

Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): Seasonal relationships with habitat structure and prey distribution in a rural landscape

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Abstract Squamate reptiles are significant components of woodland vertebrate communities in eastern Australia, but their ecology is poorly understood. We investigated seasonal variation in habitat use by the Inland Carpet Python, *Morelia spilota metcalfei* Wells and Wellington (Pythonidae), a threatened snake that inhabits the woodland environments of the Murray–Darling Basin. Nine pythons were radiotracked within and near the Mount Meg Flora and Fauna Reserve in north-eastern Victoria to investigate how habitat structure and prey distribution (namely, that of the European Rabbit, *Oryctolagus cuniculus* L. (Leporidae)) influenced seasonal movement patterns. Data were analysed over three spatial scales to allow firm interpretations regarding resource selection. Pythons exhibited distinct seasonal trends in habitat use. During the cooler spring months, snakes chose warm, well-insulated microhabitats, primarily rocky outcrops on north- and north-west-facing hillsides. Pythons moved widely during the summer months, apparently in search of prey. Snake localities could be readily linked to rabbit distribution at this time. Specifically, snakes moved to more open, disturbed habitats that contained a high density of rabbits, and consistently selected microhabitats in close proximity to rabbit burrows. In autumn, habitat use was transitional, as snakes progressively returned to the rocky hillsides where they overwintered. Thus, trends in habitat use were influenced by the snakes' thermoregulatory and foraging strategies. Careful management of specific habitats and feral prey populations is required to conserve populations of this endangered snake.

Key words: carpet python, habitat selection, rabbit, Victoria, woodland.

INTRODUCTION

Understanding patterns of spatial resource use by threatened species provides fundamental information about how these animals meet their requirements for survival (Manly *et al.* 1993), and can offer strong direction to regional strategies aimed at their conservation (Forman 1995). In eastern Australia, many forest and woodland vertebrates are threatened by ongoing habitat alteration and fragmentation. Although movement patterns and habitat selection have been studied for a range of bird and mammal taxa, there are few comparable data for many reptile species (see Webb & Shine 1997a; Fitzgerald *et al.* 2002).

Because reptiles are ectothermic, many species are reliant on specific components of their environment in order to maintain appropriate body temperatures (Huey 1982). In southern Australia, thermal requirements are thought to be a fundamental determinant of temporal variation in habitat use by snakes (Shine 1991). Relationships between the seasonal selection

of particular habitat elements and thermoregulatory behaviours have now been documented in a range of snake taxa (Shine 1987; Slip & Shine 1988a,b; Shine & Fitzgerald 1996; Webb & Shine 1997a, 1998; Pearson 2002). However, the role of other factors in affecting habitat associations is less well understood. For example, prey distribution and abundance can significantly influence seasonal movement patterns and habitat selection in snakes (Reinert 1993), yet these relationships have been studied for only two Australian species: the Diamond Python (*Morelia spilota spilota*) and Water Python (*Liasis fuscus*) (Slip & Shine 1988a; Madsen & Shine 1996). In the present study, we investigate how both habitat structure and prey distribution are related to the seasonal movements of the Inland Carpet Python, *Morelia spilota metcalfei*, a threatened snake that inhabits the woodland environments of the Murray–Darling Basin in south-eastern Australia (Barker & Barker 1994; Greer 1997).

In Victoria, the Inland Carpet Python has been listed as endangered since 1994 (NRE 2000), largely as a result of habitat changes, reductions in prey abundance and threats posed by introduced predators (Robertson *et al.* 1989). Subsequent research on the ecology and conservation status of this species in Victoria has confirmed that each of these factors are significant

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threats to remaining populations of this snake. Within the State's north-east, pythons inhabit remnant woodland, but in some localities, appear reliant on adjacent disturbed areas that harbour a high density of prey species, primarily the European Rabbit (*Oryctolagus cuniculus*) (P. Robertson, unpubl. data). Throughout northern Victoria, rabbits make up a high percentage of the prey items taken by adult pythons. In the north-east, 60% of 55 python scats collected between 1997 and 2000 contained rabbit fur (P. Robertson, unpubl. data).

We set out to investigate three basic questions: (i) How are the seasonal movement patterns of carpet pythons related to the distribution of broad habitat types and their structural components within a woodland-farmland mosaic in north-eastern Victoria?; (ii) How do these movements correspond to the distribution of their major prey species, the European Rabbit?; and (iii) How do each of the above relate to seasonal variation in microhabitat use?

METHODS

Study area

The study was undertaken within an area centred on the Mount Meg Flora and Fauna Reserve (FFR) (36°23'S, 146°05'E), approximately 22 km west-south-west of Wangaratta in north-eastern Victoria, Australia. The Mount Meg FFR represents a northerly projection of the Chesney Vale Hills and an outlying reserve of the Warby Range State Park. Both areas form a major component of Victoria's 'northern inland slopes', a distinct bioregion characterized by steep, heavily weathered granite massifs and often complex heath and woodland vegetation communities (Parks Victoria 2000). Seasonal climatic cycles are characterized by hot summers (January mean maximum temperature 31.0°C) and cool winters (July mean maximum temperature 12.8°C). Rainfall peaks in

winter (June mean rainfall 74.2 mm), although frequent cold fronts deliver rain throughout the warmer months (Bureau of Meteorology 2002).

All fieldwork was conducted within a 5-km² study area incorporating the Mount Meg FFR and adjacent hills to the east (Dave's Hill) and south-east. Mount Meg (320 m) and Dave's Hill (290 m) are divided by a narrow gully and a permanent north-flowing creek. Variations in land use, vegetation and topography within this area are further described below.

Study animals and radiotelemetry

Nine individuals of *M. s. metcalfei* were captured and radiotracked within the Mount Meg study area between April 1997 and March 2001. Snakes were primarily located by local landholders and regional land-management staff. On capture, each snake was measured (snout-vent length (SVL) to the nearest cm) using a metric tape, weighed (total mass to the nearest g) using a Pesola spring balance and sexed by probing for hemipenes. With the exception of one male, all specimens were considered sexually mature adults when judged by SVL (Shine 1991; Table 1). Each python was permanently marked by the subcutaneous injection of a passive integrated transponder tag.

All pythons were fitted with a temperature-sensitive radiotransmitter (Holohil Systems Pty Ltd, Canada; Model SI-2T). Units for larger animals had a battery life of approximately 28 months (dimensions 51 mm × 12 mm; weight 14.5 g; whip antenna 245 mm), whereas those for smaller animals operated for approximately 15 months (35 mm × 12 mm; 11.5 g; whip antenna 270 mm). Transmitters were implanted within the body cavity by a veterinarian following the procedures described by Slip and Shine (1988a) and Webb and Shine (1997a). Prior to insertion, the entire transmitter unit was coated in flowable silicon to provide a waterproof seal and reduce the risk of damage to the snake's internal organs (Webb

Table 1. Gender, morphometric data and tracking details for each python monitored within the Mount Meg study area (SVL and weight recorded on capture)

Scale clip number	Sex	SVL (mm)	Weight (g)	Capture date	Tracking period
NE04	Male	1450	939	13 February 1997	7 March 1997–5 March 2001
NE11	Female	1750	3300	12 June 1997	18 November 1997–12 March 1999
NE12	Male	1460	1100	25 September 1997	18 November 1997–15 January 1998
NE13	Male	1600	1450	31 October 1997	15 November 1997–3 December 1997
NE14	Male	1460	1050	10 October 1997	17 November 1997–23 April 1999
NE16	Female	1530	1350	13 October 1997	22 November 1997–21 December 1997
NE22	Male	1620	1510	3 September 1998	16 September 1998–23 May 2000
NE24	Male	1280	650	12 January 1999	11 March 1999–24 May 2000
NE25	Female	1600	1350	12 January 1999	11 March 1999–5 March 2001

SVL, snout-vent length.

