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Biological Conservation 86 (1998) 233–242

BIOLOGICAL
CONSERVATION

Using thermal ecology to predict retreat-site selection by an endangered snake species

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Received 14 August 1997; received in revised form 9 October 1997; accepted 13 October 1997

Abstract

Many ectotherms spend long periods in retreat-sites, where thermal conditions may strongly influence key physiological or behavioural processes (e.g. locomotion, digestion, growth rates etc). Species that rely upon specific thermal regimes may be restricted to particular types of retreat-sites, and hence vulnerable to anthropogenic habitat disturbance. We investigated the role of thermal factors in retreat-site selection by an endangered snake species: the broad-headed snake, *Hoplocephalus bungaroides*. Broad-headed snakes are restricted to sandstone rock outcrops where exfoliated boulders of different sizes and thicknesses provide a suite of retreat-sites with unique thermal characteristics. Body temperatures of snakes sheltering under rocks are determined by the degree of shading and the thickness of the rock. In the laboratory, broad-headed snakes select temperatures around 30°C, and strike speed is maximised at this temperature. From these data, we predicted seasonal patterns of habitat use by the snakes, by assuming that snakes would select retreat-sites with temperatures within their 'preferred' body temperature range. Radiotelemetric monitoring of 25 adult snakes (total of 33 snake-seasons of data) and mark-recapture data from 96 tagged snakes (including 56 juveniles) supported our predictions. During spring, snakes actively selected thin (≤ 15 cm thick) unshaded rocks. These 'hot' rocks allowed snakes to attain body temperatures within their set-point range for long periods of time. The snakes rarely moved between rocks, and a small number of rocks received frequent use by snakes of all sizes. Telemetered snakes also used cliff-top crevices exposed to the afternoon sun (i.e. with north or westerly aspects) and avoided cooler crevices (those with easterly and southerly aspects). During summer, snakes avoided thin exposed rocks which became too hot for them to tolerate (often, $> 40^\circ\text{C}$). Although some snakes moved to thicker and more shaded rocks, most snakes abandoned the rock outcrops and moved into adjacent woodland. The seasonal timing of this habitat shift varied among years, but coincided with the onset of hot weather. Thus, simple measurements of the thermal characteristics of snake retreat-sites allowed us to successfully predict major patterns of habitat use, and provide a basis from which to plan the protection and/or restoration of critical habitat components for this endangered species. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Conservation; Habitat use; Reptile; Seasonal shifts; Thermoregulation

1. Introduction

Habitat destruction appears to be the primary cause of endangerment for more than two thirds of animal taxa classed as 'endangered' in the USA (Losos et al., 1995). Animals use habitats in complex ways, however, and the reasons why particular habitat features are essential for particular taxa remain unclear for most cases (e.g. Simberloff, 1987; Caughley and Gunn, 1995). The role of abiotic variables in this respect may be unusually clearcut for animals that spend a high

proportion of their time inactive within retreat-sites. The virtue of such a study system, in pragmatic terms, is that it is far easier to characterise physical conditions within a retreat-site than to describe the entire environment experienced by a mobile animal.

The thermal regimes experienced by animals in retreat-sites are likely to differ from those experienced by surface-active animals (Andrewartha, 1961; Huey, 1982; Huey et al., 1989), and may have profound effects on the body temperatures of ectotherms and the energy budgets of some endotherms (e.g. birds: Walsberg, 1985). Selection of thermally suitable retreat-sites may be particularly important for ectotherms because their behavioural and physiological processes are temperature-dependent (Stevenson et al., 1985). The availability of

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thermally suitable retreat-sites may therefore determine patterns of habitat use by many ectotherms (Huey, 1991).

For many threatened taxa, an understanding of the thermal characteristics of retreat-sites may be useful for predicting temporal and spatial patterns of habitat use, and ultimately, for formulating appropriate management plans (e.g. butterflies: Warren and Thomas, 1992; Thomas, 1994). In the present paper, we analyse retreat-site selection by adults and juveniles of a saxicolous snake species (the broad-headed snake, *Hoplocephalus bungaroides*) that is threatened by anthropogenic habitat modifications. This small nocturnal elapid species is found under rocks in sunny localities within sandstone habitats in south-eastern New South Wales (Krefft, 1869; Swan, 1990). Its geographic range has declined considerably since the European invasion of Australia, apparently because of the removal of sandstone rocks for Sydney gardens (Krefft, 1869; Hersey, 1980; Shine and Fitzgerald, 1989). The restriction of the species to sandstone habitats, and its use of exposed exfoliated rocks as retreat-sites, suggests that thermal properties of the rocks may play an important role in habitat selection by the snakes. If major patterns of habitat use by this species are determined by thermal regimes in natural retreat-sites, we may be able to predict the species' response to habitat alteration, and hence devise more effective conservation measures.

