

SOME LIKE IT HOT: EFFECTS OF FOREST CLEARING ON NEST TEMPERATURES OF MONTANE REPTILES

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Abstract. Global climate change may affect the upper elevational limits of distribution of montane organisms, especially if those limits are set directly by temperature. Oviparous (egg-laying) reptiles are constrained in this way because of their nesting requirements. In many areas, deforestation has already subjected these animals to small-scale “climate change.” Clearing for power lines (hydrocuts) increases solar radiation to potential nest sites, and hence enables these animals to penetrate higher into montane areas than would otherwise be possible. Such small-scale anthropogenic “warming” may offer a useful model system to explore consequences of broader climate change on the distribution and biology of montane organisms. We quantified thermal effects of a hydrocut in montane eucalypt forest in the Brindabella Range of southeastern Australia. The reduced canopy cover, increased duration of sunlight exposure, and higher levels of incident radiation in cleared areas substantially modified thermal regimes in potential nest sites. Orientation and exposure were the most important determinants of nest temperature and predicted the distribution of natural nests. Such cleared corridors (for roads, power lines, ski runs, etc.) may not only extend the upper elevational limit for oviparous reptiles, but may also modify the genetic structure and demography of populations.

Key words: *Australia, southeastern; Bassiana duperreyi; climate change, global; forest clearing affects nest-site temperature; geographic distribution; montane organisms, elevational distribution limits; nesting requirements of egg-laying reptiles; oviparity; power-line clearing affects potential nest sites; Scincidae.*

INTRODUCTION

Increasing concern about global climate change has focused attention on factors that limit the upper elevational (thermal) limits to geographic distributions in montane organisms (Gibbons et al. 2000). Shifts in these elevational limits are one of the most likely impacts of global climate change, but we have little detailed information on the ways in which climatic factors directly determine the limits of distribution for fauna and flora. Such an understanding could facilitate robust predictions on the impacts of climate change. Ectothermic organisms are likely to provide excellent model systems for such studies, because of their intimate dependence on ambient thermal environments (Avery 1982). In particular, the minimum thermal requirements of developing embryos in oviparous (egg-laying) reptiles may directly determine geographic distributions of these animals (Sergeev 1940, Tinkle and Gibbons 1977, Shine 1987). The reason for this pattern is that eggs are immobile, and hence (unlike post-hatching stages of the life history) they cannot exploit the spatial heterogeneity of natural thermal environments by behavioral thermoregulation. Thus, adult reptiles can maintain relatively high and stable temperatures even in environments so cold that potential nest sites (i.e.,

the soil) do not permit embryogenesis (Mell 1929, Weekes 1933). Viviparity (uterine retention of developing embryos) allows the eggs to escape this constraint, permitting viviparous lizards and snakes to extend into much higher, colder areas than do closely related oviparous species (Greer 1989).

Oviparous reptiles near the upper elevational limit of their geographic distributions thus offer an ideal opportunity to identify exactly which attributes of the thermal environment limit distribution. Unfortunately, thermal regimes generally shift in gradual clines rather than abrupt discontinuities that correspond to the geographic limit of species. Anthropogenic activities sometimes provide “natural experiments” in this respect, providing sharp discontinuities that facilitate direct comparisons between adjacent areas that fall above and below the thermal conditions needed for successful reproduction. Such a situation allows us to identify exactly what aspects of the thermal environment are crucial to the organism, and how and why anthropogenic change can modify those parameters.

Cleared corridors such as roads and ski runs are common forms of disturbance in otherwise-forested montane areas. One widespread modification involves clear-felling of corridors within forest for the construction and maintenance of hydroelectric power lines (“hydrocuts”). Regular pruning maintains these open areas, which may thus experience a substantial increase in penetration of solar radiation. Anecdotal evidence

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FIG. 1. (Left) Hydroelectric transmission line corridor (hydrocut) at Picadilly Circus in the Brindabella Range of southeastern Australia. One of our transects ran along the area in the foreground (photograph by G. Barrott). (Right) A natural nest of the three-lined skink *Bassiana duperreyi* under a log in the Brindabella Range. The log has been turned and covering soil removed to reveal the eggs (photograph by P. Harlow).

suggests that many animals take advantage of these well-lit, warm corridors to penetrate to higher elevations than would otherwise be the case. Plausibly, this response to small-scale climate change may operate via a greater availability of potential nest sites in cleared areas relative to adjacent forests, thereby allowing oviparous taxa to reproduce successfully and, hence, extend to higher elevations.

