
- 578 Pearson, D., R. Shine, and A. Williams. 2003. Thermal biology of large snakes in cool climates: a
579 radio-telemetric study of carpet pythons (*Morelia spilota imbricata*) in south-western
580 Australia. *Journal of Thermal Biology* **28**:117-131.
- 581 Pelegrin, N. and E. H. Bucher. 2012. Effects of habitat degradation on the lizard assemblage in the
582 Arid Chaco, central Argentina. *Journal of Arid Environments* **79**:13-19.
- 583 Peterson, C. R., A. R. Gibson, and M. E. Dorcas. 1993. Snake thermal ecology: the causes and
584 consequences of body-temperature variation. Pages 241-314 in R. A. Seigel and J. T. Collins,
585 editors. *Snakes: Ecology and Behavior*. The Blackburn Press, Caldwell, New Jersey.
- 586 Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* **115**:92-112.
- 587 Pough, F. H. 1983. Amphibians and reptiles as low-energy systems. Pages 141-188 in W. P. Aspey and
588 S. I. Lustick, editors. *Behavioral Energetics: The Cost of Survival in Vertebrates*. Ohio State
589 University Press, Columbus, Ohio.
- 590 Prado, D. E. 1993. What is the Gran Chaco vegetation in South America? I. A review. *Candollea*
591 **48**:145-172.
- 592 Prevedello, J. A. and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the
593 evidence. *Biodiversity and Conservation* **19**:1205-1223.
- 594 Queensland Government. 2010. Border Rivers Maranoa-Balonne Natural Resource Management
595 Region Back on Track Actions for Biodiversity. Department of Environment and Resource
596 Management, Brisbane, Queensland.
- 597 R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for
598 Statistical Computing, Vienna, Austria <http://www.R-project.org>.
- 599 Read, J. L., J. Carter, K. M. Moseby, and A. Greenville. 2008. Ecological roles of rabbit, bettong and
600 bilby warrens in arid Australia. *Journal of Arid Environments* **72**:2124-2130.