2. Materials and methods

2.1. Role of thermal factors in habitat selection

To study the role of thermal factors in habitat selection we need to know: (1) how key behavioural or physiological processes are influenced by body temperature; and (2) how the organism perceives the 'thermal quality' of a habitat (Huey, 1991). In practice, this approach involves measuring the thermal dependence of ecologically relevant whole animal traits in the laboratory, and mapping the thermal environment from the study organism's perspective in the field (Huey, 1991). By integrating (1) and (2), we can then predict how well an organism will perform in a particular microsite, or alternatively, which microsites an ectotherm should select (or avoid) in order to maximise its fitness (Porter and James, 1979; Christian et al., 1984; Kingsolver, 1989; Huey, 1991).

2.2. Thermal dependence of physiology and behaviour

For many ectotherms the thermal dependence of key physiological and behavioural processes (e.g. development, locomotion, prey capture ability, digestion) is well documented (e.g. Huey, 1982; Ratté, 1985). For many reptiles physiological processes are optimised within the

animals' 'preferred body temperature' range, so that measurements of a species' set-point range ('preferred body temperature') and voluntary thermal maximum ($V_{T_{max}}$) in a cost-free environment (laboratory thermal gradient) provide a starting point from which the thermal quality of a habitat can be elucidated (Hertz et al., 1993; Christian and Weavers, 1996).

In the present study we use data on broad-headed snake set-point temperatures (28.1–31.1°C), $V_{T_{max}}$ (35.2°C) and strike speed (maximal at 30°C) from laboratory experiments (Webb, 1996). Strike speed is a useful measure of snake performance because broad-headed snakes ambush geckos from under rocks, where strikes are initiated from a standstill. Hence, prey capture is dependent on strike speed rather than crawling speed (Webb, 1996).

2.3. Mapping the thermal environment

In order to characterise an animal's thermal environment we need to know the range of potential equilibrium body temperatures that an animal would attain in a particular microhabitat at a particular time. Such 'operative environmental temperatures' (T_e s: Bakken and Gates, 1975) can be measured using suitable physical models of the animal (Bakken, 1992) or by complex mathematical heat transfer models (Porter et al., 1973; Tracy, 1982). For surface-active ectotherms numerous physical models are needed to accurately determine the range of T_e s available to the animal, but for inactive ectotherms sequestered in retreat-sites, well placed thermocouples provide accurate estimates of T_e s (Huey et al., 1989; Peterson et al., 1993).

We measured T_e s inside retreat-sites by placing thermocouples under eight sandstone rocks of different sizes (range 20–63 cm in diameter) and thicknesses (range 2–16 cm thick) on a single exposed rock outcrop. To assess the effects of shading on rock temperatures we artificially shaded four rocks (range 21–34 cm in diameter, 4–10 cm thick) using square frames (90 cm wide × 50 cm high) covered with two layers of 75%, beige shade cloth. We glued thermocouples onto the underside (middle) of each rock (T_r), and the substratum directly below (T_s). Temperatures were recorded every 30 min with a Campbell CR10 Data Logger (Campbell Scientific, Utah, USA). To estimate the availability of rocks with different thermal properties, we measured the length, width, maximum thickness, substratum (rock or soil) and distance to the cliff-edge, and estimated the proportion of canopy cover (= shading), of the first five rocks encountered along four transects (each 5 m long, 1 m wide) extending east, west, north, and south, from rocks selected by broad-headed snakes. T_e s inside crevices and in full sun and full shade were measured using physical models connected to miniature data loggers (see Webb, 1996).

2.4. Study sites, radio-telemetry

Study sites were located in Morton National Park, 160 km south of Sydney. We radio-tracked snakes at three sites (each approximately 3 km apart) on the western side of a sandstone plateau of 400 m elevation. Detailed descriptions of the study area, transmitters and surgical techniques are provided elsewhere (Webb and Shine, 1997a). Thirty-three broad-headed snakes were tracked over 3 yr from September 1992 to February 1995. We tracked 11 snakes each year, usually from spring until late summer when the transmitters stopped. Full details on snake body sizes, sexes, commencement of radio-tracking, and our general field procedures are presented elsewhere (see Webb and Shine, 1997a,b). Snake body temperatures were measured in the field by recording the period between radio pulses with a stopwatch, and with an automated system (see Rummery et al., 1995 for details).

2.5. Mark–recapture study

Habitat use by juvenile snakes (too small for transmitter implantation) and their main prey (velvet geckos, *Oedura lesueurii*) was documented by looking under all the rocks at our study sites at least twice per month. Small (12 mm × 2 mm) passive integrated transponder (PIT) tags were injected under the skin of all snakes to allow subsequent identification. These PIT tags do not appear to affect growth rates or locomotor performance of neonatal snakes (Keck, 1994). One advantage of using PIT tags (as opposed to other marking techniques) was that rocks could be scanned with a hand-held microchip reader to identify the snake, without overturning the rock, thereby minimising disturbance to the snakes. All rocks used by reptiles were measured, and were given a unique number to assess whether they were used by more than one snake or gecko. All geckos were given a unique toe-clip.