To test these ideas, we quantified the availability and use of potential nest sites for oviparous lizards along transects across a hydrocut in montane southeastern Australia. We predicted that potential nest sites in open areas would be exposed to higher levels of solar radiation than would forested sites, and that in consequence the hydrocut would provide opportunities for lizards to deposit their eggs in sites with higher and more variable temperatures than were available in the surrounding forest. We also predicted that lizards would disproportionately select such nest sites, because warm and variable thermal regimes accelerate embryonic developmental rates and modify hatchling phenotypes in ways that are likely to enhance the fitness of hatchling lizards (Shine and Harlow 1996, Shine et al. 1997).

METHODS

Study area

The Brindabella Range, 40 km west of Canberra in the Australian Capital Territory, extends to an elevation of ~1900 m above sea level (asl). Summers are hot (mean January air temperature at Tidbinbilla = 25.9°C) but winters are cold (July mean 10.4°C; Australian Bureau of Meteorology). The range is largely covered by eucalypt forest, but with many cleared areas for roads, hydroelectric power lines (“hydrocuts”), and forestry activities. We worked at a 60-m wide hydrocut that runs east–west at Picadilly Circus (1240 m asl; 148°50' E, 35°21' S; see Fig. 1). First cleared >35 yr ago (Pengilley 1972), regrowth in this area is removed inter-

mittently by the power company. The hydrocut is dominated by low clumps of snowgrass, as occur in clearings within the surrounding forest; there are few exotic or weedy invaders in this system (Fig. 1). Because work to control regrowth occurs rarely (less than once per 10 yr) and usually involves manual pruning rather than heavy machines, soil compaction is minimal.

Study species

Several lizard species are abundant at lower elevations in this region, but only viviparous taxa extend to >1650 m (Pengilley 1972). The most abundant oviparous taxa at Picadilly Circus are three-lined skinks (*Bassiana duperreyi*, to 80 mm snout–vent length). Female *Bassiana* produce a single clutch of 3 to 9 eggs in early to mid-December each year. The eggs are often laid in communal clutches, and are typically found under logs and rocks in exposed situations within the hydrocut rather than in the surrounding forest (Fig. 1; Pengilley 1972, Shine and Harlow 1996). Females actively select relatively “hot” nesting sites, and such sites accelerate embryonic development, hasten hatching, and optimize phenotypic traits of the resulting hatchlings (Shine 1995, Shine and Harlow 1996, Shine et al. 1997). Hydric conditions vary considerably among natural nests, but laboratory experiments suggest that this variation in moisture levels does not exert any significant influence on the phenotypes of hatchling lizards (Flatt et al. 2001).

Methods

On 12 January 2001 we set out three parallel transects running from north to south across the hydrocut at Picadilly Circus. The transects were 70 m apart. Each was 70 m long, extending from the forest on one side to the other. We then selected 10 equally spaced points along each transect (i.e., 7.8 m apart), in such a way that the two outermost points at each end fell within the forest. The next two points on each side were clas-

sified as “edge” sites, and the middle two as “central hydrocut.” We then selected the potential nest site closest to each of these points. Our criteria for this judgment (based on studies of previous nests at this site) were rocks >10 cm long, or logs >30 cm long. In two cases, the shelter item closest to the transect point was in use as a nest, and had also been used in previous years.