- 601 Rhodes, J. R., C. McAlpine, A. F. Zuur, G. M. Smith, and E. N. Ieno. 2009. GLMM Applied on the
602 Spatial Distribution of Koalas in a Fragmented Landscape. Pages 469-492 in A. F. Zuur, E. N.
603 Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith, editors. Mixed Effects Models and
604 Extensions in Ecology with R. Springer, New York.
- 605 Richardson, R. 2008. Draft Queensland Brigalow Belt Reptile Recovery Plan 2008 - 2012. World
606 Wildlife Fund, Brisbane, Queensland.
- 607 Sattler, P. and R. Williams, editors. 1999. The Conservation Status of Queensland's Bioregional
608 Ecosystems. Environmental Protection Agency, Brisbane, Queensland.
- 609 Schutz, A. J. and D. A. Driscoll. 2008. Common reptiles unaffected by connectivity or condition in a
610 fragmented farming landscape. *Austral Ecology* **33**:641-652.
- 611 Seabrook, L., C. A. McAlpine, and R. Fensham. 2006. Cattle, crops and clearing: Regional drivers of
612 landscape change in the Brigalow Belt, Queensland, Australia, 1840–2004. *Landscape and
613 Urban Planning* **78**:373-385.
- 614 Seebacher, F. and R. A. Alford. 2002. Shelter microhabitats determine body temperature and
615 dehydration rates of a terrestrial amphibian (*Bufo marinus*). *Journal of Herpetology* **36**:69-
616 75.
- 617 Shine, R. and D. J. Slip. 1990. Biological aspects of the adaptive radiation of the Australasian pythons
618 (Serpentes: Boidae). *Herpetologica* **46**:283-290.
- 619 Simbotwe, M. P. 1984. Resource partitioning in a woodland reptile community of the Kafue flats,
620 Zambia. *African Journal of Ecology* **22**:281-287.
- 621 Slip, D. J. and R. Shine. 1988. The reproductive biology and mating system of diamond pythons,
622 *Morelia spilota* (Serpentes: Boidae). *Herpetologica* **44**:396-404.
- 623 Spellerberg, I. F. 1972. Temperature tolerances of southeast Australian reptiles examined in relations
624 to reptile thermoregulatory behaviour and distribution. *Oecologia* **9**:23-46.
- 625 Swaine, M. D., D. Leiberman, and J. B. Hall. 1990. Structure and dynamics of a tropical dry forest in
626 Ghana. *Vegetatio* **88**:31-51.
- 627 Tews, J., U. Brose, V. Grimm, K. Tielborger, M. C. Wichman, M. Schwager, and F. Jeltsch. 2004.
628 Animal species diversity driven by habitat heterogeneity/diversity: the importance of
629 keystone structures. *Journal of Biogeography* **31**:79-92.
- 630 Vitt, L. J. and L. D. Vangilder. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-
631 Reptilia* **4**:273-296.
- 632 Warner, J. K. 2009. Conservation biology of the gaboon adder (*Bitis gabonica*) in South Africa.
633 Dissertation. University of Witwatersrand, Johannesburg, South Africa.
- 634 Whitney, K. D. and T. B. Smith. 1998. Habitat use and resource tracking by African *Ceratogymna*
635 hornbills: implications for seed dispersal and forest conservation. *Animal Conservation*
636 **1**:107-117.
- 637 Whittington-Jones, G. M., R. T. F. Bernard, and D. M. Parker. 2011. Aardvark burrows: a potential
638 resource for animals in arid and semi-arid environments. *African Zoology* **46**:362-370.
- 639 Williams, C. K. and R. J. Moore. 1995. Effectiveness and cost-efficiency of control of the wild rabbit,
640 *Oryctolagus cuniculus* (L.), by combinations of poisoning, ripping, fumigation and
641 maintenance fumigation. *Wildlife Research* **22**:253-269.
- 642 Williams, J. B., B. I. Tieleman, and M. Shobrak. 1999. Lizard burrows provide thermal refugia for larks
643 in the Arabian desert. *The Condor* **101**:714-717.
- 644 Williams, R. J., G. A. Duff, D. M. J. S. Bowman, and G. D. Cook. 1996. Variation in the composition and
645 structure of tropical savannas as a function of rainfall and soil texture along a large-scale
646 climatic gradient in the Northern Territory, Australia. *Journal of Biogeography* **23**:747-756.
- 647 Wilson, D., R. Heinsohn, and S. Legge. 2006. Age- and sex-related differences in the spatial ecology of
648 a dichromatic tropical python (*Morelia viridis*). *Austral Ecology* **31**:577-587.

649 Wilson, S. K. and D. G. Knowles. 1988. Australia's Reptiles: A photographic reference to the
650 terrestrial reptiles of Australia. Collins Publishers Australia, Sydney, New South Wales.
651 Woodbury, A. M. 1954. Study of reptile dens. *Herpetologica* **10**:49-53.

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Tables

Table 1: Habitat variables assessed at each radio-tracked woma python location (used) and each random site (available).

Variable code	Variable type	Method	Categories	Hypotheses
domveg	Categorical	Most abundant tree or shrub species within 20 m radius	Cleared, bendee, mulga, poplar box, other [†]	2 & 5
status	Categorical	Clearing status, based on visual assessment of canopy height, stem density and DBH of the largest trees. Confirmed using aerial photographs with approximately 10-year intervals from 1953-2006	Cleared, regrowth or intact	2 & 5
debris	Ordinal	Visual estimation of the amount of fallen woody debris within 10 m radius: 0 = no woody debris visible, 1 = scattered pieces of woody debris, 2 = clumps of woody debris that do not inhibit researcher momentum, 3 = ground	na	3, 4, & 5

		strewn with fallen timber, or large pushed up piles of woody debris		
grveg	Ordinal	Visual estimation of ground vegetation cover within 10 m radius: 0 = < 25%, 1 = 25-50%, 2 = 50-75%, 3 = > 75%	na	3, 4, & 5
shrub	Ordinal	Visual estimation of shrub cover within 10 m radius: 0 = < 25%, 1 = 25-50%, 2 = 50-75%, 3 = > 75%	na	3, 4, & 5
burrows	Categorical	Ground burrow entries with diameter > 5 cm within 10 m radius	present, absent	3, 4, & 5