3. Results

3.1. Thermal characteristics of snake retreat-sites

3.1.1. Rocks

A full description of thermal profiles in retreat-sites is provided elsewhere (Webb, 1996), but key results are summarised here. Thermal regimes under rocks were determined primarily by rock thickness and the degree of shading. Thick rocks heated more slowly than thin rocks, and shaded rocks were cooler than similarly-sized unshaded rocks (Fig. 1). During spring, exposed thin (≤ 15 cm thick) rocks provided thermal regimes that allowed snakes to attain body temperatures within their set-point range, whereas thicker rocks did not (Fig. 1a).

During summer, temperatures under exposed thin rocks exceeded the voluntary thermal maximum of snakes (35.2°C) during sunny weather, whereas, T_e s under large boulders were favourable for snakes, as were temperatures under shaded rocks (Fig. 1b). The proportion of days during which rocks were too hot for snakes depended on rock thickness as well as weather (Fig. 2). For example, very thin rocks (2 cm thick) were too hot for snakes to use on over 70% of days during January, whereas thicker rocks (16 cm thick) were too hot on only 3% of days. Weather conditions were also important, because rocks were significantly cooler (and thus, could safely be used by snakes) during overcast periods, even in mid summer.

3.1.2. Crevices

During spring, crevices with easterly and southerly aspects remained in shade throughout the day, whereas crevices with westerly aspects were in full sun for most

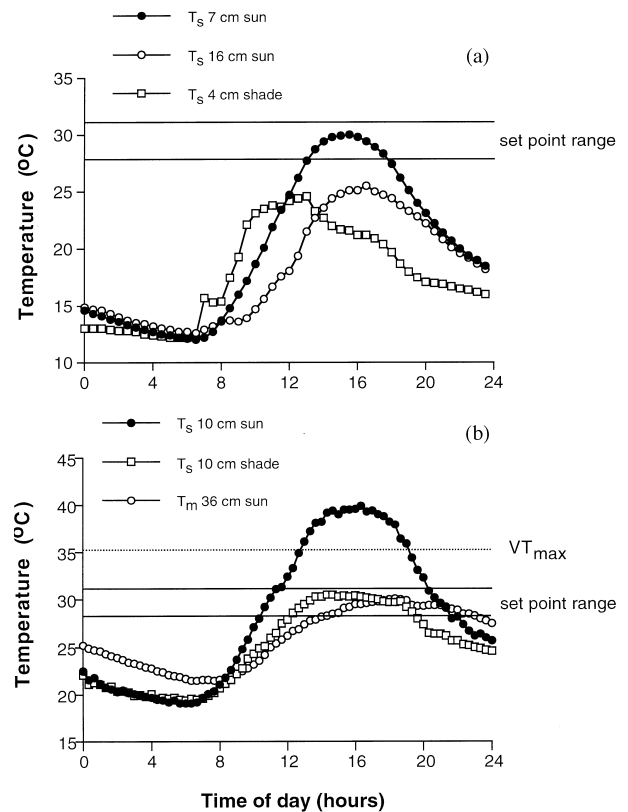


Fig. 1. Daily cycle of substratum temperatures (T_s) under rocks on sunny days during spring (a) and summer (b). Shown are T_s under: (a) exposed thin (7 cm thick) and thick (16 cm thick) rocks, and a shaded thin rock (4 cm thick) during spring (24 October 1994); and (b) thin rocks (10 cm thick) in sun and full shade, and a snake model (T_m) placed under the centre of a large exposed boulder (36 cm thick) in summer (12 January 1995). Solid horizontal lines indicate the snakes' preferred temperature range (set-point range), and the dotted horizontal line is the snakes' voluntary thermal maximum (VT_{max}) based on laboratory studies (Webb, 1996). Measurements were taken at 30 min (a) and 20 min (b) intervals.

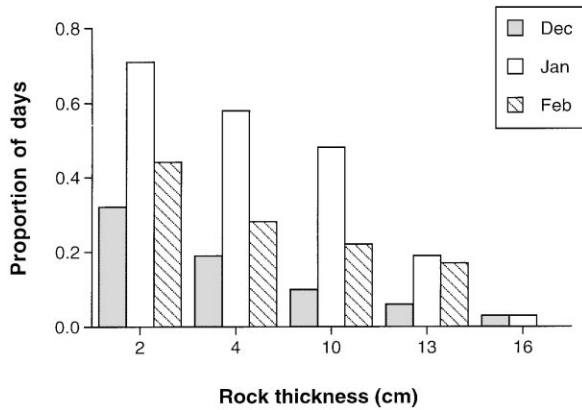


Fig. 2. Proportion of summer days that substratum temperatures ($T_{s,s}$) under exposed rocks of varying thicknesses (2, 4, 10, 13 and 16 cm thick) exceeded the voluntary thermal maximum ($VT_{max} = 35.2^{\circ}\text{C}$) of telemetered broad-headed snakes. Temperatures under rocks were recorded every 30 min at a single exposed cliff-edge site during 1993–1994. A total of 80 days of temperature data was collected during summer (31 days during December and January, 18 days during February).

of the afternoon (see Webb, 1996). During sunny weather in summer, $T_{e,s}$ deep inside exposed cliff-top crevices with westerly aspects remained within the snakes' set point range for long periods of time. In contrast, $T_{e,s}$ deep within crevices with easterly and southerly aspects were much cooler, and rarely exceeded 25°C (Webb, 1996).