We measured the length, width, and thickness of each of these cover items, as well as its orientation and slope. A 35-mm camera with a 180° hemispherical lens (Canon F1 7.5-mm fisheye lens) was placed on each cover item and used to take a photograph pointing directly upwards. The resulting photographs were scanned and specialized gap-light-analyzer image-analysis software used to extract information on canopy cover, light penetration, etc., from the digitized version (Frazer et al. 1999). A miniature thermal data-logger (Thermochron iButton, Dallas Semiconductor, Dallas, Texas, USA; diameter 15 mm, height 6 mm) was placed under the cover item in the place that we judged most likely to contain eggs in a natural nest. The thermochrons were set to record temperatures every 15 min. We then scored the numbers of potential nest sites (cover items fulfilling the above criteria) within a 5-m-diameter circle around each point on the transects. Lastly, we searched the surrounding area for natural nests of *Bassiana*, and quantified thermal regimes and canopy exposure for these nests in the same way as for the transect points. We returned to Picadilly on 18 January 2001 to retrieve and download the thermochrons.

Analysis

Data were analyzed using the software programs Statview 5 (SAS Institute 1998) and SuperANOVA 1.1 (AbacusConcepts 1991) on an Apple Macintosh G4 computer. Assumptions of statistical tests were checked prior to analysis. In some cases, ln-transformation was required to remove variance heterogeneity. Comparisons among locations were made with nested ANOVAs, in which the main effect (location) was nested within transect, and tested against the nested term.

RESULTS

The cover items that we selected as “potential nests” were similar in size to natural nests. For rocks, lengths averaged 23.2 ± 9.09 cm (mean \pm 1 SD) for 9 potential nests, vs. 24.1 ± 6.5 cm for 13 natural nests. Widths (15.4 ± 6.3 cm vs. 15.8 ± 4.0 cm) and thicknesses (7.1 ± 2.8 cm vs. 8.7 ± 3.1 cm) were also similar between the artificial and natural nest sites, respectively. For logs, the two sets (artificial and natural, respectively) of cover items ($n = 21$ and 22 logs) displayed approximately equal lengths (144.4 ± 100.9 cm vs. 164.7 ± 85.1 cm), widths (15.8 ± 7.8 cm vs. 23.4 ± 9.9 cm) and thicknesses (8.3 ± 5.5 cm vs. 9.5 ± 3.0 cm). A two-factor multivariate ANOVA with type of cover item (rock or log) and natural vs. potential nest

as factors, and length, width, and thickness of cover items as dependent variables, revealed a strong size difference between rocks and logs ($F_{3,59} = 13.40$, $P < 0.0001$ with Wilks' lambda), but no difference between potential and natural nests ($F_{3,59} = 1.49$, $P = 0.23$), and no significant interaction term ($F_{3,59} = 1.03$, $P = 0.39$).

Unsurprisingly, canopy cover was much lower in the hydrocut than in the surrounding forest (Figs. 1 and 2). In consequence, sites within the hydrocut were exposed to direct sunlight for almost twice as long each day, and had 80% higher incident radiation than did sites in the forest (Fig. 2; nested ANOVA with location nested within transect as the factor gives $F_{4,15} = 20.32$, $P < 0.0001$ for percent canopy cover; $F_{4,15} = 33.38$, $P < 0.0001$ for duration of direct exposure to sunlight; $F_{4,15} = 18.92$, $P < 0.0001$ for total incident solar radiation). All of these characteristics showed strong north-south asymmetry, however. The southern edge of the hydrocut had a lower canopy cover, longer exposure to direct sunlight, and higher total incident radiation (Fig. 2).

The extent of canopy cover over a potential nest site largely determined the duration of time to which it was exposed to direct solar radiation ($n = 30$ potential nest sites, $r = 0.94$, $P < 0.0001$). In turn, that exposure duration largely determined total incident radiation exposure ($n = 30$ potential nest sites, $r = 0.97$, $P < 0.0001$). The higher radiation input at southern sites was not a simple consequence of the lower canopy cover; because the sun was to the north, sites at the southern edge of the hydrocut received more radiation than did sites with similar canopy cover at the northern edge. Thus, even holding canopy cover constant, radiation load was higher for southern edges than northern edges (ANCOVA with canopy cover as the covariate, location as the factor, and total incident radiation as the dependent variable, $F_{4,10} = 8.15$, $P < 0.004$; Tukey-Kramer post-hoc tests show that all sites differed significantly [$P < 0.05$] except for the south edge vs. hydrocut, and the north forest vs. south forest).

