

CANOPY STRUCTURE, MICROCLIMATE, AND HABITAT SELECTION BY A NOCTURNAL SNAKE, *HOPLOCEPHALUS BUNGAROIDES*

ROBERT M. PRINGLE,¹ JONATHAN K. WEBB, AND RICHARD SHINE²

School of Biological Sciences, Building A08, University of Sydney, New South Wales 2006, Australia

Abstract. Forest structure strongly influences ambient environmental conditions such as light and temperature, but most studies on habitat selection by mobile organisms have either ignored canopy structure or treated it as a dichotomous variable (e.g., “shady” or “sunny”). Furthermore, the predominance of active diurnal species as model organisms in such studies has left many unanswered questions about the importance of vegetation-related variables for nocturnal and sedentary species (e.g., what does “shade” mean to an organism that moves at night and sits in a cave all day?). We used hemispherical photography to quantify canopy structure and examine its role in determining the thermal microenvironments available to a rock-dwelling nocturnal snake (*Hoplocephalus bungaroides*) across two different spatial scales. The narrow plateaus inhabited by the snakes in southeastern Australia are highly heterogeneous with respect to vegetation: east-facing aspects are densely covered whereas west-facing aspects are patchy mosaics. We found that temperatures of potential retreat sites increased with increasing canopy openness, but the definitive determinant of retreat-site temperature was incident radiation intensity, which depended upon the location of canopy gaps relative to the sun path. This factor restricted the snakes to west-facing cliff tops, and there only to an optimal subset of rocks that received adequate irradiance. Moreover, thermal regimes of retreat sites displayed higher maxima and were evening shifted relative to randomly sampled rocks in the same area. Our results suggest that thermally suitable retreat sites are a limiting resource, and that local increases in vegetation density might contribute to the decline of this endangered species.

Key words: conservation management; ectotherm; endangered species; fire regime; *Hoplocephalus bungaroides*; hemispherical photography; historical vegetation change; New South Wales, Australia; patch heterogeneity; retreat site; thermoregulation.

INTRODUCTION

Vegetation density is a dynamic habitat characteristic, and changes in this variable will prompt changes in other habitat attributes such as light intensity, air and ground temperatures, wind speed, and refuge availability. Historically, vegetation changes have been driven by climate changes, wildfire, faunal extinctions, and anthropogenic landscape modification. The persistence of these factors, in addition to the more recent anthropogenic increase in atmospheric CO₂ (Betts et al. 1997), promise that shifts in vegetation density will continue. Although there has been a great deal of research on vegetation dynamics (Miles 1979, Tallis 1991, Whitlock and Bartlein 1997), there are fewer data on how these changes might affect native fauna.

Theory predicts that in a directionally shifting environment, a population must adapt genetically, track its environment spatially, or go extinct (Pease et al. 1989). Some observational evidence supports this prediction: long-term studies have implicated changes in

vegetation density in the local extinctions and emigrations of various populations (Fitch 1999, Holmes and Sherry 2001). However, species with high habitat specificity and small ranges may not be able to emigrate successfully, and local extinction may thus be tantamount to species extinction.

Because the ecology and physiology of ectotherms depend on the thermal attributes of their habitat (Huey 1982, 1991, Huey and Kingsolver 1989), they may be particularly sensitive to the thermal consequences of changes in habitat structure. Numerous studies on habitat selection by active diurnal ectotherms have confirmed the importance of habitat structure in creating opportunities for basking and other forms of behavioral thermoregulation (for recent examples, see Hertz et al. 1994, Vitt et al. 1997, Litzgus and Brooks 2000, Bryant et al. 2002). However, little attention has been paid to the role of habitat structure in determining the thermal attributes of retreat sites used by sedentary and/or nocturnal ectotherms (but see Huey et al. 1989, Kearney 2002). This situation is ironic, because these organisms cannot bask and are less mobile in response to thermal cues. Thus, the long-term costs of any “mistakes” made with respect to habitat selection will be severe. For example, if an individual chooses a retreat site that approaches its critical thermal maximum during the day, then it will have to move, thereby expending en-

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¹ Present address: St. John's College, University of Oxford, Oxford OX1 3JP UK.