& Shine 1997a). Complete units represented less than 2% of python bodyweight in all cases.

Snakes were released at their points of capture and subsequently located weekly during spring, summer and autumn. Pythons were located during the day (usually morning to early afternoon) using a directional 'H' antenna and miniature radio receiver (Telonics Inc., AZ, USA). Location accuracy was generally to within 1 m, and was achieved either by direct visual observation or by triangulation. A range of microhabitat variables was recorded at each location to examine seasonal variation in microhabitat use. Shaded air temperature (1 m above the ground, 1 m horizontal from the snake's location) and shaded surface temperature (1 m from the snake's location) were measured to the nearest 0.1°C using a pocket digital thermometer. The microhabitat utilized by each snake was classified into eight structural categories: on or in rock outcrop; on ground; in rabbit burrow; on or in log; in tree; in shrub; in water; or inside a building. To assess microhabitat level associations with rabbit distribution, the distance to the nearest rabbit burrow was estimated at all relocation sites. The coordinates of each location were recorded in the Universal Transverse Mercator system (White & Garrett 1990) using a differential global positioning system (Trimble 10 channel Ensign XL GPS Unit), providing an accuracy of ± 5 m on most occasions.

Landscape variables

Sampling grid

During September 2000, a sampling grid was established within the Mount Meg study area to investigate the relationships between python movement patterns and variation in habitat structure and rabbit abundance. The grid extended 2 km eastwards from the western boundary of the Mount Meg FFR to the eastern side of Dave's Hill and ran north-south for 2.5 km, encompassing the majority of sites utilized by the telemetered pythons. Grid cells 1 ha (100 m \times 100 m) in size represented the basic sampling unit and were chosen to minimize within-cell variation in habitat features, while providing a broad scale at which to investigate the spatial relationships in question. *M. spilota* are capable of travelling more than 500 m per day (Slip & Shine 1988a; P. Robertson, unpubl. data), and therefore could easily relocate to a new grid cell between tracking events (see Cross & Peterson 2001). Restrictions of time and accessibility to some areas resulted in the exclusion of 83 cells from the sampling area. The remaining 417 active cells were identified using markers placed on nine parallel transect lines that ran north-south across the grid, at a distance of 200 m apart (following Southwell 1987).

Habitat structure

To examine seasonal habitat associations displayed by these pythons, six macrohabitat types were described within the study area based on variation in topography, vegetation and disturbance history:

1. Granitic woodland: structurally complex remnant woodland found on steep slopes and hill crests; canopy vegetation is dominated by *Eucalyptus blakelyi*; stands of the shrubs *Calytrix tetragona* and *Grevillea alpina* often form a dense understorey layer.
2. Disturbed granitic woodland: structurally disturbed remnant woodland found on the lower slopes; overstorey consists of *E. blakelyi*, *Eucalyptus albens* and *Eucalyptus macrorhyncha*; understorey vegetation heavily depleted by sheep grazing and consists of introduced weeds; granite outcrops are numerous.
3. Degraded woodland: remnant woodland in which the overstorey has been largely removed and understorey shrubs are restricted to localized rocky ridges; exotic weeds (primarily *Echium plantagineum*, *Marrubium vulgare* and *Hypericum perforatum*) form a dense layer of vegetation at ground level.
4. Wetland: several spring-fed dams at the head of a small gully surrounded by dense heath of *Leptospermum continentale* with an overstorey of sparse *Eucalyptus camaldulensis*.
5. Gully: a narrow strip of open riparian vegetation following the creek-line north through the study area; overstorey consists of *E. albens* and *E. camaldulensis*, whereas the understorey layer is dominated by *Acacia implexa*.
6. Grazed land: undulating agricultural land to the north the study area; almost entirely cleared and replaced by exotic pasture.

Because of sharp topographical and land-use divisions within our study area, we are confident that the categories identified above are ecologically significant. The distribution of each macrohabitat was subsequently mapped over the entire study area by visually assigning each grid cell to one of the six habitat types. An illustration of each macrohabitat type is provided elsewhere (Heard & Black 2003).

Within-habitat variation of 10 structural and compositional habitat attributes was sampled in a random set of 200 grid cells to examine relationships between python movement patterns and structural habitat attributes. Variables chosen were either distinguishing features used in the habitat classifications described above, or those found to be important to carpet pythons elsewhere (Slip & Shine 1988a; Shine & Fitzgerald 1996). Cover estimates for seven structural variables were recorded using 10 evenly placed point surveys within each cell (Table 2). All point surveys

consisted of a circular plot with a radius of 10 m. Visual cover estimates were made within each quarter section of these plots and were combined to give an overall estimate for the entire plot. Cell-wide cover estimates for each variable were based on the mean of all 10 point surveys.

A visual estimate of the extent of remnant vegetation cover was made while traversing each grid cell. Both altitude and slope were calculated with the use of a topographical map (digital topographical information courtesy of Parks Victoria, Wangaratta). Altitude was recorded in metres at the cell centre, and slope was expressed as the difference in height (m) between the highest and lowest points within each cell (Southwell 1987).

Rabbit distribution

Rabbit-burrow and dung-pellet counts were carried out in each grid cell between October 2000 and February 2001, to quantify rabbit distribution within the study area and identify its relationship with python movement patterns. Both these measurements provide reliable indices of rabbit abundance within temperate Australian environments (Williams *et al.* 1995). All rabbit-burrow entrances (active and inactive) located within 5 m of either side of each transect were counted and mapped on a cell-by-cell basis on four separate occasions. Within a random set of 137 grid cells, the ability of these counts to predict patterns of cell-wide burrow abundance was investigated by comparing them to similar counts within 10 systematically placed point surveys (a sample of those described above). Relative burrow abundance within each grid cell was recorded as the maximum number of burrows counted along the transect during the four sampling periods. Relative dung-pellet abundance in each grid cell was also measured during these four sampling periods using a 1-m² quadrat. During each sampling period, the quadrat was placed 20 m north of that sampled previously in order to ensure that individual pellets were not repeatedly counted. For each count, the quadrat was placed 15 m from the transect line, perpendicular to the line. All intact pellets within the

quadrat were counted, and pellet abundance within each grid cell was expressed as the mean number recorded during the four transect samples.

Data analysis

Telemetry data

For each individual python, locational datasets were divided by season (all years combined) and mapped onto a base map of the sampling grid using the mapping package *MapInfo version 7.0* (MapInfo Inc, New York, NY, USA). All locations were then assigned to one of the 417 individual grid cells. Those that were located outside of the grid were excluded from further analysis (including all six locations recorded for python NE12). Python locations were aggregated within the northern half of the sampling grid. Therefore, we restricted all analyses to the portion of the grid contained within an outer-minimum convex polygon surrounding all python locations, following Kenward (2001). Polygon borders were based on the boundaries of all grid cells bisected by lines linking the outer-most locations utilized by these snakes. The resultant grid consisted of 282 cells.