3.2. Behaviour and body temperatures of snakes in retreat-sites

During spring, most telemetered broad-headed snakes were found under rocks or inside crevices (and occasionally, inside fallen logs), where they spent long periods of time inactive both by day and night (mean time inactive: rocks = 7.5 days, $SD = 7.4$, range 1–30, $n = 19$; crevices = 9.0 days, $SD = 9.0$, range 1–41, $n = 25$). There were no significant differences in the time spent inactive

in retreat-sites (crevices vs rocks) during the three years of the study (two factor ANOVA: retreat sites $F_{1,37} = 0.23$, $p = 0.63$; years $F_{2,37} = 0.80$, $p = 0.46$; non-significant interaction term $F_{2,37} = 0.23$, $p = 0.80$). Rock use by the snakes was highly non-random: snakes avoided rocks on soil, even though these rocks were abundant on the study sites (Table 1). The snakes' preference for rocks with rock substrata meant that they could not burrow, and hence, their body temperatures were highly correlated with substratum temperatures under rocks ($r^2 = 0.96$, 1, 990 df, $p < 0.0001$, $n = 5$ snakes). Thus, the snakes had little opportunity for behavioural modification of body temperatures unless they were prepared to bask outside their rocks, but such behaviour was rarely observed (Webb, 1996).

3.3. Predicted patterns of retreat-site selection

The strong dependence of snake $T_{b,s}$ on rock $T_{s,s}$, coupled with the snakes' sedentary, cryptic behaviour, allows us to accurately predict the $T_{b,s}$ of snakes under different types of rocks at different times of the year. Thus, we can predict patterns of retreat-site selection by broad-headed snakes using our thermal data. Two assumptions are needed: (i) snakes should select retreat-sites with temperatures within the preferred T_b range (28.1 – 31.1°C); (ii) snakes should avoid sites where temperatures exceed the voluntary thermal maximum ($VT_{max} = 35.2^{\circ}\text{C}$, Webb, 1996). Thus, during spring we predict that snakes should select: (i) crevices with westerly or northerly aspects, because these are warmer than are southerly or easterly crevices (see earlier); (ii) thin (≤ 15 cm thick), unshaded rocks, because thicker rocks and rocks shaded by vegetation do not warm to the snakes' preferred T_b range.

During summer, temperatures under exposed thin rocks are too hot for snakes to tolerate (see earlier), and we predict that: (i) snakes should avoid thin unshaded rocks and select thicker or more shaded rocks; and (ii) the timing of movements away from exposed thin rocks

Table 1

Numbers of rocks available to and used by *H. bungaroides* on study sites. Rocks were classified as five 'rock types' based on physical and thermal attributes: rock substratum (soil vs rock); thickness, thin (≤ 15 cm thick) vs thick (> 15 cm thick); and degree of shading, exposed ($\leq 30\%$ canopy cover) vs shaded ($> 30\%$ canopy cover). To assess whether snakes were selecting or avoiding particular habitat (rock) types, we used the methods of Neu et al. (1974) to construct 95% confidence intervals around the proportions of each habitat type used by snakes. If p_a fell within the confidence intervals of p_u then the null hypothesis of no habitat selection was accepted

Rock type	No. rocks available	No. rocks used by snakes	Expected number	Proportion of rocks available (p_a)	Proportion of rocks used by snakes (p_u), with 95% confidence intervals	Selective use of rocks?
Soil substratum	872	3	58.6	0.437	$0.009 \leq 0.022 \leq 0.035$	avoidance
<i>Rock substratum</i>						
Thin, exposed	632	111	42.4	0.317	$0.744 \leq 0.828 \leq 0.912$	selection
Thin, shaded	139	5	9.3	0.070	$0.021 \leq 0.037 \leq 0.053$	avoidance
Thick, exposed	305	15	20.5	0.153	$0.085 \leq 0.112 \leq 0.139$	avoidance
Thick, shaded	47	0	3.2	0.023	0	avoidance
Totals	1995	134				

should coincide with the seasonal onset of high (>35°C) temperatures under exposed thin rocks.

Later, we review patterns of retreat-site selection by broad-headed snakes during spring and summer, and evaluate whether our predictions are supported by our radio-telemetric and mark-recapture data.