² Corresponding author. E-mail: rics@bio.usyd.edu.au

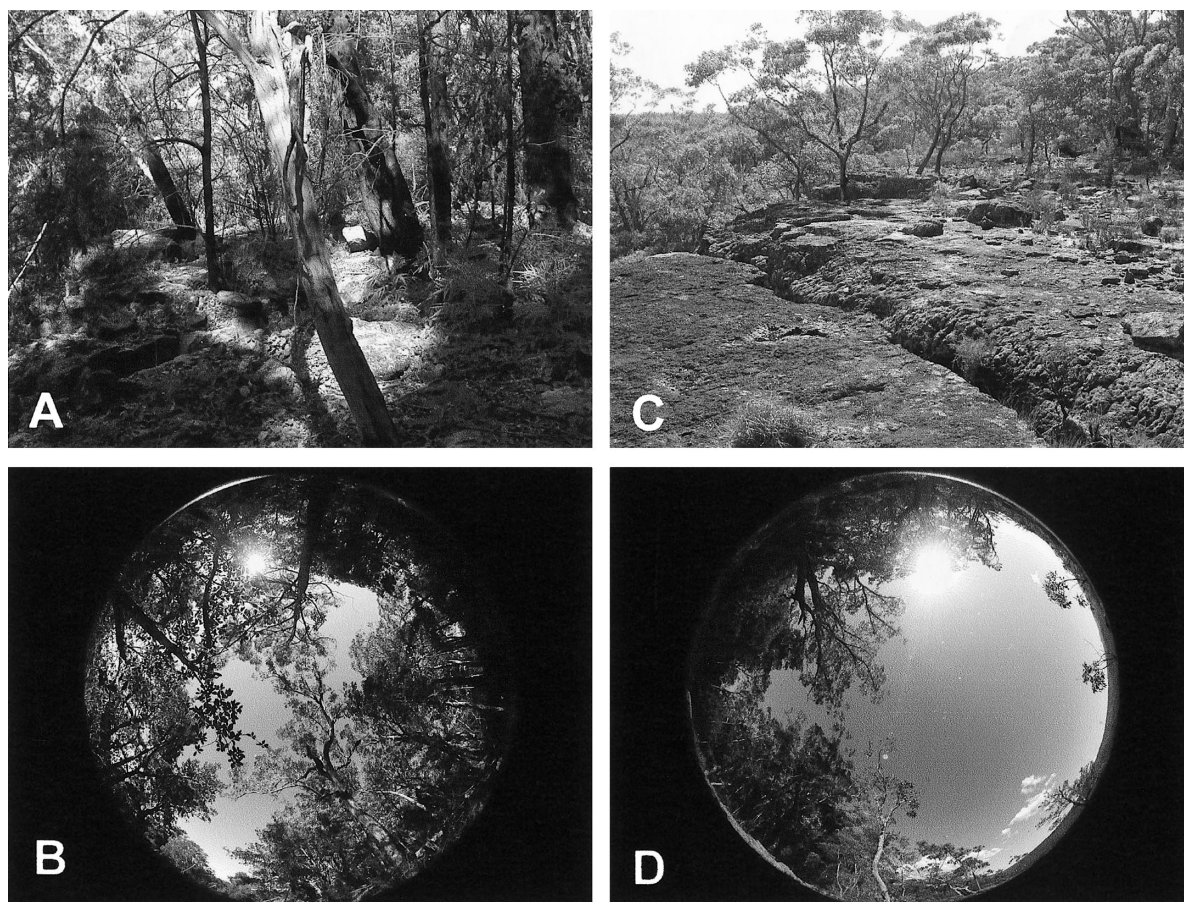


FIG. 1. Broad spatial variation in plateau habitat in Morton National Park, Australia, with representative hemispherical photographs. Exfoliated sandstone rocks are abundant on both (A, B) easterly and (C, D) westerly cliff tops, but the two sides differ substantially in vegetation density.

ergy and exposing itself to predators. Alternatively, if the retreat site is too cold, physiological performance (and even survival) may suffer.

Despite the widely cited importance of vegetation as a structural characteristic of habitat (Heatwole 1977, Reinert 1984, Orians and Wittenberger 1991), most studies on habitat selection have either ignored vegetation or treated it vaguely. This is partly because it is difficult to quantify vegetation density in a given area. However, increasingly precise techniques to estimate canopy structure and related variables (Barrie et al. 1990, Frazer et al. 1999) provide a solution to this problem.

We used hemispherical photography and gap analysis to investigate the role of canopy structure in determining the thermal attributes of retreat sites for a nocturnal species (the broad-headed snake, *Hoplocephalus bungaroides*) in a heterogeneous environment. Using existing data on the natural history of this species, we examined patterns of retreat-site choice with respect to vegetation across both broad (macrohabitat) and narrow (microhabitat) spatial scales to ask how vegetation influences habitat availability for this endangered spe-

cies. We then extrapolated from these findings to suggest answers to the questions: would a gradual increase in vegetation density threaten the survival of this species, and if so, can the habitat be managed effectively to prevent its extinction?

METHODS

Study area and species

Our study was conducted in Morton National Park ~160 km south of Sydney, Australia. The area is dominated by evergreen heathland vegetation and eucalypt forest; *Eucalyptus gummifera*, *Eucalyptus agglomerata*, *Syncarpia glomulifera*, and *Banksia* spp. were common at our sites. A series of flat-topped plateaus of ~400 m elevation traverse the park from south to north, edged by well-defined steep cliffs on either side. East-facing (hereafter easterly) and west-facing (hereafter westerly) ridges are similar geologically, but easterly ridges generally have denser vegetation, whereas westerly ridges are mosaics of varying vegetation cover (Fig. 1).

Hoplocephalus bungaroides is a small (<90 cm total length) snake of the family Elapidae that occurs only

on sandstone outcrops within 250 km of Sydney (Cogger 2000). Although its numbers have declined in recent years (Shine et al. 1998, Goldingay and Newell 2000, Webb and Shine 2000, Webb et al. 2002a), historical evidence suggests that the species has long been confined to a small geographic range (Krefft 1869). The population examined here has been the subject of a long-term radiotelemetry and mark-recapture study, and its ecology and life history are described in detail elsewhere (Webb and Shine 1998a). This species is an extreme ambush predator, often remaining within a single retreat for as long as four weeks and preying on small reptiles and mammals that enter the retreats. It is also a thermophilous species: laboratory experiments have shown that it voluntarily selects body temperatures between 28.1° and 31.1°C and that its physiological performance is positively correlated with temperature (Webb and Shine 1998b). During the colder months of the year (April–November), broad-headed snakes shelter under exfoliated rocks and in crevices in sandstone outcrops. During summer, most individuals migrate from the outcrops and shelter within hollow trees (Webb and Shine 1997b). Individuals demonstrate strong site fidelity, often returning to the same rocks over several consecutive years (Webb and Shine 1997a). However, despite these relatively long-range migrations (up to 1 km) and the comparable distances between easterly and westerly cliffs (150 m to 2 km; Fig. 2), telemetered individuals have never been observed sheltering under rocks on the easterly cliff tops (J. K. Webb, *unpublished data*).

Four replicate study sites were chosen on two adjacent plateaus 4 km apart (Fig. 2). Each site consisted of a 100 × 15 m transect on the easterly cliff top and another on its westerly counterpart. At sites 1–3, transects were located directly opposite each other across the plateau, but at site 4, reptile collectors had extensively disturbed the cliffs opposite our easterly transect so we shifted the westerly transect to the south (Fig. 2). However, in no case did the distance between a pair of transects exceed 1 km, which is the maximum dispersal distance observed during this species' seasonal migrations. Thus, the easterly ridgetops could have been reached and colonized by the snakes. The number of potential habitat rocks (defined as all rocks >20 cm in length, <20 cm in thickness, and lying flush on solid rock substrate; Webb and Shine 1998c) was estimated for each transect by counting and measuring all rocks within two randomly selected 10 × 5 m plots. Estimates of reptile abundance and diversity in each transect were made by a systematic sweep in which all rocks were turned and animals were scored as either "active/basking" or "sheltering." All manipulated rocks were replaced precisely in their original locations.