[†]'Other' = sites dominated by belah (*Casuarina cristata*; n = 1), brigalow (*Acacia harpophylla*; n = 4), honey myrtle (*Melaleuca uncinata*; n = 3), lancewood (*A. shirleyi*; n = 1), and silver-leafed ironbark (*Eucalyptus melanophloia*; n = 17).

Table 2: Relative fit of six models, representing five alternative hypotheses about the drivers of woma habitat use patterns.

Hypothesis	Rank	Model	Parameters [†]	df	logLik	AIC	ΔAIC	ω
Habitat + shelter (#5)	1	m21	habitat, debris, grveg, burrows	10	-525.6	1071	-	1.0000
Multiple shelters (#4)	2	m15	debris, grveg, shrub, burrows	6	-559.1	1130	59.0	0.0000
Multiple shelters (#4)	3	m14	debris, grveg, burrows	5	-561.9	1134	62.6	0.0000
Single shelter (#3)	4	m8	burrows	3	-589.4	1185	113.6	0.0000
Habitat (#2)	5	m4	habitat	7	-645.7	1305	234.2	0.0000
Null (#1)	6	m1	nil	2	-709.1	1422	350.9	0.0000

[†]habitat = a combination of woodland type and clearing status; debris = cover of fallen woody debris; grveg = cover of ground vegetation; burrows = presence or absence of underground burrows; shrub = cover of shrubs