To reduce the influence of temporal autocorrelation in the locational dataset, only locations recorded at least 6 days apart were used in further analysis. This length of time was thought necessary on the assumption that animals that had not moved since the previous location had freely chosen not to do so (i.e. any factors possibly inhibiting movement, such as weather conditions, should have abated over this time). Within each season, the utilization rate of each grid cell was calculated as the sum of all records located within that cell. Unless otherwise stated, all subsequent data analysis was undertaken using the statistical package *SPSS version 10.0* (SPSS Inc., Chicago, IL, USA) or *JMP version 5.0* (SAS Institute, Cary, NC, USA).

Macrohabitat level

Within each season, the total number of python locations recorded within each macrohabitat was

Table 2. Structural habitat variables sampled within a random set of 200 grid cells, each of 1 ha in size, within the Mount Meg study area

Variable	Definition
Per cent bare ground	Cover of bare soil or leaf-litter in plot
Per cent rock	Cover of bare granitic rock in plot; usually outcrops or individual boulders
Per cent ground vegetation	Foliage cover of weeds, grasses, sedges, herbs and lilies in plot
Per cent understorey vegetation	Foliage cover of all shrubs and juvenile trees <3 m in height in plot
Per cent overstorey vegetation	Foliage cover of all trees >3 m in height in plot
Log density	Number of fallen logs >10 cm in diameter in plot
Per cent fallen vegetation	Cover of fallen vegetation (branches and foliage) in plot

calculated by adding the totals from all grid cells assigned to that macrohabitat type (White & Garrett 1990). For each season, we performed a χ^2 goodness-of-fit test to determine whether the observed distribution of radio-locations between macrohabitat types differed from that expected, based on their availability (availability being habitat area, expressed as the number of grid cells assigned to that habitat), following White and Garrett (1990). Within each season, python 'preference' for or 'avoidance' of each macrohabitat was calculated as the difference between the rank of availability and the rank of usage obtained for each habitat type (Johnson 1980).

Pooling of data across pythons was necessary for statistical testing in this study. Within radio telemetric studies of snakes, problems of individual variability with respect to habitat use are recognized, and previous authors warn against the effect of this variation on the trends observed from a collective group (Shine 1987; Charland & Gregory 1995). Although our locational dataset was adequately large, it was obtained from a small sample of snakes, and several contributed significantly more data than others. It should be recognized, therefore, that the trends observed from the group could be biased by these individuals. Nonetheless, the monitored pythons displayed similar seasonal patterns of movement and habitat use, and we are confident that the data obtained are not significantly affected by aberrant behaviour. Additionally, python home-ranges overlapped extensively, and habitat availability does not appear to have been effected by conspecific exclusion.

Spearman's rank correlation coefficient was used to determine the relationship between rabbit-burrow abundance recorded along the transect line with that measured from the point surveys. Subsequent calculation of relative rabbit-burrow abundance between macrohabitats was made as follows:

$$rba_i = [(b_i/t) \times 100]/ha_i \quad (1)$$

where rba_i is the relative burrow abundance within macrohabitat i , b_i is the sum of burrows within grid cells assigned to macrohabitat i , t is the total number of burrows counted over the entire study area and ha_i is the percentage of the total area covered by macrohabitat i . The observed distribution of burrow abundance between macrohabitats was tested against that expected based on macrohabitat area using χ^2 goodness-of-fit.

Grid-cell level

Correlations between habitat variables were tested using a Spearman's rank correlation matrix. Altitude and slope were highly correlated ($r > 0.8$) and thus altitude was discarded from further analyses. Because of relatively low altitudinal variation within the study area, slope was considered a more important determinant of habitat variation. For each season, we

classified grid cells as 'used' or 'unused' by the eight snakes tracked and employed binary logistic regression (McCullagh & Nelder 1989) to determine which habitat variables (including rabbit distribution) correlated with grid-cell utilization. Individual models were constructed for each season using a backward stepwise procedure to reduce the number of explanatory variables included. Under this method, models are constructed using all candidate variables and the explanatory power of the model assessed using Akaike's information criterion (AIC). The variables explaining the least proportion of deviance were removed successively until no further improvement in AIC was noted. The resulting model with the minimum AIC was considered the most parsimonious, and was retained for the purposes of inference and prediction. Rabbit-pellet abundance and burrow-presence/absence variables were excluded from the regression analysis because of strong correlations to rabbit-burrow abundance. All regression analyses were undertaken using the *R* statistical software package (Ihaka & Gentleman 1996).

Receiver-operating characteristic (ROC) plots (DeLong *et al.* 1988; Zweig & Campbell 1993) were subsequently used to evaluate the performance of the regression models. ROC plots are derived by plotting the proportion of true-positive cases identified by the model ('sensitivity': the proportion of occasions when the model correctly predicts species' presence) against false positive cases ('specificity': the proportion of occasions when the model incorrectly predicts species' presence) at a number of prediction threshold values (the probability value at which the model is considered to have predicted presence). The area under the resulting curve (AUC) provides a measure of a model's predictive performance between 0.5 (a model with no predictive value) and 1.0 (a model with perfect predictive ability). Further discussion on the application of this method is provided by Fielding and Bell (1997), Pearce and Ferrier (2000) and Luck (2002). ROC analysis was undertaken using the statistical package *R*, using a version of S script devised by D. Mahoney and E. Atkinson (Mayo Clinic, Rochester, MN, USA)

Microhabitat level

Seasonal variation in microhabitat use was expressed as the per cent of locations falling within each microhabitat category. For each season, relationships between microhabitat use and variation in shaded air and surface temperatures were explored graphically (only microhabitats used on more than five occasions were included in this analysis). Seasonal changes in the proximity of relocation sites to rabbit burrows were tested using a non-parametric Kruskal-Wallis test. The data were significantly non-normal (Shapiro-Wilks *W*-test) and displayed variance inequality (Bartlett's