Measurements of canopy cover and thermal regimes

At each site, 10 rocks were selected randomly (but using the criteria previously described) on both the

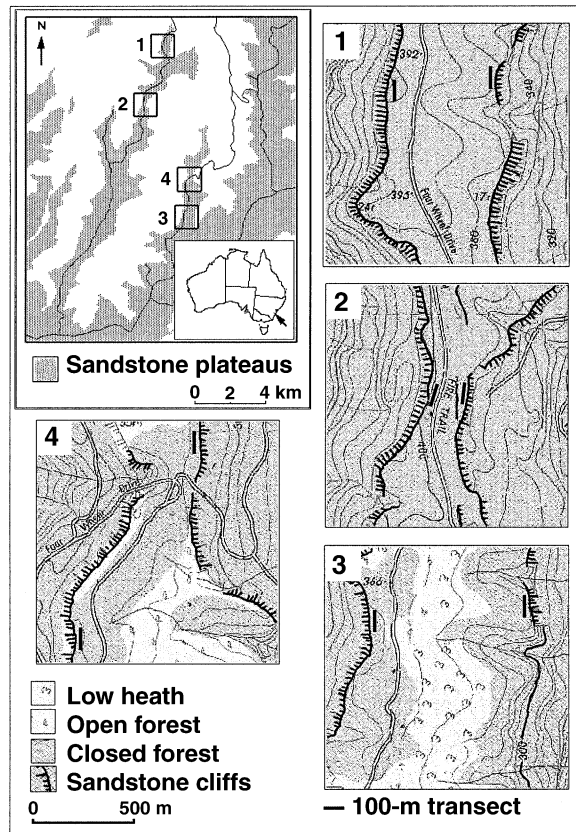


FIG. 2. Location of our study sites in Morton National Park, southeastern Australia. Each site consisted of a 100-m transect on the easterly side and an opposing 100-m transect on the west side. Rectangles indicate the location of sites on the plateaus (top left corner) and the four topographical maps (numbers 1–4) show the exact locations of the 100-m transects (solid bars) on the plateaus. Topographical maps show 10-m contour intervals, cliffs, vegetation, and fire trails.

easterly and westerly sides, and another set of rocks from the westerly sides were selected because they were known to have been used by *H. bungaroides* (J. K. Webb, *unpublished data*). In subsequent analyses, rocks were grouped according to these three categories (easterly, westerly, or known retreat site). The dimensions of each rock and its distance to the cliff edge were measured, and a small thermal data logger (Thermochron iButton by Dallas Semiconductor, Dallas, Texas, USA; diameter 15 mm, height 6 mm) was glued to the center of the underside of the rock. The rock was then replaced in its original position. The thermochrons recorded the temperature every 10 minutes for one cloudless 24-h period (midnight to midnight) before being retrieved. Temperatures were sampled on 5 May 2002 (first plateau) and 12 May 2002 (second plateau). Temperatures from both plateaus were later grouped for analysis.

Canopy cover and incident radiation were estimated for each rock using hemispherical photography and gap analysis (Frazer et al. 1999). A Nikon Coolpix 995

digital camera with Nikon FC-E8 fisheye converter was used to take hemispherical photographs. The camera was mounted pointing upward on a small tripod (18 cm tall), placed atop the rock, oriented to magnetic north, and leveled using a cross-check level. Aperture and ISO sensitivity were held constant. All exposures used the camera's self-timer to minimize camera shake and were recorded in black and white to minimize chromatic aberration (Frazer et al. 2001).

Experimental canopy manipulation

To investigate the effects of vegetation clearing on habitat thermal regime, a nearby outcrop was selected where overhanging vegetation had shaded potential habitat rocks. Sixteen rocks were randomly allocated to control ($n = 8$) and experimental ($n = 8$) groups. Rock dimensions, their diel thermal regimes, and their canopy covers were measured on 10 May as previously described. Accessible branches and scrub were then trimmed from above the experimental rocks, whereas the vegetation above control rocks was not changed. "After" photos were taken to quantify change to the canopy, and temperature data were recorded over another cloudless 24-h period (12 May) before the thermochrons were retrieved.

Analysis

Hemispherical photographs were broken down into binary bitmaps (black, canopy; white, sky) and were analyzed using Gap Light Analyzer Version 2.0 (GLA; Frazer et al. 1999). The program estimates percent canopy openness, plots the sun's path, and uses geographical and seasonal data to produce estimates of incident radiation intensity per day (in units of megajoules per square meter per day). Because our sample of known habitat rocks had been used by snakes at various times from April to November, comparisons between habitat rocks and randomly sampled rocks used a single estimate of mean incident radiation intensity per day over that eight-month period. However, for comparisons that involved temperature, an estimate was calculated for the day on which the thermal regime was sampled. Temperature data were downloaded from thermochrons and used to create two indices of thermal quality for each rock. The first was simply the average of the 144 temperature readings taken over the course of the 24-hour sampling period. However, it has been suggested that high body temperatures at dusk (defined as the two-hour period around sunset) are important to these snakes, because their nocturnal prey are most active during this time and high body temperatures may increase predation success (Webb and Shine 1998b). Thus, average dusk temperature was also used as a potentially more biologically meaningful estimate of thermal quality.

All statistical analyses were performed on StatView 5.0 for the Macintosh (SAS Institute 1998). Unpaired t tests were used to make broad comparisons between

easterly and westerly cliff tops. Two-factor ANOVA and ANCOVA (with site and rock category as factors) were used for comparisons between our three rock categories unless otherwise stated. Tukey's honestly significant difference test (hsd) was used for multiple comparisons between these categories. Prior to all analyses, data were examined for violations of assumptions. F tests and Kolmogorov-Smirnov tests were used to check for heterogeneity of variance and non-normality, respectively. In cases in which data did not conform to the assumption of homogenous variances, log transformation was used to remove heteroscedasticity. When a covariate was used, we verified that the slope of the relationship between the covariate and the dependent variable was homogenous prior to eliminating interaction terms. Results of statistical tests were considered significant at $P \leq 0.05$. Descriptive statistics are reported as means ± 1 SE unless stated otherwise.