3.4. Observed patterns of retreat-site selection

3.4.1. Rocks

Our 33 radio-tracked snakes used a total of only 45 different rocks during spring. The mean number of rocks used by each telemetered snake in a single year was 2.03 (SD=1.13, range 1–5), and this number did not differ significantly among years (one-factor ANOVA, $F_{2,30}=2.33$, $p>0.05$). Pooling all rocks used by all broad-headed snakes during the 3 yr of the study, a total of 134 rocks were used by 115 individual broad-headed snakes during late winter and spring. Multiple use of the same rock by different snakes (at different times) was common, and some ‘snake’ rocks were used by up to nine different snakes (mean number of snakes using each rock = 1.45, SD = 1.10, range 1–9).

Did broad-headed snakes select thin exposed rocks, as predicted? Under the null hypothesis of no habitat selection, analysis of availability vs use of the five major categories of rocks revealed that snakes did not select rocks according to their availability (Chi-square goodness of fit test, $\chi^2=170.4$, 4 df, $p<0.0001$, see Table 1). Instead, snakes selected thin exposed rocks with rock substrata, but avoided rocks on soil, or rocks with rock substrata which were thick or shaded by vegetation (Table 1, 95% confidence intervals; see Neu et al., 1974). The snakes’ preference for exposed rocks with rock substrata meant that most rocks used by snakes were close to cliffs (mean distance = 5.0 m, range 0–21 m). Did snake body size influence the choice of rocks? We compared key characters of rocks (thickness, canopy cover, diameter) used by three size-classes of snakes (juveniles, SVL < 35 cm; subadults, $35 \leq \text{SVL} \leq 45$ cm; adults, SVL > 45 cm). Regardless of body size, broad-headed snakes used thin rocks (mean thickness = 8.6 cm) with little or no canopy cover (mean canopy cover = 4.5%; one factor ANOVAs, 1, 120 df, $p>0.05$ in both cases). However, rocks used by juvenile snakes were significantly smaller than those used by adults (mean diameters of 45.9 vs 53.4 cm, one-factor ANOVA on rock diameter, $F_{2,120}=6.23$, $p=0.003$).

Fewer snakes were found under thin rocks during summer than in spring (Fig. 3). Indeed, no snakes were found under exposed thin rocks during the summers of 1993–1994 and 1994–1995. Telemetry studies confirm this pattern. In summer, most telemetered broad-headed snakes moved long distances away from exposed cliffs (up to 780 m, Webb and Shine, 1997b) where they sheltered inside the hollow branches of large trees. Snakes

spent long periods of time sequestered inside tree-hollows (mean = 7 days, range 1–48 days; Webb and Shine, 1997a), and were rarely observed during summer.

The timing of the movements away from exposed rocks occurred during the hottest months of the year, as predicted. The timing varied from year to year and was clearly influenced by the weather (Fig. 4). For example, during the first field season (1992–1993) it was atypically wet and cool during November and early December, and most snakes did not move into the forest until the onset of hot weather during January 1994. During the second field season (1993–1994) most telemetered snakes began moving away from the cliffs in late November (Fig. 4), when temperatures under rocks started to approach the VT_{\max} of the snakes. During the final year (1994–1995) most snakes did not move away from cliffs until December (Fig. 4).

In the few cases where telemetered broad-headed snakes used rocks during hot weather, the rocks were in relatively shaded positions in the forest. As predicted, rocks used by telemetered snakes during summer were significantly thicker than those used during spring (means of 20.0 vs 9.7 cm thick; one-factor ANOVA, $F_{1,57}=11.14$, $p<0.01$) and had significantly more vegetative cover (33.9 vs 8.1% canopy cover, one-factor

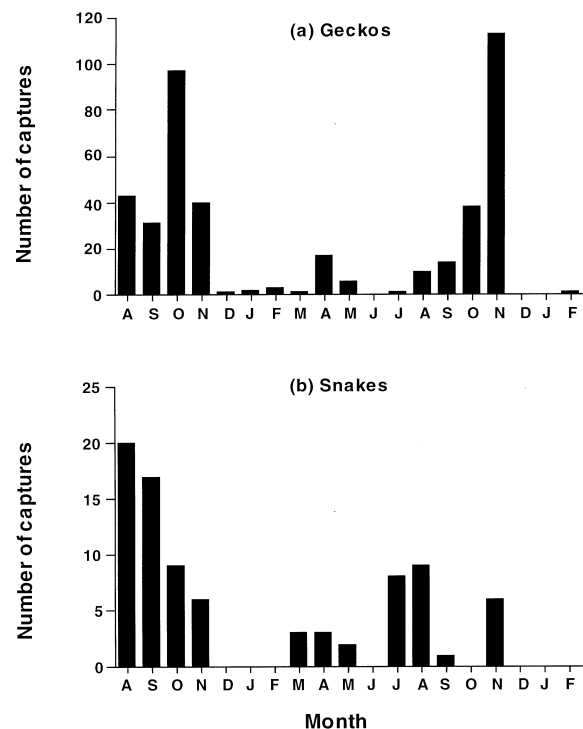


Fig. 3. Capture rates of (a) velvet geckos and (b) broad-headed snakes under exposed thin (≤ 15 cm thick) rocks on the cliff-edge from August 1993 to February 1995. A total of 228 numbered rocks (including 128 ‘snake’ rocks) from four field sites were checked twice each month for the presence of geckos and snakes, except during June 1994 when we did not visit the sites. No snakes were found under these rocks during summer (December to February).