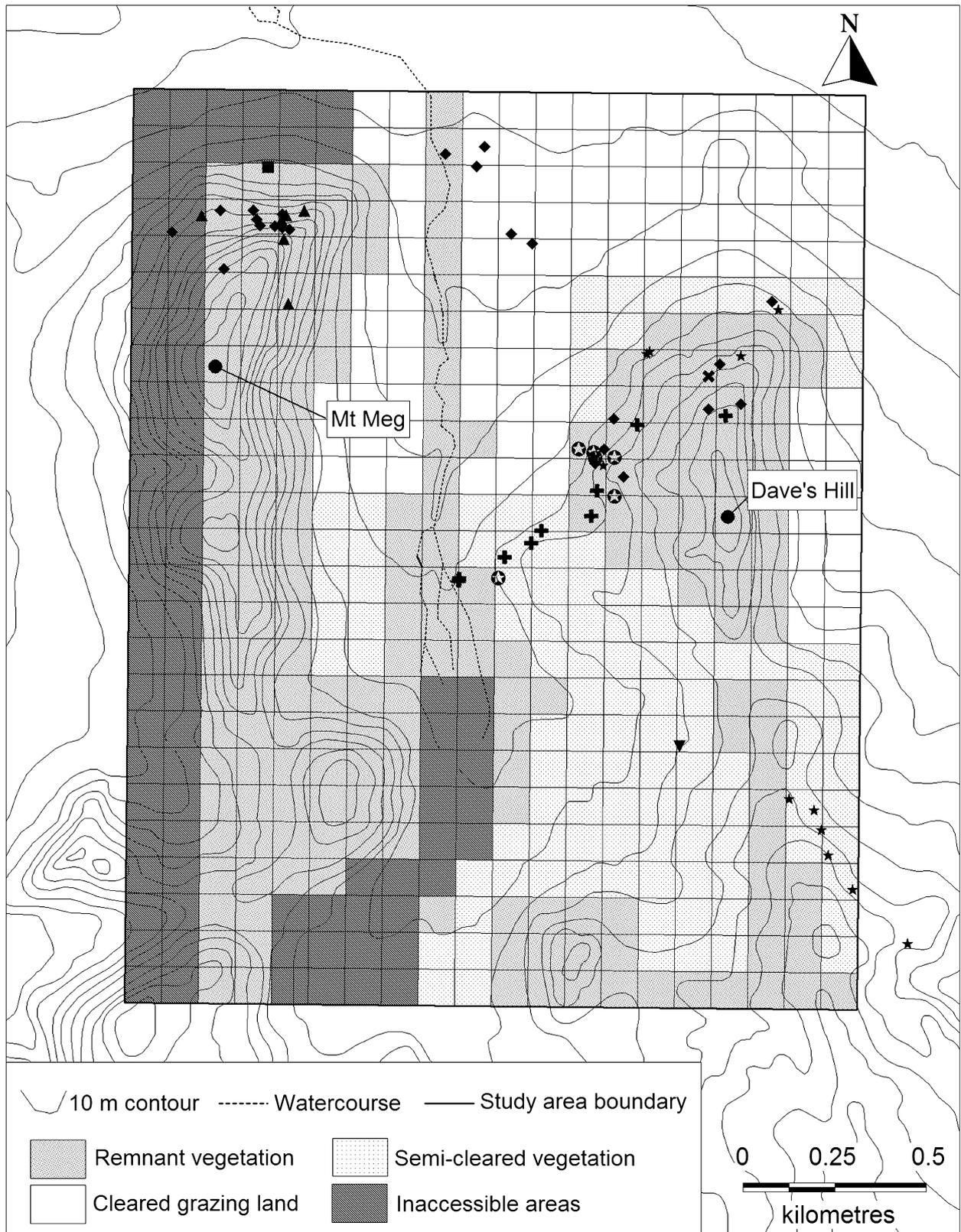


Fig. 1. The distribution of python radio-locations recorded during spring in relation to remnant vegetation cover and topography at the Mount Meg study area. Data were gathered from eight carpet pythons monitored between April 1997 and March 2001: (◆), male NE04; (×), female NE11; (■), male NE13; (▲), male NE14; (▼), female NE16; (+), male NE22; (⊕), male NE24; (★), female NE25.

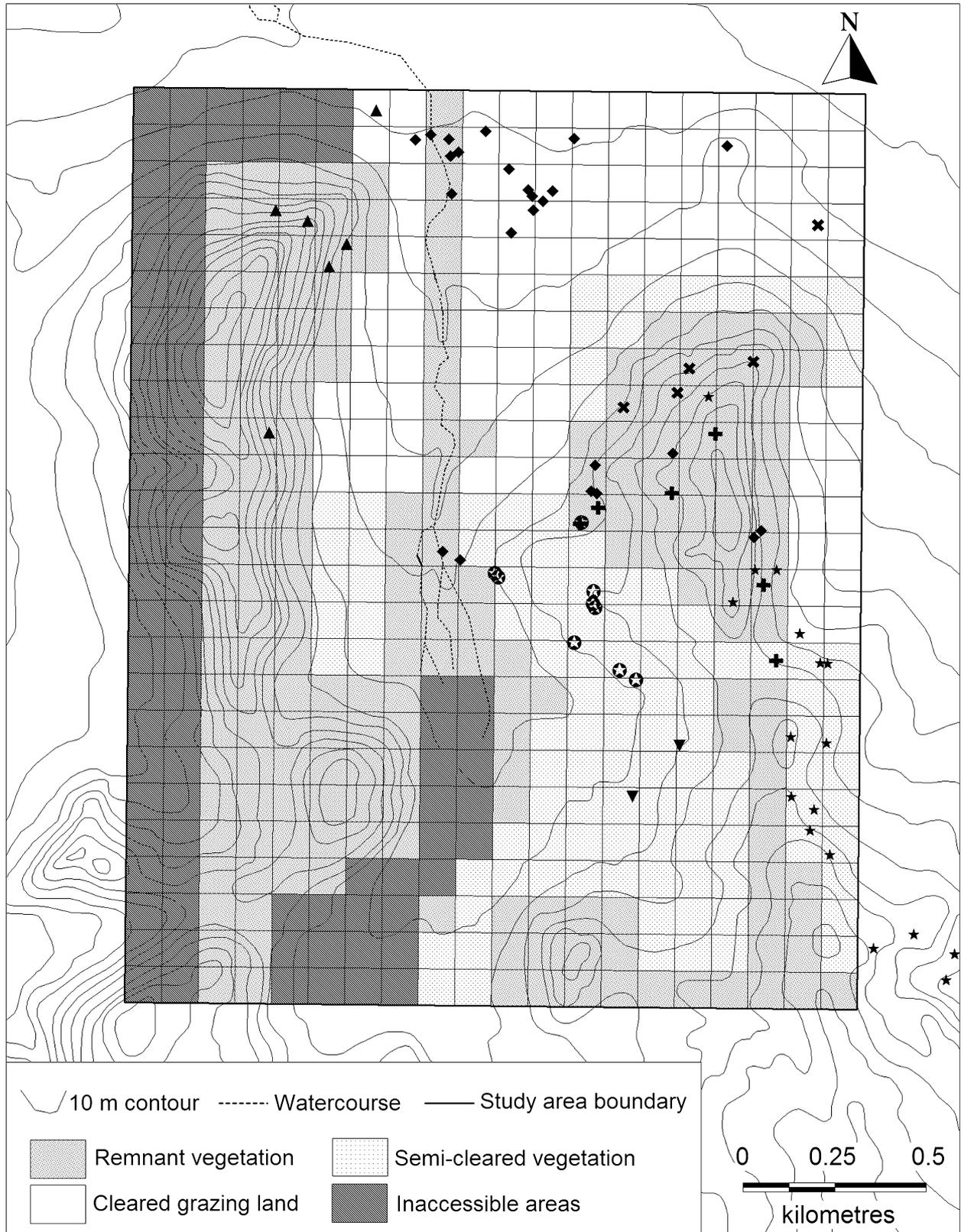


Fig. 2. The distribution of python radio-locations recorded during summer in relation to remnant vegetation cover and topography at the Mount Meg study area. Data were gathered from seven carpet pythons monitored between April 1997 and March 2001: (◆), male NE04; (×), female NE11; (▲), male NE14; (▼), female NE16; (+), male NE22; (⊗), male NE24; (★), female NE25.