RESULTS

Site characteristics

Rock density was higher on easterly (0.60 ± 0.12 rocks/m²) than on westerly (0.33 ± 0.04 rocks/m²) transects. Despite nonrandom sampling of rocks with respect to size, retreat-site rocks were significantly longer and wider than randomly sampled rocks on both transects at every site (Table 1). This variation presumably arose because we deliberately set the lower bounds of our sample equal to the minimum dimensions ever observed in a retreat-site rock. Rock thickness varied within and among sites, and there were no significant differences among groups. Thorough searches of the transects revealed that westerly transects supported a strikingly higher abundance and diversity of reptiles than did easterly transects (Table 2). Both of these differences were statistically significant ($t = -5.28$, $df = 6$, $P = 0.002$ for number of individual reptiles, and $t = -5.55$, $df = 6$, $P = 0.001$ for number of species). Interestingly, all species represented on the easterly cliff tops are diurnal active foragers, whereas the species occurring on the westerly cliff tops employ a variety of activity patterns and foraging strategies.

Canopy cover and thermal regimes

The mean characteristics of our three rock categories are summarized in Table 1. Analysis of hemispherical photographs revealed substantial differences in canopy cover among categories (Fig. 3; $F_{2,95} = 65.56$, $P < 0.0001$). Tukey's post hoc comparisons showed that canopy cover was significantly less dense ($P < 0.05$) on the westerly transects than on the easterly transects and that the known retreat sites had marginally less ($P \approx 0.05$) canopy cover than randomly sampled rocks on the westerly side. In two cases, there were significant differences between individual sites.

Transmitted radiation intensity also differed significantly according to aspect (Fig. 3; $F_{2,95} = 76.88$, $P <$

TABLE 1. Characteristics (mean \pm 1 SD) of sampled rocks according to category.

Characteristic	Rock category		
	East	West	Retreat sites
Length (cm)	44 \pm 13	40 \pm 8.5	55 \pm 16
Width (cm)	32 \pm 10	27 \pm 7.7	38 \pm 8.5
Thickness (cm)	8 \pm 2.4	7 \pm 2.5	7 \pm 2.4
Canopy openness (%)	3 \pm 7.1	46 \pm 7.1	51 \pm 9.1
Radiation intensity (MJ·m ⁻² ·d ⁻¹)	2.6 \pm 0.60	3.7 \pm 0.65	4.2 \pm 0.56
24-h average temperature (°C)	15 \pm 1.4	17 \pm 1.1	18 \pm 1.4
Dusk average temperature (°C)	17 \pm 1.4	22 \pm 2.0	24 \pm 2.7

0.0001); westerly rocks received more radiation than easterly rocks, and retreat sites received more than the average rock on the westerly transects (Tukey's hsd, all P 's $<$ 0.05). There were no differences in mean radiation intensity among sites. Predictably, canopy openness was a major determinant of transmitted radiation intensity, with some scatter due to the location of canopy gaps relative to the path of the sun (Fig. 4; $n = 107$ sampled rocks, $r = 0.89$, $P < 0.0001$). Canopy openness and radiation intensity decreased slightly but nonsignificantly with distance from the cliff edge ($n = 107$; $r = 0.16$, $P = 0.09$ for canopy openness, and $r = 0.15$, $P = 0.12$ for transmitted radiation), but retreat sites were significantly closer to the cliff edge than were random rocks on the westerly side (one-factor ANOVA; $F_{1,65} = 7.15$, $P = 0.01$).

Both indices of thermal quality also varied significantly among rock categories (Fig. 5; $F_{2,95} = 54.42$, $P < 0.0001$ for average 24-h temperature, $F_{2,95} = 128.79$, $P < 0.0001$ for average dusk temperature). Random westerly rocks were warmer than easterly rocks, and retreat sites were warmest of all (Tukey's hsd, all P 's $<$ 0.05). Mean temperatures also varied between in-

dividual sites. Radiation intensity, as estimated by the GLA software, was a major determinant of temperature (Fig. 6; $n = 107$, $r = 0.69$, $P < 0.0001$ for 24-h temperature; $n = 107$, $r = 0.74$, $P < 0.0001$ for dusk temperature), and it was a more accurate predictor of a potential retreat site's temperature than was canopy openness per se ($r = 0.57$ for 24-h temperature and $r = 0.66$ for dusk temperature). Rock dimensions had no significant effect upon either 24-h or dusk temperature averages in an ANCOVA (ANCOVA with temperature as the dependent variable and rock length, width, and thickness as covariates; all P 's $>$ 0.15).

Because of the correlation between overall canopy openness and transmitted radiation intensity, more exposed rocks should generally be warmer. However, depending on the location of canopy gaps relative to the sun's path, there is often substantial variation in radiation intensity (and, hence, in temperature) even between rocks with equivalent overall canopy openness (Fig. 4). Thus, retreat-site choice should be driven by transmitted radiation intensity rather than canopy openness, and retreat sites should receive more radiation than random rocks that have the same overall canopy

TABLE 2. Reptile abundance and diversity as estimated by thorough searches of each study site.

Location	East			West		
	Species	No. individuals	Behavior†	Species	No. individuals	Behavior†
Site 1	<i>Eulamprus tenuis</i>	2	A	<i>Bassiana platynota</i>	2	S
				<i>Ctenotus taeniolatus</i>	1	A
				<i>Oedura lesueurii</i>	10	S
				<i>Hoplocephalus bungaroides</i>	2	S
				<i>Rhinoplocephalus nigrescens</i>	5	S
Site 2				<i>Cryptoblepharus virgatus</i>	3	M
				<i>Oedura lesueurii</i>	7	S
				<i>Rhinoplocephalus nigrescens</i>	2	S
Site 3	<i>Ctenotus taeniolatus</i>	1	A	<i>Bassiana platynota</i>	2	A
				<i>Cryptoblepharus virgatus</i>	1	S
				<i>Egernia cunninghami</i>	1	A
				<i>Hoplocephalus bungaroides</i>	2	S
Site 4	<i>Pseudechis porphyriacus</i>	1	A	<i>Bassiana platynota</i>	1	A
				<i>Cryptoblepharus virgatus</i>	4	M
				<i>Hoplocephalus bungaroides</i>	2	S

† Behavior codes are: A, active/basking; S, sheltering; M, mixed behaviors.