These differences in exposure and orientation across our transects generated substantial variation in thermal regimes under cover items. Diel variation in temperature was considerable, but the ranking of the locations remained relatively consistent through time (Fig. 3). Thus, the southern edge of the hydrocut heated up sooner—and to higher temperatures—than did the northern edge. In consequence, temperatures underneath cover items in the middle of the hydrocut and on its southern edge were higher and more variable than were those of the northern edge. The forest sites were cooler and less variable than any other locations (Fig. 4; one-factor nested ANOVA; for mean temperature, $F_{4,15} = 6.54$, $P < 0.008$; for standard deviation, $F_{4,15} = 5.38$, $P < 0.014$; for minimum temperature, $F_{4,15} = 11.70$, $P < 0.001$; for maximum temperature, $F_{4,15} = 4.61$, $P < 0.03$).

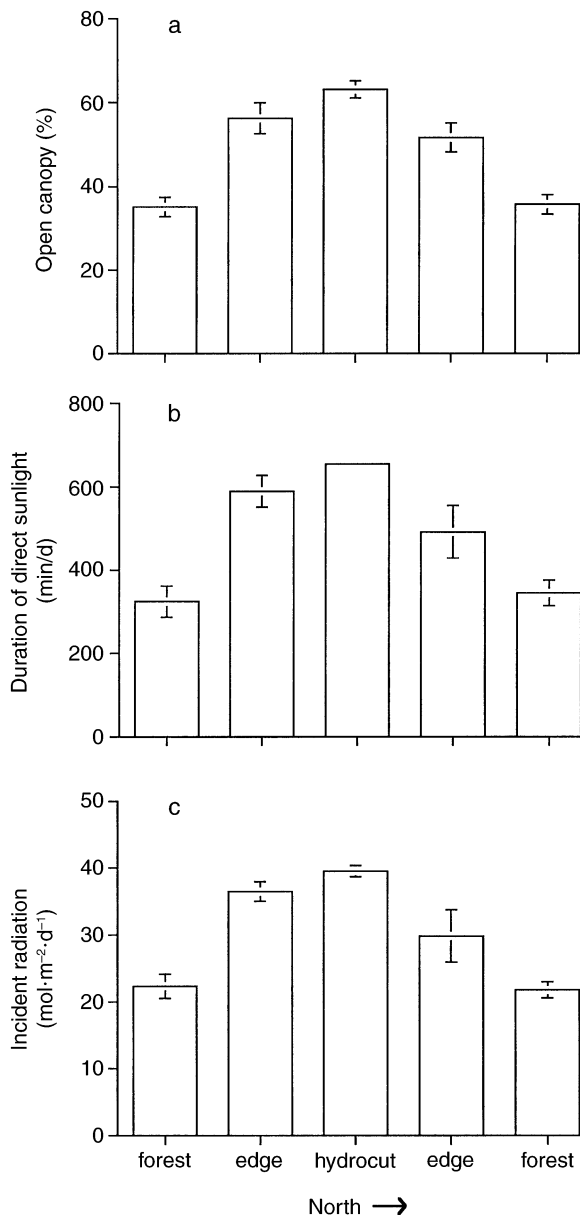


FIG. 2. Nest-site characteristics at sites across a hydrocut at Picadilly Circus in the Brindabella Range, Australia: (a) canopy cover, (b) duration of direct sun exposure, and (c) intensity of solar radiation. All histograms show means \pm 1 SE, based on two replicate sites for each type of location, along each of three parallel transects.

Is there a direct causal connection between exposure to radiation and “nest” temperature? If the thermal regime under a cover item is driven by its exposure (and thus, radiation), we expect to see a correlation between mean temperature at a site and its duration of exposure to direct sunlight (or radiation intensity). In contrast, if thermal regimes are determined mainly by insulation (type and thickness of cover objects), or by orientation or local soil type (and thus, moisture level, etc.), we would not expect to see such a correlation.