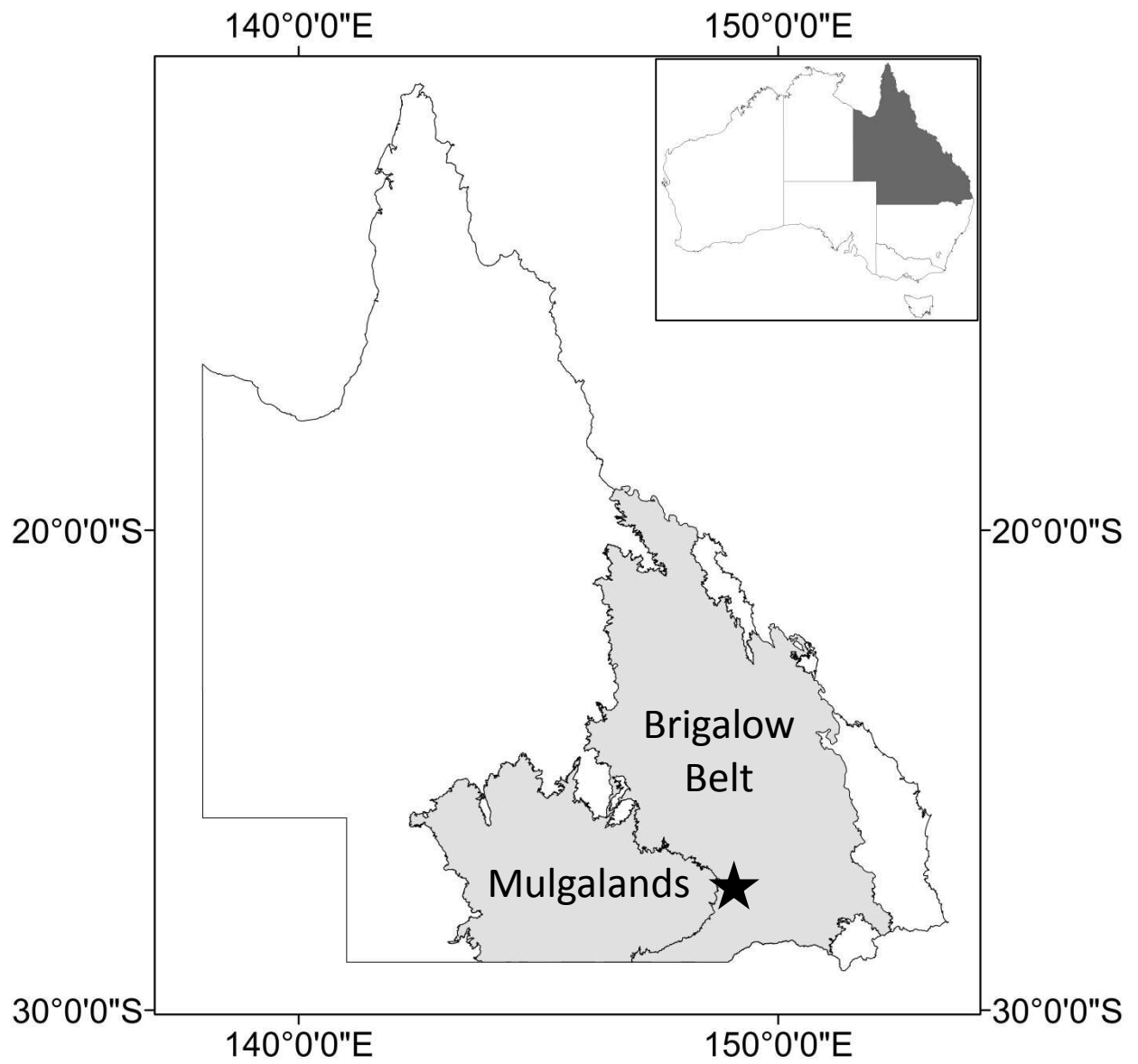


Figure 1: Location of the study site (star) on the boundary of the Brigalow Belt and Mulgalands Bioregions in southern Queensland, Australia.