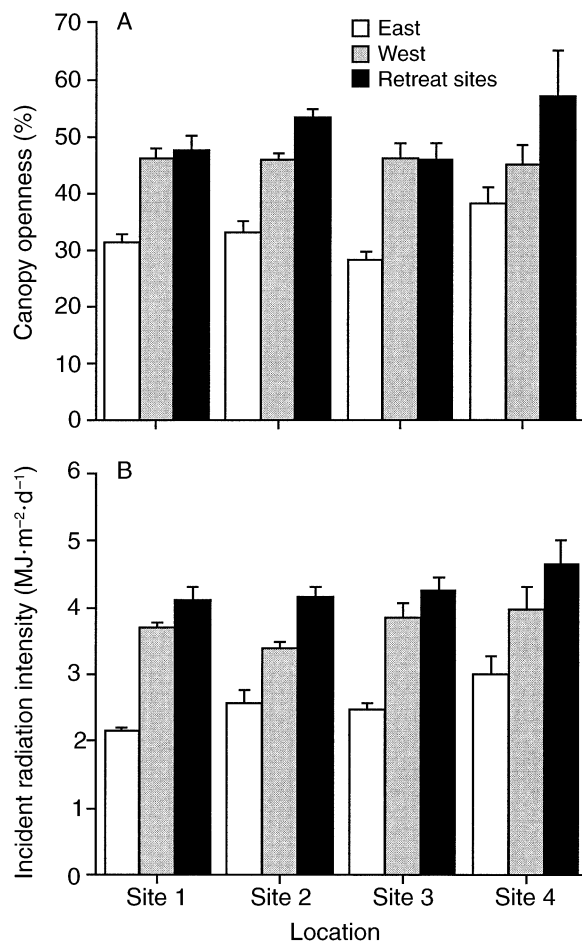


FIG. 3. Variation among sites in (A) canopy openness and (B) incident radiation intensity among replicate sites and rock categories. Values are means \pm 1 SE.

openness. This prediction can be tested with ANCOVA, using transmitted radiation intensity as a dependent variable and entering overall canopy openness as a covariate to adjust for its effect on transmitted radiation. A homogeneity-of-slopes test for an ANCOVA with site and aspect as factors revealed several confounding interaction terms. However, the important comparison is between known and potential retreat sites on the west side. When the analysis was restricted to these two categories, the regression slopes were very similar (0.054 for known retreat sites and 0.074 for potential retreat sites), and the difference between used and unused rocks was significant (two-factor ANCOVA with canopy cover as the covariate, site and rock category as factors, and transmitted radiation intensity as the dependent variable, $F_{1,79} = 17.64$, $P < 0.0001$; see Fig. 4).

Although the density and pattern of canopy determines transmitted radiation intensity, it is not possible to ascribe the difference in temperature between east and west aspects entirely to their differing canopy cov-

er. If this were the case, there should be no significant difference between aspects when the effects of radiation intensity are removed. However, the differences in temperature between easterly and westerly transects do not disappear in an ANCOVA with radiation intensity as a covariate ($F_{2,100} = 4.99$, $P = 0.009$ for 24-h temperature average; $F_{2,100} = 30.22$, $P < 0.0001$ for dusk temperature average; see Fig. 6). The explanation is that our estimate of radiation intensity is in units of megajoules per square meter per day and makes no allowances for differing radiation intensity in a given spot over the course of the same day. Holding daily radiation intensity constant does not remove the effects of the direct irradiance received by the westerly rocks (which have already been substantially warmed by rising air temperatures during the day) in the hours preceding dusk. Of course, this has less effect when averaged over 24 h than it does for the two hours of dusk, which explains the magnitudes of the differences for those two indices (as reflected by their respective F values). Fig. 5A shows that although rocks on the easterly cliff top begin warming up sooner than those on the west, they are still relatively cool as the westerly side shifts into direct sunlight. Moreover, the temperatures under rocks used by snakes are more evening shifted than unused rocks on the west side, supporting the hypothesis that snakes select retreat sites on the basis of high evening temperatures (Fig. 5B).

Experimental canopy manipulation

Canopy openness was increased by an average of $15 \pm 2\%$ for our eight experimental rocks, which corresponded to an average increase of $1.4 \pm 0.3 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in radiation intensity. There were no significant a priori differences between the two groups in rock size, temperature regime, or canopy openness (one-factor ANOVAs, Tukey's hsd, all P 's > 0.05). Average temperature differences between the groups as measured before and after canopy removal had heterogeneous variances, and log transformation did not remove the heteroscedasticity. However, ANOVA is usually robust to violations of the assumption of homogenous variances when sample sizes are equal (Lindman 1974), so we proceeded with the analyses. Rocks from both groups were colder over 24 h on the second day of measurement than the first, due to lower air temperatures. However, this decrease was smaller in the manipulated group than in the control group (one-factor ANOVA, $F_{1,14} = 9.43$, $P = 0.008$).

More striking was the difference between the two groups at dusk: whereas all rocks in the control group decreased in temperature from the first day to the second, all but one rock in the experimental group actually *increased* in temperature on the second day, and this difference between the two groups was again significant (Fig. 7; $F_{1,14} = 16.73$, $P = 0.001$). The mean difference between the two groups in average dusk temperature was nearly 2°C (Fig. 7), which is similar in