In practice, our data show that temperatures under potential cover items were affected both by the thickness of the cover item and by exposure to radiation, but the latter factor was by far the most important. Multiple regression showed that the radiation exposure had more influence on nest temperatures than did thickness (or any other attribute) of the cover item. Both the mean and the variance of nest temperature affect hatching success and hatchling phenotypes of *Bassiana* (Shine et al. 1997), so we examined both of these traits:

Mean temperature.—For 21 logs, mean temperature was predictable from a combination of cover-item thickness and radiation exposure ($r = 0.86$, $P < 0.0001$), but radiation contributed more to this result ($t = 5.39$, $P < 0.0001$) than did the shelter-item characteristics ($t = 1.14$, $P = 0.27$). The same was true for nine rocks (overall, $r = 0.94$, $P < 0.0001$; radiation, $t = 5.63$, $P < 0.002$, shelter-item thickness, $t = 1.81$, $P = 0.12$).

Variance in nest temperature.—For 21 logs, the standard deviation in temperature was predictable from a combination of cover-item thickness and radiation exposure ($r = 0.81$, $P < 0.0001$), but radiation contributed more to this result ($t = 3.82$, $P < 0.002$) than did the shelter-item characteristics ($t = 1.65$, $P = 0.12$). The same was true for nine rocks (overall, $r = 0.92$, $P < 0.004$; radiation, $t = 4.78$, $P < 0.004$, shelter-item thickness, $t = 1.98$, $P = 0.09$).

If exposure to radiation is the primary determinant of nest temperatures, then the thermal differences among different sites across the transects (Fig. 4) should disappear once radiation exposure is held constant. We can test this with ANCOVA, using radiation input as the covariate, location as the factor, and mean temperature as the dependent variable. As predicted, sites in different parts of the transect, but with the same level of exposure to solar radiation, did not differ in mean nest temperatures (slopes, $F_{4,20} = 1.25$, $P = 0.32$; intercepts, $F_{4,24} = 0.29$, $P = 0.88$). We thus conclude that temperature regimes of potential nest sites are largely determined by radiation exposure, and thus, by canopy cover.

Because we also surveyed a 5-m-diameter circle around each transect point for potential nesting sites (i.e., cover items), we can compare nest-site availability along the transects as well. These data showed a slight but nonsignificant trend for more potential nest sites (usually logs) in the forested areas than in the more open sites ($F_{4,25} = 1.49$, $P = 0.24$; see Fig. 5). In strong contrast, natural nests of *Bassiana* were concentrated in the middle of the hydrocut and along its southern edge (Fig. 5; comparing availability to usage, $\chi^2 = 128.11$, 4 df, $P < 0.0001$).

Reflecting their highly exposed locations, natural nests were similar to mid-hydrocut and south-edge sites on our transects in terms of the duration and intensity of their exposure to solar radiation (ANOVA including nests as an additional group; for duration of direct solar