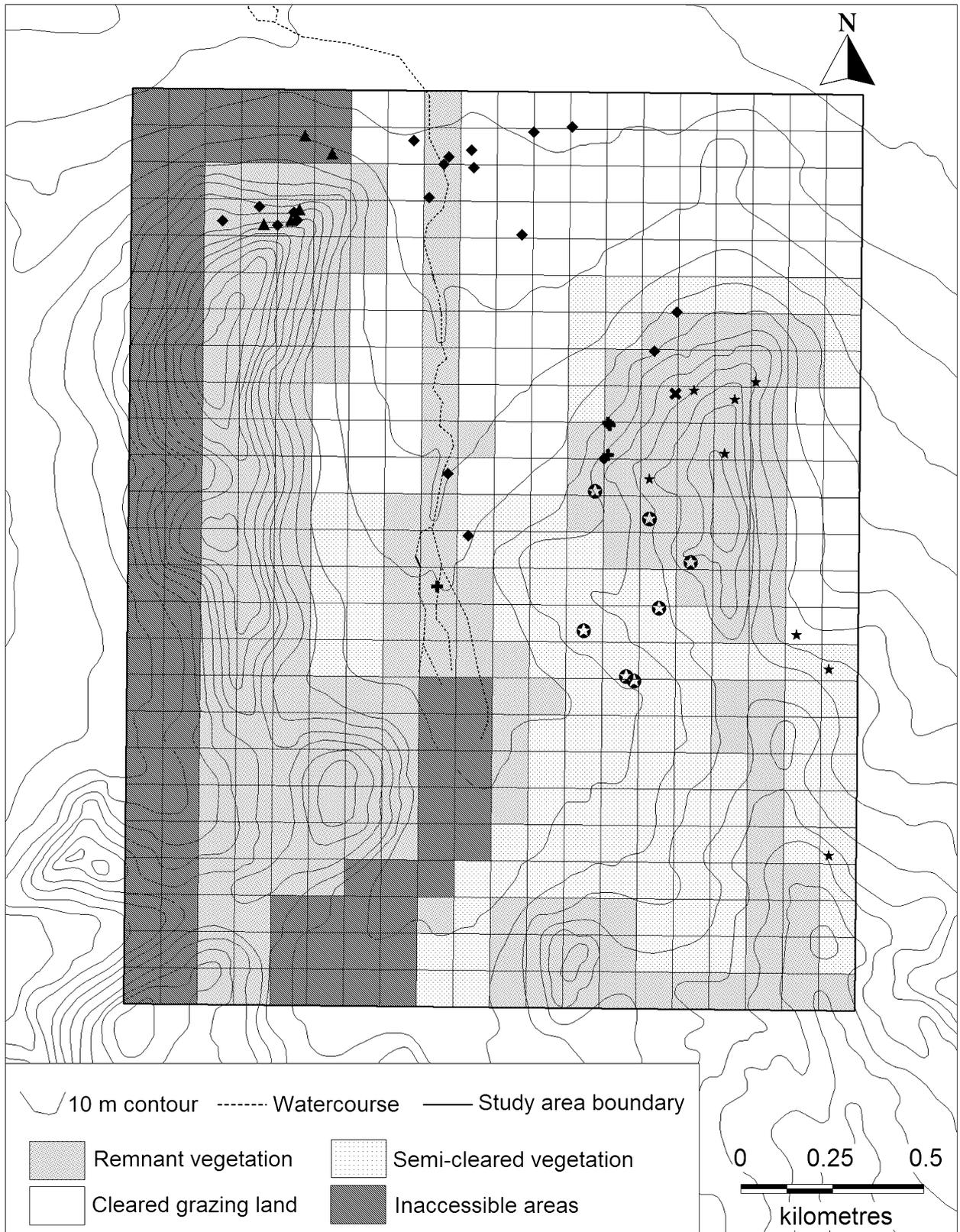


Fig. 3. The distribution of python radio-locations recorded during autumn in relation to remnant vegetation cover and topography at the Mount Meg study area. Data were gathered from six carpet pythons monitored between April 1997 and March 2001: (◆), male NE04; (×), female NE11; (▲), male NE14; (⊕), male NE22; (⊛), male NE24; (★), female NE25.

F-test) (Sokal & Rohlf 1995). We limited this analysis to occasions when burrows were located within 100 m of the snake locations, because of the likely inaccuracy of visual estimates made over longer distances. The

Tukey–Kramer honestly significant difference (HSD) test was used to determine which of the seasonal means varied significantly.

RESULTS

Macrohabitat level

Python habitat use

During spring, python macrohabitat use varied significantly from that expected based on macrohabitat availability ($\chi^2 = 65.3$, degrees of freedom (d.f.) = 5, $P < 0.001$). Snakes primarily used sites located on the north- or north-west-facing slopes of Mount Meg and Dave's Hill (Fig. 1), primarily within granitic woodland and disturbed granitic woodland. The wetland area was used infrequently during the study period; however, one snake (NE22) sheltered within this macrohabitat type continuously between 29 September 1998 and 19 November 1998. Degraded woodland, gully areas and grazed land were largely avoided.

Snakes dispersed widely across the study area during summer (Fig. 2) and used macrohabitats in proportions similar to their availability ($\chi^2 = 4.3$, d.f. = 5, $P > 0.50$). Pythons generally moved away from the densely wooded slopes used during spring, preferring more open habitat types, particularly degraded woodland. Although generally avoided, grazed land was utilized frequently by one male python (NE04), usually whilst visiting several farm buildings in the north of the study area.

In autumn, snakes generally moved away from the more open habitat types utilized during the summer months (particularly degraded woodland), and again frequented granitic woodland and disturbed granitic woodland. In the later months of autumn, telemetred pythons gradually returned to the steeper hill slopes inhabited during spring (e.g. the north face of Mount Meg; Fig. 3). During autumn, python NE04 used remnant vegetation along the gully while returning to Mount Meg from either Dave's Hill or the farm buildings in the north of the study area. Patterns of macrohabitat utilization displayed during autumn differed significantly from those expected based on macrohabitat availability ($\chi^2 = 41.4$, d.f. = 5, $P < 0.001$). Figure 4 displays seasonal macrohabitat preferences displayed by carpet pythons within the Mount Meg study area.

Rabbit abundance across macrohabitat types

Rabbit-burrow abundance as recorded from the transect line correlated highly with that observed using point surveys ($r = 0.5$, $P < 0.001$), validating transect