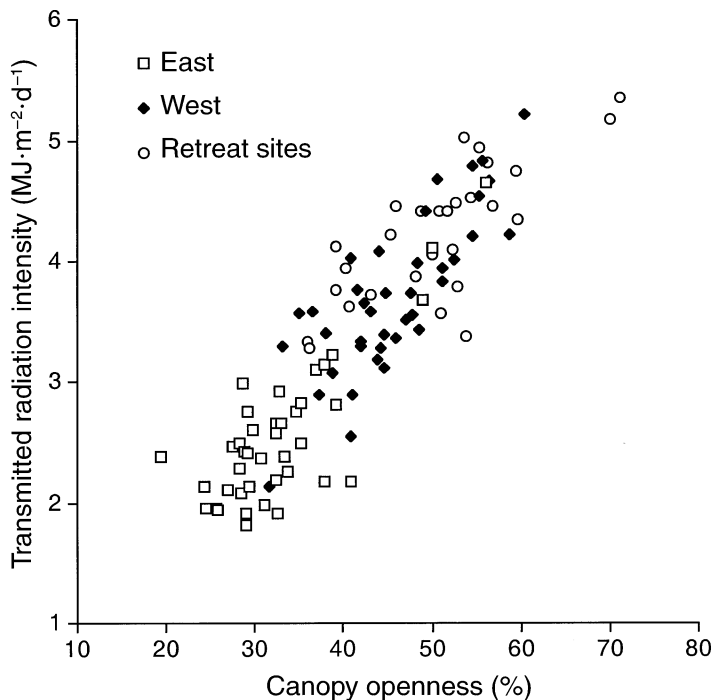


FIG. 4. The relationship between incident radiation intensity and canopy openness for all sampled rocks ($n = 107$).

magnitude to the thermal difference between retreat sites and random rocks on the westerly side (Fig. 5). Hence, an increase in canopy openness of only $\sim 15\%$ had a biologically significant impact on the thermal regimes of potential retreat sites.

DISCUSSION

Even within a small plateau, there are substantial variations in habitat characteristics. This occurred on two different spatial scales within our study sites, both broadly (between cliff tops with easterly and westerly aspects) and narrowly (at different points within the westerly transects), and the consequences for ectothermic vertebrates were striking. As suggested by a previous radiotelemetric study and supported by thorough searches of our study sites, neither *Hoplocephalus bungaroides* nor any other nocturnal reptiles settle on the east sides of the plateaus, despite the small distances between aspects and the abundance of otherwise suitable rocks. The only reptiles that do occur on the easterly cliff tops of these plateaus are diurnally basking species that can exploit transient patches of sunlight that filter through the thicker canopy. Nocturnal species cannot shuttle between sun and shade, and their choice of retreat sites will effectively determine the range of body temperatures available to them during the daylight hours. That these retreat sites are among the warmest available rocks anywhere on the plateaus suggests that thermally suitable microhabitat is a limiting resource for *H. bungaroides*. In addition, our results show that evening temperatures are crucial determinants of a retreat site's suitability.

The causality of retreat-site temperature is complex, and it will vary with such physical properties as wind speed and direction, reflectivity and microtopography of rocks, evaporation from the rock surface, etc. (Porter and Gates 1969, Huey et al. 1989, Bakken 1992). It would be difficult to measure these characteristics in the field and even more difficult to disentangle their relative contributions to retreat-site temperature. However, it is clear that a substantial amount of variation in temperature is driven directly by differences in the amount of radiation incident upon the rocks, and that the amount of radiation, in turn, is determined by the size and location of canopy gaps. The distinct differences in temperature between our experimentally trimmed and control groups of potential retreat sites demonstrate that whatever other factors might be operating, an increase in incident radiation can elevate temperatures in biologically meaningful increments.

Previous work showed that rock thickness affects temperature at these sites, and that broad-headed snakes shelter beneath thin (< 20 cm) rocks on solid rock substrate (Webb and Shine 1998c). Our decision to sample only rocks that fit these criteria therefore limited temperature variation. By ensuring that these physical features of the rocks were relatively constant across the categories, we were able to isolate the effects of vegetation cover on rock temperature. This is not to imply that there is complete thermal homogeneity under individual rocks; our analysis does not exclude the possibility of thermoregulation *within* retreat sites (Licht et al. 1966, Kearney 2002), which may explain

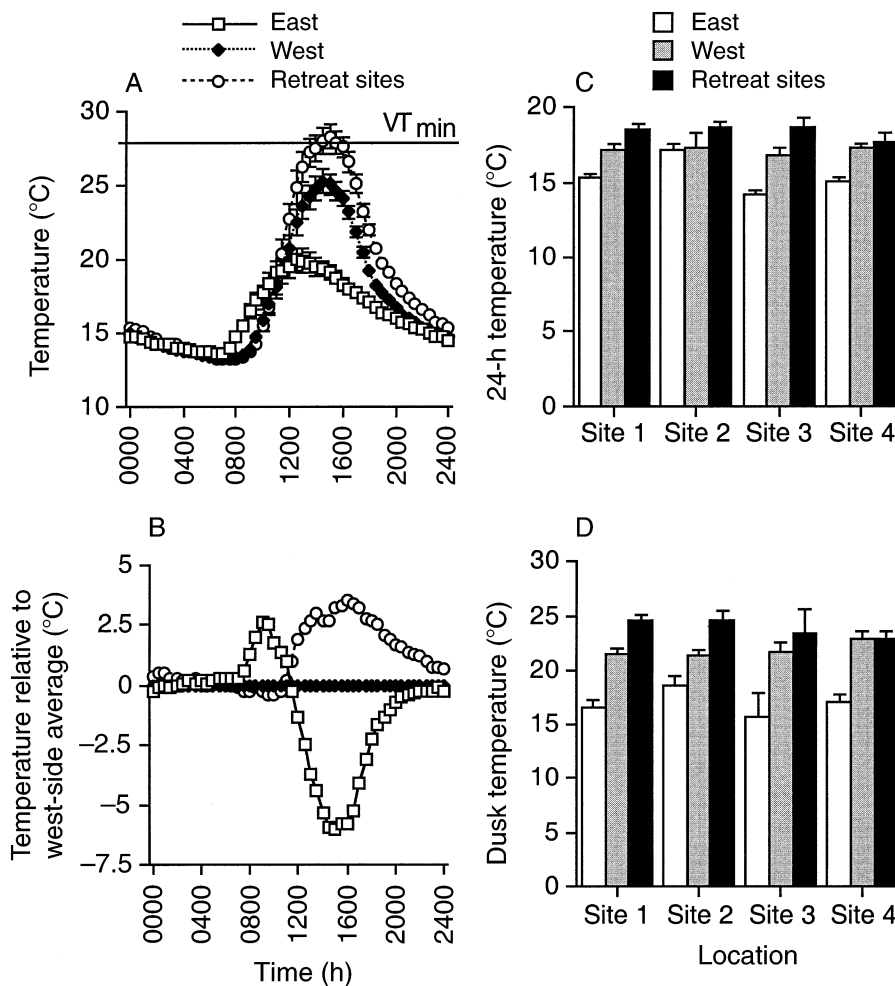


FIG. 5. Variation in temperature among sites and rock categories. (A) Average 24-h temperature cycle from our first replicate ridge. Superimposed horizontal bar represents the minimum temperature preferred by snakes in the laboratory (VT_{min} ; Webb and Shine 1998b). (B) Temperature variation of rock categories relative to the average of randomly sampled rocks on the west. (C) Average 24-h temperature variation. (D) Average temperature variation at dusk (1600 to 1800 hours). Histograms show means \pm 1 SE.