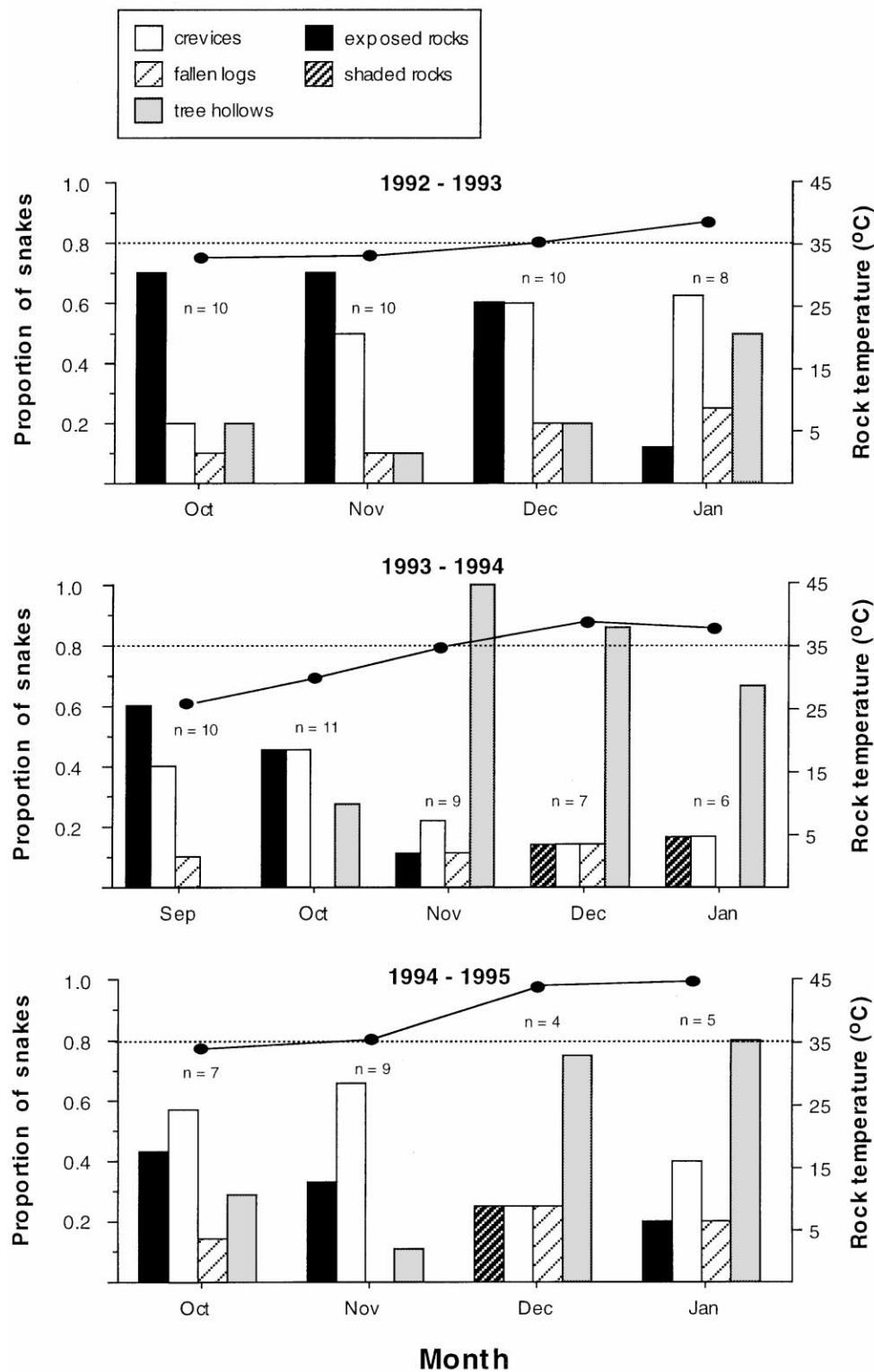


Fig. 4. Retreat-sites selected by telemetered broad-headed snakes during each month during the three years of the study. The most commonly used retreat-sites were rocks, crevices and tree hollows. Snakes occasionally used logs on the ground. Proportions of snakes using each type of retreat-site are indicated by histograms. Note that because most telemetered snakes used more than one type of retreat-site each month, proportions of snakes using the four types of retreat-sites do not sum to 1.0. Mean monthly substratum temperatures (T_{s}) under thin rocks (10 cm thick) are shown by circles connected by a solid line. Note that rocks used by snakes in summer were usually located in shaded locations in the forest, well away from exposed sandstone cliffs (see text for statistical analyses).