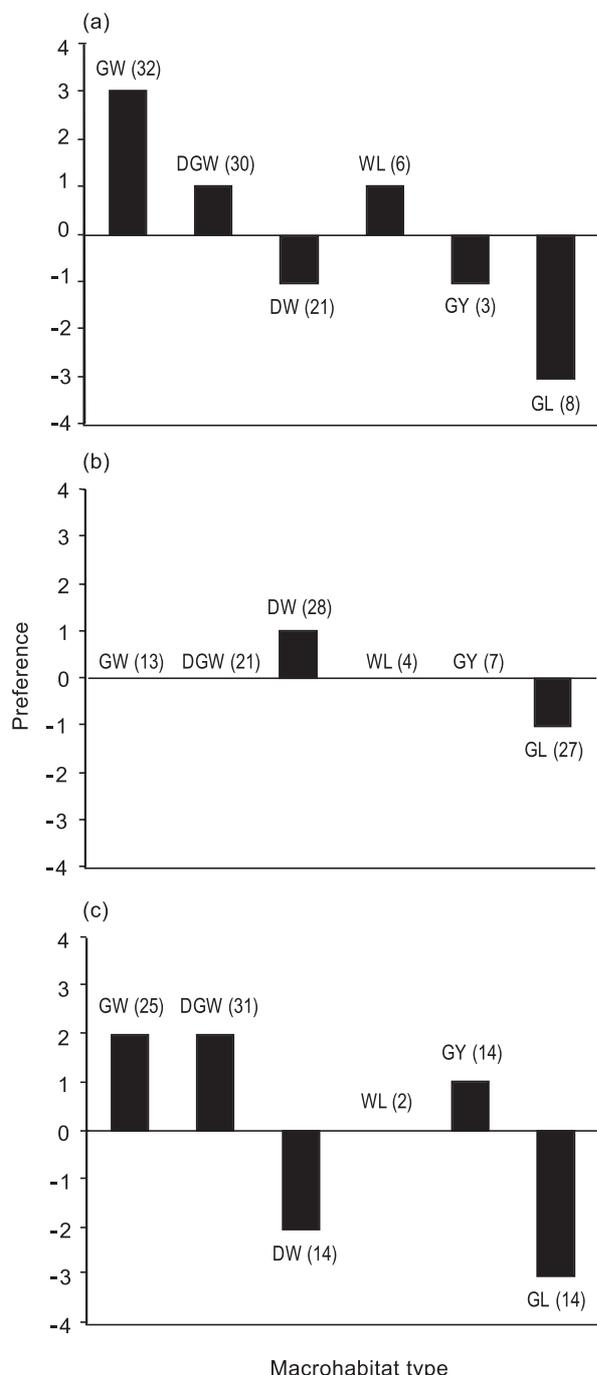


Fig. 4. Seasonal macrohabitat preferences displayed by carpet pythons at the Mount Meg study area in (a) spring ($n = 66$), (b) summer ($n = 75$) and (c) autumn ($n = 59$). Numbers in parentheses indicate the percentage of radiolocations deriving from each habitat type. DGW, disturbed granitic woodland; DW, degraded woodland; GL, grazed land; GW, granitic woodland; GY, gully; WL, wetland.

counts as a reliable indicator of cell-wide burrow abundance. Burrow abundance varied significantly between the six macrohabitat categories ($\chi^2 = 838.8$, d.f. = 5, $P < 0.001$). Relative burrow abundance (*rba*) was highest in degraded woodland (*rba* = 2.3) and

disturbed granitic woodland (*rba* = 1.4) – far greater than in all remaining habitats (*rba* < 0.5) (Fig. 5).

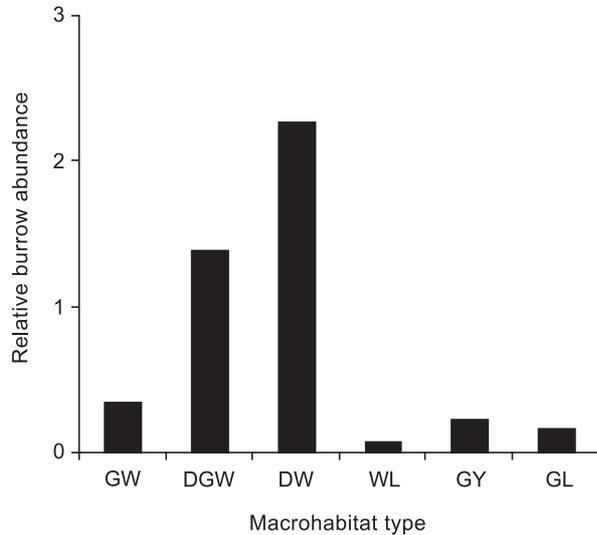


Fig. 5. Relative rabbit burrow abundance between macrohabitat types within the Mount Meg study area. Relative burrow abundance is measured in proportion to the available habitat area. DGW, disturbed granitic woodland; DW, degraded woodland; GL, grazed land; GW, granitic woodland; GY, gully; WL, wetland.

Grid-cell level

Areas occupied by telemetred carpet pythons displayed consistently higher structural habitat complexity than those that were not inhabited during the study period. This was particularly apparent during spring (Table 3).

In all seasons, locations used by pythons were characterized by relatively steep topography, high rock and understorey vegetation cover, higher fallen-log density and relatively low ground-vegetation cover. Note, however, that the latter association resulted from a consistent avoidance of cells covering open pasture, where ground vegetation cover was generally 80–100%. Our cell-by-cell estimates of remnant-vegetation cover showed that telemetered pythons consistently inhabited cells with less vegetation disturbance than neighbouring areas; on average, the extent of remnant vegetation cover was 34% higher in used grid cells.

Grid-cell level associations between python activity and rabbit distribution also varied seasonally. Cells inhabited during spring and autumn showed little relationship with rabbit distribution. During the summer months, however, snakes were found in cells with higher burrow and pellet abundance (burrow means \pm standard error (SE): used cells = 5.8 ± 1.4 ,

Table 3. Grid-cell relationships between python activity and nine biophysical attributes recorded across the Mount Meg study area. The sample size of grid cells utilized by pythons in each season (n) is provided in parenthesis

Variable	Relationship [†]		
	Spring (n = 23)	Summer (n = 29)	Autumn (n = 18)
Per cent bare ground	+3.8	+2.6	+5.4
Per cent rock	+25.4	+18.5	+18.4
Per cent ground vegetation	-16.9	-14.1	-14.0
Per cent understorey vegetation	+10.3	+6.4	+11.4
Per cent overstorey vegetation	+7.8	+7.2	+10.2
Log density	+4.0	+3.0	+4.4
Per cent fallen vegetation	+6.3	+2.6	+6.7
Per cent remnant vegetation cover	+30.1	+24.7	+31.3
Slope (m)	+9.6	+5.5	+6.3

[†]Relationships are the mean variable score for cells used by the eight snakes tracked minus that obtained from cells that were avoided by these snakes.

Table 4. Summary of binary logistic regression analysis of the relationships between python activity and nine biophysical attributes recorded within grid cells across the Mount Meg study area

Model	Variables included	Estimate	Standard error	P
Spring	Per cent rock	+0.06	0.01	<0.001
	Per cent overstorey vegetation	-0.04	0.02	0.07
Summer	Per cent rock	+0.03	0.01	0.01
	Per cent ground vegetation	-0.02	0.01	0.09
	Per cent understorey vegetation	-0.04	0.02	0.08
Autumn	Per cent remnant vegetation cover	+0.02	0.01	<0.01

unused cells = 3.8 ± 0.7 ; pellet means \pm SE: used cells = 23.8 ± 4.2 , unused cells = 17.4 ± 2.5), and more frequently inhabited cells in which rabbit burrows were present (burrows present: used cells = 65%, unused cells = 43%).

Logistic regression analysis confirmed significant seasonal variation in the relationships between python activity and the biophysical attributes measured. However, few of the original nine variables proved useful for predicting python movement patterns at the grid-cell level (Table 4). Regression models indicated that occurrence in particular cells was most consistently related to high rock cover and low to moderate overstorey-vegetation cover during spring; high rock cover, low ground-vegetation cover and low understorey-vegetation cover during summer; and high remnant-vegetation cover during autumn. However, only rock cover and remnant-vegetation cover were significantly associated with python distribution ($P < 0.05$; Table 4). The logistic regression analyses did not show a significant correlation between rabbit distribution and python grid-cell occupancy in any season.