the snakes' preference for larger rocks (Dial 1978, Kearney and Predavec 2000).

The difference in incident radiation between used and unused retreat sites on the westerly transects was greater and more consistent than the difference in canopy openness, and it persisted even when the analysis was adjusted for the effects of overall canopy openness. Hence, canopy openness is thermally important only insofar as it determines transmitted radiation. Stated so simply, this seems obvious (how could the presence of a canopy gap exert a direct effect on temperature in and of itself?). Nevertheless, it suggests the need for a slight modification of how we think about habitat characteristics for nocturnal ectotherms. Many studies on habitat selection in reptiles have focused on the importance of canopy cover as a structural feature, the implication being that structural characteristics, which are relatively "stable" over time, will be the stimuli

used as cues in habitat selection (Heatwole 1977). This has led to the adoption of a vernacular that describes habitats as either "exposed" or "shaded" (or variations thereof), which is an oversimplification. A retreat site might appear shaded (i.e., have higher absolute canopy cover), but actually offer greater thermal benefits than a rock that appears more exposed, depending on the location of the canopy gaps relative to the path of the sun.

The assumption that relative abundance of sun and shade is the cue used to assess thermal suitability may be an artifact of the predominance of diurnal organisms in such studies; the sun/shade dichotomy is a perfectly reasonable criterion to use in a model of habitat selection by black rat snakes (Weatherhead and Charland 1985), wood turtles (Compton et al. 2002), or iguanid lizards (Adolph 1990, Vitt et al. 2002), but it has no meaning for species that only move and select habitat

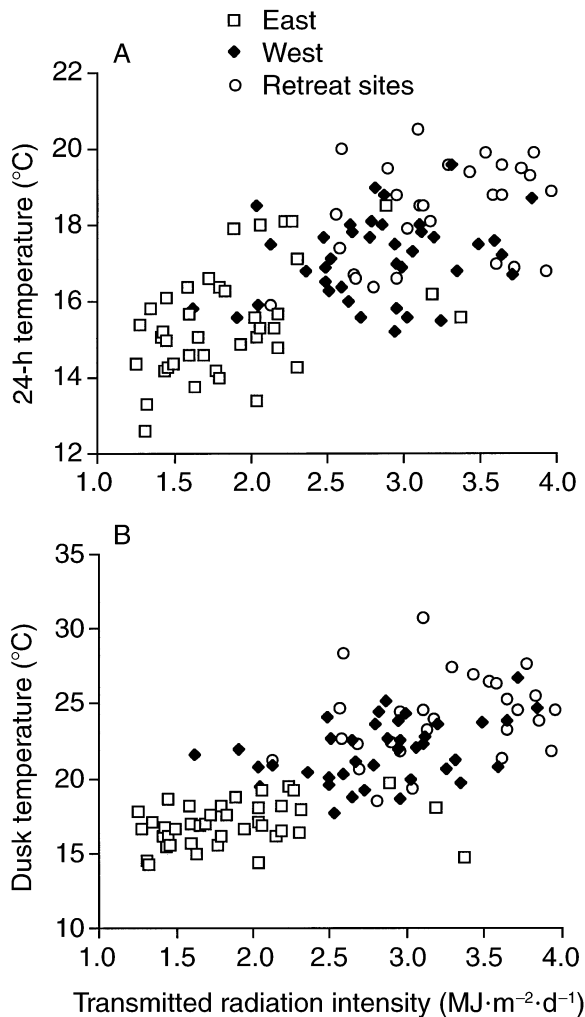


FIG. 6. Correlation of (A) 24-h temperature average and (B) dusk temperature average with incident radiation intensity for all sampled rocks.

at night when there is neither shade nor sun. Kearney (2002) recognized this problem in his study of retreat-site selection by the nocturnal gecko *Christinus marmoratus*: the degree of shading is difficult to estimate for a given rock because it varies with time of day. It seems likely that, given a set of potential retreat sites with appropriate crevice width, rock temperature in the evening (when snakes move between retreat sites) will be the dominant proximal cue in habitat selection by *H. bungaroides*.

Moreover, the classification of habitat simply as "shaded" or "not shaded" might obscure subtle yet potentially important factors influencing habitat selection. For instance, it has been hypothesized that vegetation cover plays a crucial role in concealing snakes from predators (Janzen 1976). Our study area supports populations of both diurnal (*Dacelo gigas*, *Milvus sphegnurus*, *Falco subniger*) and nocturnal (*Ninox strenua*, *Tyto alba*) birds of prey, and snakes are occasion-

ally found sporting beak marks (J. K. Webb, *personal observation*). If there is a trade-off between thermal concerns and safety from predators, then the optimal retreat site would not be the rock with the highest canopy openness, but the rock with canopy gaps located so as to transmit high levels of radiation while retaining some of the protection against avian predators afforded by vegetation. Such a trade-off between thermal benefit and predation risk has been demonstrated in a sympatric species of nocturnal reptile, the velvet gecko *Oedura lesueurii* (Downes and Shine 1998).

What then does the relationship between vegetation density and retreat-site quality mean for *H. bungaroides* as an endangered species? Several studies have implicated successional vegetation changes in the local extinction of reptile populations (Ballinger and Watts 1995, Fitch 1999, Jäggi and Baur 1999), but in each case the species studied (e.g., *Agkistrodon contortrix*, *Coluber constrictor*, *Crotalus horridus*, and *Sceloporus undulatus* in North America; *Vipera aspis* in Europe) are very wide-ranging geographically. In contrast, a few local extinctions of *H. bungaroides* would result in species extinction.