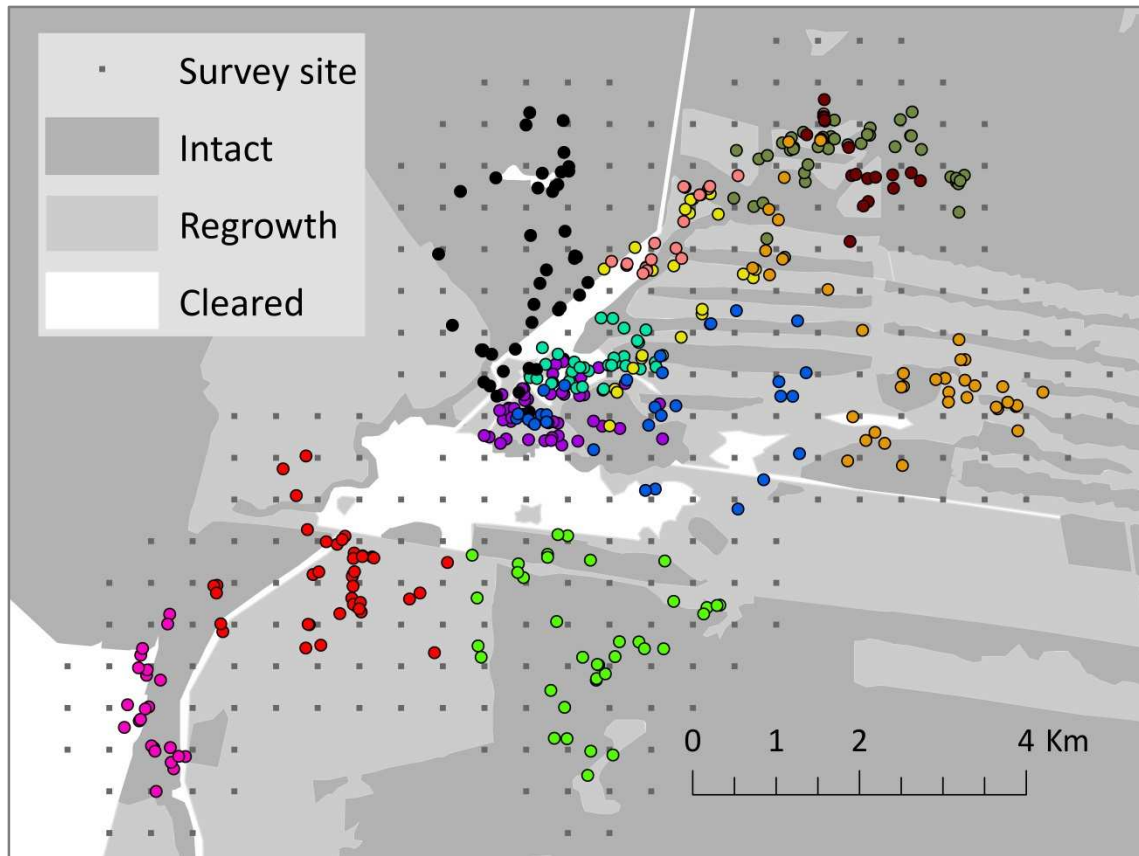


Figure 2: Distribution of the unique woma locations (large circles) and random survey sites (small squares). In the online colour version, each colour represents the recorded locations of an individual woma python.

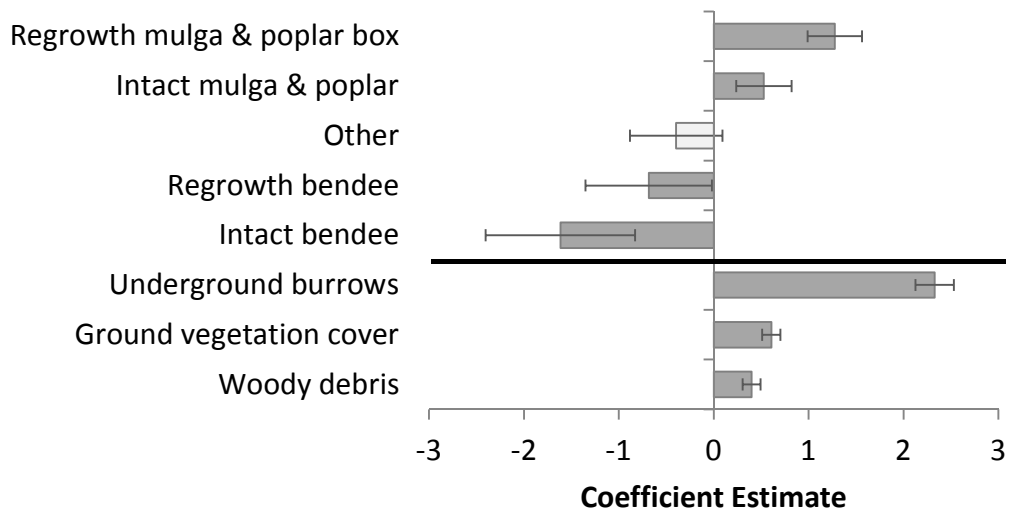


Figure 3: The effects of woodland type and clearing status, and shelter type, on woma occurrence in disturbed dryland landscapes. Values are derived from the best-fit mixed-effects model. Variables with a positive coefficient estimate have a positive effect, and variables with a negative coefficient estimate have a negative effect on woma occurrence. The use of each habitat type (above the line) is relative to cleared paddocks. Lighter shading highlights habitats that were used no more or less often than cleared paddocks as indicated by the error bars, which represent confidence interval estimates (i.e. $1.96 \cdot SE$).