Although few explanatory variables proved significant, the predictive ability of each derived habitat model was acceptable. AUC of the resulting ROC plots (Fig. 6) indicated predictive ability was highest for the spring model (AUC = 0.80, SE = 0.05, $P < 0.001$) and moderate for those constructed using the summer and autumn datasets (summer: AUC = 0.75, SE = 0.05, $P < 0.001$; autumn: AUC = 0.74, SE = 0.05, $P < 0.001$).

Microhabitat level

Carpet pythons were terrestrial during the cool spring months and sheltered within complex granite outcrops, particularly rock crevices or gaps between large boulders (Table 5). Snakes were frequently recorded basking on the ground adjacent to such structures during mild, sunny conditions throughout this period (Fig. 7). When on the ground, snakes preferred areas with woody debris or some vegetation cover, generally the foliage of native lilies (*Stypantra glauca*, *Dianella* spp.) or exotic weeds (particularly *Marrubium vulgare*). Arboreal behaviour increased during summer when pythons were most frequently located sheltering within tree hollows 2–10 m above-ground (particularly within *E. blakeyi*, *E. albens* and *E. macrorhyncha*). All snakes located at ground level during summer were sequestered in rock crevices or rabbit burrows. Over the autumn months, snakes used rock crevices and tree hollows at similar frequencies, and again used hollow logs, which they avoided during summer. The snakes' use of hollow logs often coincided with low air and surface temperatures during autumn (Fig. 7). Tele-

metered pythons were rarely found on shrubs or in aquatic situations (although one animal spent a period of 4 weeks among dense emergent vegetation), and, with the exception of NE04, seldom ventured into buildings.

The proximity of microhabitats to rabbit burrows varied significantly between seasons (Kruskal–Wallis: $\chi^2 = 26.9$, d.f. = 2, $P < 0.001$). Distance to the nearest rabbit burrow was significantly greater during spring (median = 50 m, $n = 42$) than summer (median = 5 m, $n = 60$) or autumn (median = 20 m, $n = 41$) (Tukey–Kramer HSD: spring vs summer, difference = 20.8, $P < 0.05$; spring vs autumn, difference = 8.2, $P < 0.05$; summer vs autumn, difference = -3.5 , $P > 0.05$). Similarly, the use of rabbit warrens as shelter sites was almost entirely restricted to the summer (spring = 0 locations; summer = 12 locations; autumn = 2 locations). Burrow use was often associated with high daily air and surface temperatures (Fig. 7). During summer, air temperatures exceeded 29°C on eight of the 12 occasions in which snakes were recorded sheltering within rabbit burrows.

DISCUSSION

The results of the present study show distinct seasonal shifts in habitat use by this population of *M. s. metcalfei*, and provide evidence that prey distribution plays a significant role in seasonal habitat selection. However, from the data presented, we believe that thermal requirements are the overriding determinant of temporal variation in habitat use by these snakes. The population studied here is of particular interest in this regard as it occurs at the south-eastern extremity of carpet python distribution across mainland Australia – a thermally challenging and climatically variable environment. Therefore, the following discussion focuses on interpreting the patterns observed in terms of annual thermoregulatory and foraging strategies, relating both to the structure and composition of the habitats available within the Mount Meg study area.

The telemetered pythons occupied structurally diverse habitats during spring, primarily using sites located on north- and north-west-facing slopes, and favouring sites dominated by complex granite outcrops and low canopy cover. Several temperate Australian snake species display preferences for unshaded, fractured or exfoliated rock microhabitats during the cooler months of the year (elapids: Fyfe & Booth 1984; Webb & Shine 1998; colubrids: Fitzgerald 2000), including other members of the carpet python complex (e.g. *M. s. spilota*: Slip & Shine 1988a; *Morelia spilota bredli*: Fyfe 1990). Deep rock crevices and caves provide dry, thermally stable microhabitats during cool weather, whereas the surrounding outcrops heat

quickly during sunny conditions and offer excellent basking opportunities (Prior & Weatherhead 1996). The north- and north-west-facing outcrops frequented in this study area provide enhanced basking opportunities, particularly late in the day, which might assist these snakes to maintain body temperatures above ambient at night. All Victorian populations of *M. s. metcalfei* are subjected to night-time temperatures below freezing in late winter and early spring, and might rely heavily on the combination of well-insulated shelter sites and frequent thermoregulatory opportunities to survive the cooler months.

In temperate environments, many snakes maintain relatively stable body temperatures during the summer months (Gibson & Falls 1979; Slip & Shine 1988b;

Pearson 2002) and disperse and hunt widely at this time (Webb & Shine 1997b, 1998; Fitzgerald *et al.* 2002). In coastal areas of central New South Wales, non-reproductive *M. s. spilota* move large distances from their overwintering sites to areas in which prey are

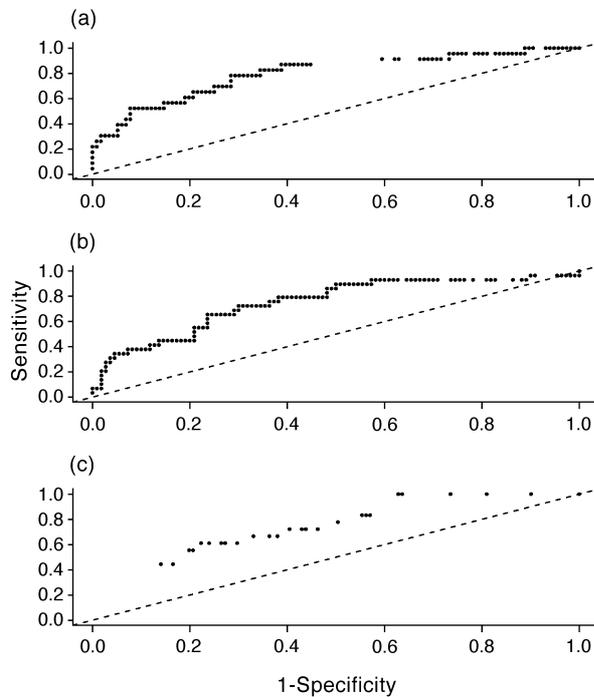


Fig. 6. Receiver-operating characteristic plots for each binary logistic regression model constructed to describe the seasonal relationships between python activity and habitat attributes within the Mount Meg study area in (a) spring, (b) summer and (c) autumn. The diagonal dashed line indicates the curve expected for a model with predictive capabilities no better than random (area under curve = 0.5).