The issue of vegetative encroachment and habitat availability for this species raises two questions. The first is whether there is indeed a trend toward increasing vegetation density in southeastern Australia, as hypothesized by Flannery (1994). Briefly, the explanation for this putative increase in vegetation density is that the elimination of Aboriginal landscape-burning practices (which had maintained open woodland) since the arrival of Europeans in Australia has allowed encroachment of woody vegetation. This is a difficult hypothesis to address quantitatively, and efforts to address it qualitatively (by interpreting the journals of early explorers; e.g., Ryan et al. 1995, Benson and Redpath 1997) have been subjective, acrimonious, and inconclusive. Nevertheless, it is generally accepted that burning was used extensively by Aborigines as a land management tool (Bowman 1998). Furthermore, studies of ecotone shifts

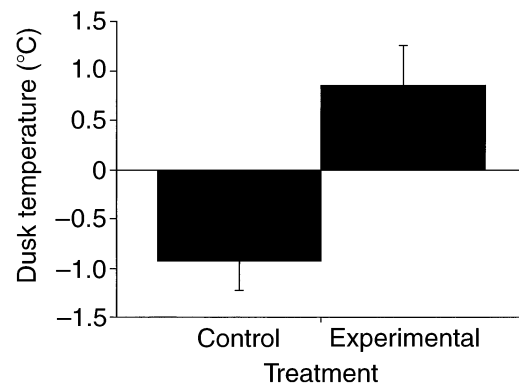


FIG. 7. Difference in average dusk temperature between control and experimental groups. Histograms show means \pm 1 SE.

in North America and northern Australia using historical aerial photographs have clearly demonstrated increases in vegetation density and have attributed them to fire suppression practices (Mast et al. 1997, Bowman et al. 2001). Morton National Park, the location of our study sites, was inhabited by several Aboriginal groups at the time of European exploration (New South Wales Parks and Wildlife Service 2001), and we consider it quite likely that fire deterrence since European arrival has led to an increase in vegetation density in that area as well. Objective efforts to address this issue are clearly needed to enhance our understanding of long-term habitat dynamics in this area.

The second question is whether it is reasonable to assume that future canopy encroachment could have a significant negative impact upon *H. bungaroides*. This seems a likely scenario, especially when we consider the other factors affecting habitat availability for this species at the macrohabitat (ridgetop) level. Of the total number of rocks on a given plateau, approximately half are on the easterly aspect and thus are thermally unsuitable as retreat sites for *H. bungaroides*. Of the rocks on the westerly side, many are stolen (by bush-rock collectors; see Shine et al. 1998), disturbed, or broken (by reptile collectors; see Webb et al. 2002a). Of the remaining westerly, undisturbed, and intact rocks, a smaller number are exposed to sufficient solar radiation to be thermally suitable and most of these are within several meters of the cliff edge. Furthermore, not all of the remaining westerly, undisturbed, intact, and thermally suitable rocks will be available to a given snake: individuals occupy distinct home ranges, and two males will not cohabit the same area or retreat site (Webb and Shine 1997a). This restriction is important because several adjacent rocks on a given stretch of cliff top may often receive appropriate levels of radiation. Finally, there may well be shared preference competition (Rosenzweig 1991) for high-quality retreat sites between *H. bungaroides* and the sympatric small-eyed snake *Rhinoplocephalus nigrescens* (Webb et al. 2002b; J. K. Webb, unpublished data). Under these conditions, under- and overstory encroachment of westerly cliff tops may well be contributing significantly to the decline of this species.

However, as demonstrated by our experimental manipulations, a modest increase in canopy openness can increase the temperatures by an amount equivalent to the temperature difference between used and unused retreat sites. We do not advocate drastic measures (e.g., tree felling or burning); the sandstone ridges favored by *H. bungaroides* are rich and fragile ecosystems, and overzealous efforts in the name of the broad-headed snake may have unintended and unfortunate consequences for other species (some of which are also endangered; Burrows 2001). *Hoplocephalus bungaroides* inhabits large dead trees during its summer migrations (Webb and Shine 1997b), and would itself be sensitive to misapplied forestry practices. However, the cutting

of overhanging branches and clearing of understory weeds in areas deemed important to *H. bungaroides* could be an important tool in future plans to manage the habitat of this species. Specifically, this pruning can be aimed at vegetation to the west of the cliff tops, particularly where trees from below the cliff are growing up to shade the crucial cliff edges. Such targeted management will confer the greatest amount of thermal benefit to snake habitat while causing minimal disturbance to the surrounding area. It would be wise to spread these efforts over several westerly plateaus, maintaining some relatively open areas on each, as this would facilitate dispersal between plateaus and the establishment of stable subpopulations.

The snakes are extremely selective with respect to the physical properties of their retreat sites. The thin slabs of sandstone that weather and break off the plateau are unique in shape and fit perfectly into the exact spot on the underlying substrate whence they split. Personal observations and a previous study with concrete pavers (Webb and Shine 2000) indicate that whereas geckos and invertebrates are not particularly selective, broad-headed snakes are reluctant to shelter under wobbly, ill-fitting rocks. Hence, moving "new" rocks into ideal locations to augment the habitat is probably not a viable option.

In summary, our study supports the hypothesis that vegetative succession can have a significant impact upon habitat availability for ectotherms by affecting the thermal characteristics of potential habitats (Thomas and Morris 1994, Meik et al. 2002), and that this impact is especially profound for diurnally sheltering species that cannot exploit transient patches of sunlight. However, we suggest that this relationship is more complex than has traditionally been acknowledged, and that precise methods of quantification may enable the detection of more subtle aspects of habitat selection. Furthermore, we believe that our study highlights the importance of long-term natural history studies (e.g., Fitch 1999) and objective environmental histories in conserving biodiversity (Bowman 2001). A better understanding of the relationship between long-term successional changes and habitat availability will lead to increasingly efficient conservation plans for *H. bungaroides* and similar species.

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