ANOVA, $F_{1,57} = 12.73$, $p < 0.001$). Three snakes were observed sheltering in caves under rocks, where temperatures may be much cooler (Huey et al., 1989). Although snakes rarely used exposed rocks on the cliff-edge during summer, three snakes used rocks on the cliff-edge for brief periods (2 days) in mid-December 1992 following a long period of cool wet weather. One snake used large boulders (with dimensions > 100 cm, thicknesses > 40 cm) on an isolated rock outcrop 15 m below the cliffs in late January and early February 1993. In the final year one snake used an exposed thin rock on the cliff-edge on a cool January morning; however, this rock was lying directly over a vertical crevice, so the snake could easily avoid lethally high temperatures by retreating into the crevice.

3.4.2. Crevices

In spring, telemetered snakes used horizontal crevices with westerly (27 observations) or north-westerly aspects (15 observations), but avoided crevices with easterly aspects. Although our study sites were located on the western side of a plateau, crevices with easterly aspects were abundant because the cliff-edge was deeply dissected by numerous chasms (up to 5 m wide and 100 m long) that ran in a northerly direction. Many crevices were also available under huge cliff-top boulders, so that snakes had access to a wide variety of crevice types.

Some snakes continued to use crevices year round (Fig. 4), and although snakes could theoretically spend very long periods of time in their preferred temperature range by selecting cliff-top crevices, few snakes did so (Webb, 1996). Telemetered snakes avoided hot cliff-top crevices during summer, but use of crevices with southerly or easterly aspects was rare (3 of 16 observations). Instead, most snakes selected crevices further below the cliff tops (and hence, were partly shaded by vegetation): crevices selected by snakes in summer were an average of 6.4 m below cliffs (SD = 4.5, $n = 20$ observations) compared to 1.8 m (SD = 1.5, $n = 42$ observations) during spring (one-factor ANOVA, $F_{1,60} = 34.3$, $p < 0.0001$).

4. Discussion

Why do broad-headed snakes tend to select retreat-sites that allow them to attain body temperatures close to 30°C? Several answers to this question are possible, including:

1. *Phylogenetic inertia*—mean selected body temperatures of a wide range of snake species, including several Australian elapids, are close to 30°C (Avery, 1982; Lillywhite, 1987). Thus, the thermoregulatory preferenda of *H. bungaroides* may simply represent retention of an ancestral trait, with

no adaptive significance in its current habitat. The massive consequences of this preference for habitat selection, however, cast doubt on this explanation.

2. *Maximisation of ability to capture and digest prey*—snakes that are warmer can strike faster, and thus should be more capable of catching the agile lizards that are their main prey (Webb, 1996). Conceivably, the high temperatures under the rocks chosen by broad-headed snakes may also optimise their ability to digest prey (e.g. Lillywhite, 1987). Thermophilic responses to feeding are widespread among snakes (Peterson et al., 1993) and may influence patterns of retreat-site selection by snakes in the field (Reinert, 1993).
3. *Maximisation of ability to encounter prey*—if a sit-and-wait predator is to maximise its probability of encountering potential prey, it must wait in ambush in the habitats used by the prey. If the prey uses thermal cues for habitat selection, the simplest ‘rule’ a predator could use to maximise its probability of encountering prey would be to use the same cues used by the prey. Velvet geckos (*Oedura lesueurii*), the major prey species for broad-headed snakes (Webb, 1996), select shelter-sites based on a complex set of structural cues, including temperature (Schlesinger and Shine, 1994a). In practice, our data show that these ‘rules’ result in velvet geckos in our study area exploiting thin rocks in full sun, at least during spring (see Fig. 3). Indeed, many of the rocks used by broad-headed snakes were also used by geckos. Of 128 ‘snake’ rocks that we regularly checked, 49 (38%) were also used by velvet geckos. During spring, the geckos were highly selective in their choice of retreat-sites: they selected thin rocks with rock substrata, but avoided rocks on soil, and thick or shaded rocks with rock substrata (248 of 268 rocks used by 373 individual geckos were ≤ 15 cm thick, exposed, and had rock substrata). Thus, the end result of thermally-mediated habitat selection by the snakes may have been to maximise their chances of encountering potential prey items.

4.1. Implications for conservation

Our results have significant implications for future conservation strategies aimed at protecting the habitat of broad-headed snakes, or recolonising areas previously inhabited by this species. Later we use our data to evaluate two hypotheses that were put forward to explain the disappearance of *H. bungaroides* from much of its former range:

4.1.1. Bush rock collection

Several authors have suggested that removal of exfoliated rocks from sandstone rock outcrops is one of the

major causes of the broad-headed snake's decline in distribution and abundance (Kreffit, 1869; Hersey, 1980; Shine and Fitzgerald, 1989). Our study supports this hypothesis, and identifies two unique features of habitat selection by broad-headed snakes that makes them especially vulnerable to bush-rock removal: their frequent dependence on a small number of thermally distinctive rocks for shelter-sites; and the use of the same sorts of rocks by velvet geckos, the major prey of these snakes. Are rocks stolen by rock thieves similar in size to the hot rocks favoured by *H. bungaroides*? Elsewhere we and our colleagues have shown that rock thieves select hot rocks (Schlesinger and Shine, 1994b; Webb, 1996; Shine et al., in press), because thicker 'cooler' boulders are too heavy for humans to lift, and very thin rocks break easily during transportation.