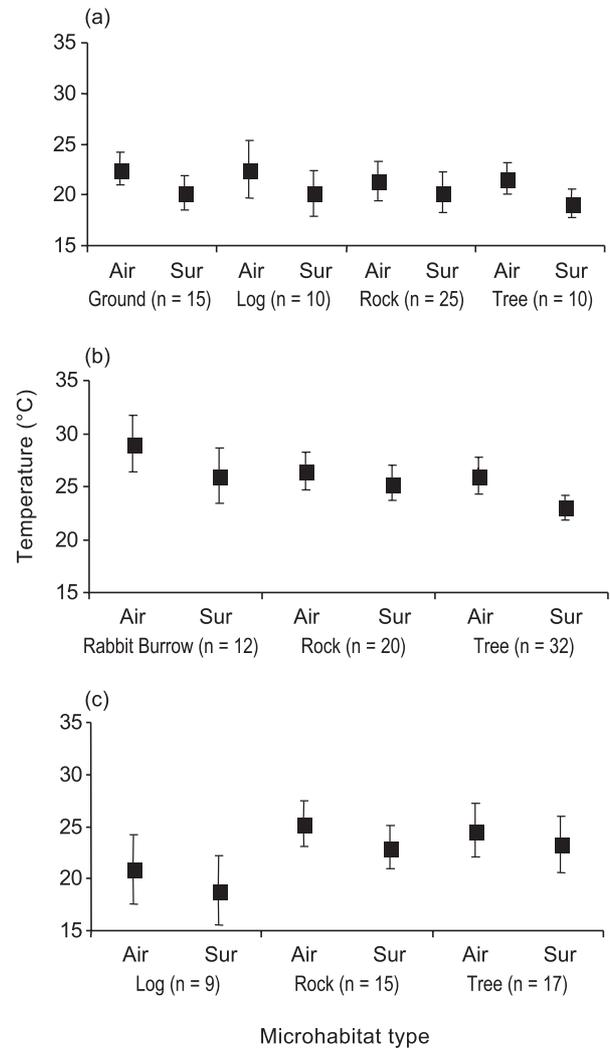


Fig. 7. Mean air (Air) and surface (Sur) temperatures recorded when carpet pythons used different microhabitats over the three seasons in which radiotelemetry was conducted: (a) spring; (b) summer; (c) autumn. Only microhabitats used on more than five occasions are displayed. Error bars = 95% confidence intervals.

Table 5. Seasonal variation in microhabitat use (percentage of radio-locations) displayed by carpet pythons monitored at the Mount Meg study area

Season	Sample size (<i>n</i>)	Building (%)	Ground (%)	Rabbit burrow (%)	Rock (%)	Log (%)	Tree (%)	Shrub (%)	Water (%)
Spring	69	5.8	20.3	0.0	37.7	17.4	17.4	0.0	1.4
Summer	80	8.8	0.0	15.0	26.3	2.5	41.3	1.3	5.0
Autumn	63	12.7	6.3	3.2	30.2	17.5	30.2	0.0	0.0
Total	212	9.1	8.9	6.0	31.4	12.5	29.6	0.4	2.1

more abundant, and they frequent microhabitats where they can ambush their mammalian quarry (e.g. light vegetation cover next to mammal runways; Slip & Shine 1988a). Our pythons also displayed movements of this kind. During the summer months, pythons dispersed across the study area, preferred macrohabitats with high rabbit abundance, consistently chose microhabitats in close proximity to rabbit burrows and entered burrows frequently (particularly in December and January). Concomitant with increased burrow use at times of high environmental temperatures, snakes were recorded to have fed (as evidenced by a large abdominal bolus) after entering rabbit burrows during summer (S. Reid, Parks Victoria, pers. comm.; G. Heard, P. Robertson, pers. obs.). In one case (on 20 February 2000), a recently suffocated rabbit was discovered lying at the entrance of a burrow inhabited by a telemetered python (G. Heard, P. Robertson, pers. obs.). Although ambush or 'sit and wait' strategies are primarily used to capture prey by carpet pythons elsewhere in Australia (Slip & Shine 1988c; Shine & Fitzgerald 1996), active searching can also be a productive adjunct to these activities (Fearn *et al.* 2001; G. Barrow, Parks Victoria, pers. comm.). It is probable that entering burrows in search of rabbits could be a commonly used foraging strategy of *M. s. metcalfei*.

Although the logistic regression analyses did not support a significant relationship between rabbit abundance and python movements in any season, snakes inhabited grid cells with a relatively high abundance of rabbits during the warmer months. At Mount Meg, rabbits are distributed patchily throughout the rocky slopes favoured by pythons, but are most abundant on the flat, more open land where extensive warrens are easily excavated. Assuming that the measures of rabbit abundance used here reflect their availability to the snakes, this pattern suggests that the coincidence of habitat structure and prey availability plays a greater role in habitat preference than prey availability alone. Pythons might maximize foraging success by moving into areas with greater prey abundance, but only into areas that also provide microhabitats necessary for both thermoregulation and shelter from predators. Farm buildings are an interesting example of this interaction. At Mount Meg, these structures occur in the cleared areas generally avoided by pythons. However, they provide numerous above-ground shelter sites (roof cavities etc.) and support an abundance of commensal prey species. As has been observed for *M. s. spilota* and *Morelia spilota mcdowelli* (Slip & Shine 1988a; Shine & Fitzgerald 1996; Fearn *et al.* 2001), one of our snakes made regular journeys to these buildings during the summer months, apparently taking advantage of both features. While residing in these structures, this snake primarily consumed introduced rodents (*Rattus rattus*, *Mus musculus*), but was also seen raiding the nest of a

Willie Wagtail (*Rhipidura leucophrys*; P. Robertson, unpubl. data; G. Walters, local landholder, pers. comm.).

Considering the restrictions low environmental temperatures place on thermoregulation and activity, it follows that pythons display a somewhat transitional pattern of habitat use during autumn. Pythons at Mount Meg continued to feed at this time, even when nightly air temperatures dropped below 5°C (G. Heard, pers. obs.). However, snakes generally moved away from the prey-rich habitats used during summer (specifically degraded woodland) and once again frequented areas where warm, insulated microhabitats were most abundant (e.g. the north face of Mount Meg). By doing so, snakes may reduce their opportunities to capture prey, but will maximize their chances of maintaining appropriately high body temperatures for digestion and other metabolic processes (Reinert 1993).

Seasonal variation in habitat use by this population of carpet pythons is, in many aspects, analogous to that shown by other temperate Australian snakes. Fundamental patterns appear to be mediated by thermal constraints, which tightly control the timing of annual movement and feeding patterns. In contrast, Australian pythons inhabiting climatically benign environments (e.g. subtropical regions) can show little seasonality in thermoregulatory behaviour, movement patterns and feeding rates (Shine & Fitzgerald 1996; Fearn *et al.* 2001). In the wet-dry tropics, some species are more strongly influenced by other environmental stimuli such as rainfall (Madsen & Shine 1996, 2002; Shine & Madsen 1996). In all environments, however, habitat selection by individual snakes can vary greatly depending on reproductive status (Reinert 1993). Throughout the telemetry study described here, the only reproductive activity noted was an isolated mate-pairing record involving a telemetered male. As such, we cannot assess the extent to which reproductive activities might have affected the results presented here.

This study has significant implications for python habitat management in northern Victoria. The data presented here highlight (i) the need to maintain large remnant woodland patches as core habitat for these snakes and to promote mosaics of dense, highly connected remnant vegetation to facilitate seasonal movement patterns; (ii) the need to maintain the structural integrity of these woodland habitats (particularly by excluding grazing, timber extraction and firewood collection, which are extensively practised in northern Victoria) to insure the availability of microhabitats such as rock outcrops, standing and fallen hollow timber, and complex shrub and ground-layer vegetation; and (iii) the need to modify rabbit control techniques to allow low-moderate rabbit populations to persist in significant python habitat, and to avoid warren ripping or fumigation during the summer

months when snakes are most likely to inhabit rabbit burrows.

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