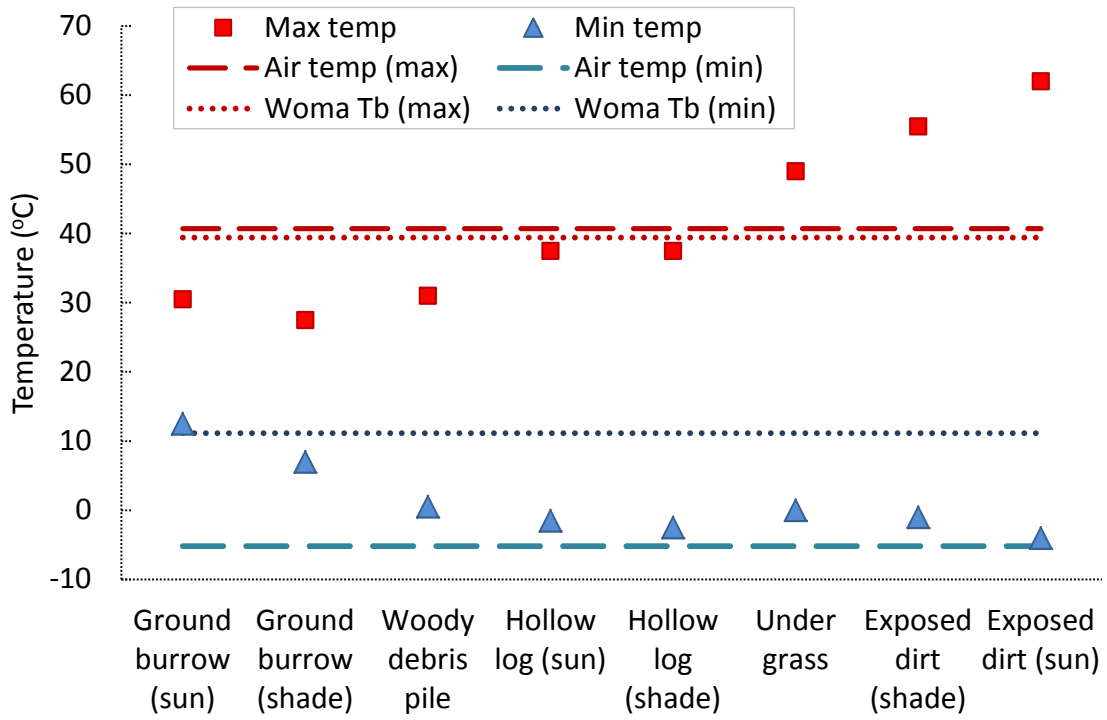


Figure 4: Thermal buffering capacity of eight terrestrial microhabitats at the study site, in comparison with the highest and lowest recorded air and woma body (T_b) temperatures during this study.

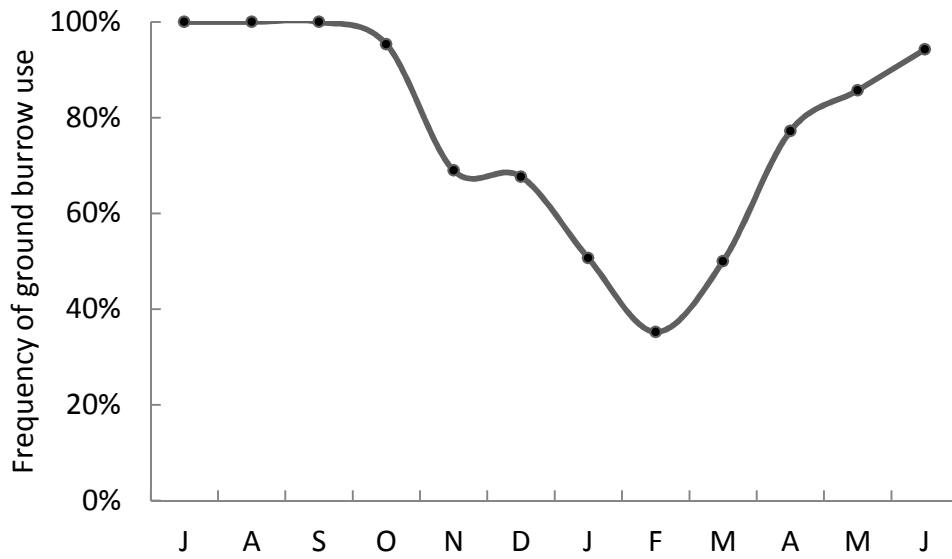


Figure 5: Frequency of ground burrow use per month by radio-tracked womas.