What are the consequences of the removal of hot rocks for *H. bungaroides*? Rock removal could negatively affect broad-headed snakes in several ways. Firstly, the snakes might be forced to bask more frequently (in order to digest prey etc.), thereby increasing their vulnerability to avian predation (Christian and Tracy, 1981; Webb, 1996). Alternatively, the use of suboptimal (i.e. cooler) retreat-sites by snakes could lead to lower growth rates in juveniles or decreased fecundity in adult females (Adolph and Porter, 1993). Lastly, a reduction in the availability of hot rocks could lead to a reduction in prey density, thereby reducing the carrying capacity of snakes on rock outcrops.

Given the current political stance on bush-rock collection in New South Wales (the activity is still legal, and rocks are regularly stolen from National Parks where *H. bungaroides* is present: Webb, 1996), it is clear that any program designed to ensure continued habitat preservation will have to consider the replacement of rocks that were removed. If thermal characteristics are indeed the prime determinant of rock suitability, it should be feasible to 'restock' disturbed outcrops with artificial 'rocks' (e.g. concrete pavers or concrete rocks poured in situ) with the appropriate thermal characteristics. The general similarity in rock characteristics (size, thickness) used by broad-headed snakes of different body sizes (and their prey) simplifies such an undertaking.

4.1.2. Overgrowth of rock outcrops by vegetation

In Australia, changes to endemic fauna and to fire regimes have substantially altered the vegetation cover over the continent since human occupation, especially over the last 200 yr (Kohen, 1996). When Europeans first settled in the Sydney region, the vegetation was considerably more open in many areas than it is today (trees were widely spaced and there was little understorey), chiefly because the local aboriginal population regularly burnt the forest (Kohen, 1996). Hence, the decline of *H. bungaroides* across much of its former

geographic range might be due, at least partially, to the overgrowth of rock outcrops by vegetation. Such overgrowth would transform formerly 'hot' rocks into cooler rocks that are less suitable for broad-headed snakes. In the same way, overgrowth of winter rattlesnake (*Crotalus horridus*) dens by vegetation may have contributed to the species' decline, and lopping of overhanging vegetation was suggested as one management option (Brown, 1993). In Europe, successful conservation of an endangered butterfly was brought about by carefully planned tree-lopping in coppice woodlands (Warren and Thomas, 1992). Thus, to conserve *H. bungaroides*, reserve managers must prevent the overgrowth of rock outcrops by vegetation. Pilot studies to investigate the cost-effectiveness (and ecological effects) of controlled burns versus tree-lopping would be extremely useful.

In conclusion, our study suggests that simple biophysical modelling of habitat use by ectotherms may provide insights into the ways in which these organisms use available spatial resources. Seasonal shifts in habitat use are a consistent feature of the ecology of many snake species (Reinert, 1993) as well as other types of reptiles (Paulissen, 1988), but the causal factors generating such shifts usually remain elusive (but see Christian et al., 1983). Undoubtedly, seasonal shifts in prey availability play a major role in many such migrations (King and Duvall, 1990; Madsen and Shine, 1996), but our work suggests that the role of the physical (especially, thermal) environment should not be overlooked in this respect. For animals that spend much of their time inactive within thermally distinctive retreat-sites, it may be possible to predict patterns of habitat use through space and time from a relatively simple study such as our own. Such predictive power may be of considerable value for the future management and conservation of these kinds of animals.

Acknowledgements

The authors thank the following volunteers for their assistance in the field: P. Doughty, R. Drury, M. Gardener, P. German, P. Harlow, J. Hines, S. Keel, J.S. Keogh, T. Madsen, M. McCloskey, M. Olsson, K. Russell, S. Smith, A. Stow, L. Tasker, M. Thompson, G. Torr, R. Van Damme, J. Walker, G. White and M. Ypma. We thank M. Pincombe for allowing us to use his field hut, and K. Christian and two anonymous reviewers for their thoughtful comments on the manuscript. J. Webb is particularly indebted to M. Runcie for her help in the field and continued support throughout the project. J. Webb thanks the Nowra National Parks and Wildlife Service staff for charging batteries and rescuing Professor Shine's 4WD from a flooded creek crossing. This study was supported by grants to R.S.

from the Australian Nature Conservation Agency and the Australian Research Council, and an Australian Museum Postgraduate Award and Ethel Mary Read Award to J.K.W. The research was approved by the NSW National Parks and Wildlife Service (Licences B995, B996 to J.K.W.) and the University of Sydney Animal Care and Ethics Board. The work formed part of the senior author's Ph.D. research at the University of Sydney.

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