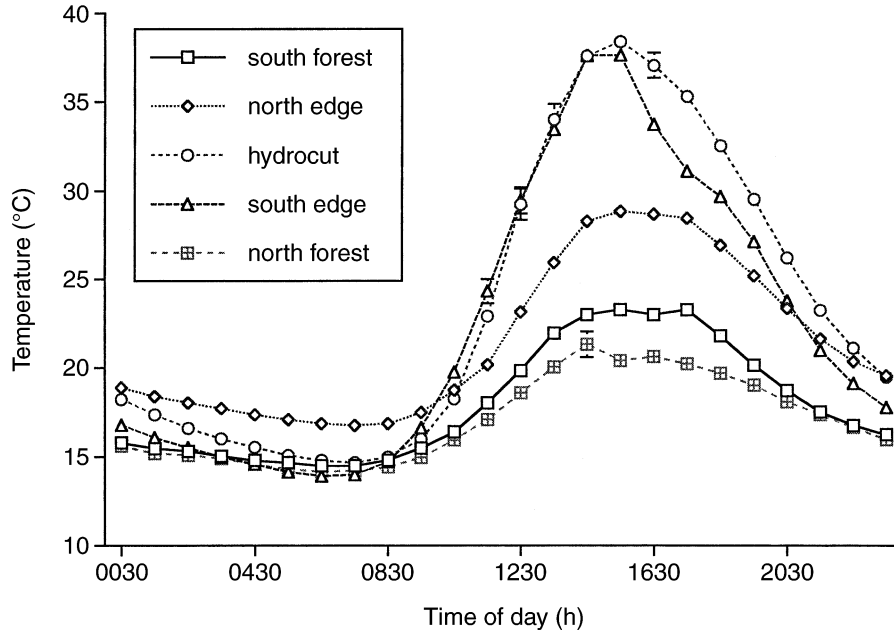


FIG. 3. Diel cycle in temperatures along one of the transects across a hydrocut at Picadilly Circus in the Brindabella Range, Australia. Data points show means \pm 1 SE, based on two replicate sites for each type of location.

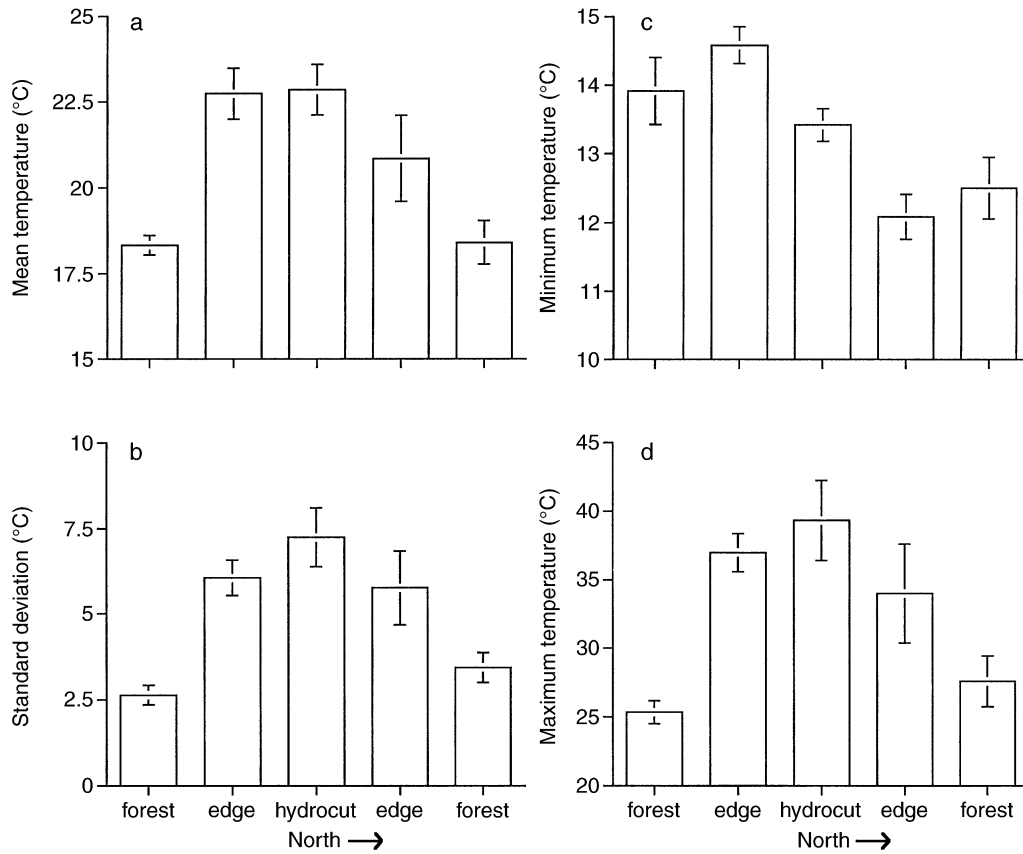


FIG. 4. Variation in temperature regimes along transects across a hydrocut at Picadilly Circus in the Brindabella Range, Australia. Histograms show means \pm 1 SE, based on two replicate sites for each type of location along each of three parallel transects.

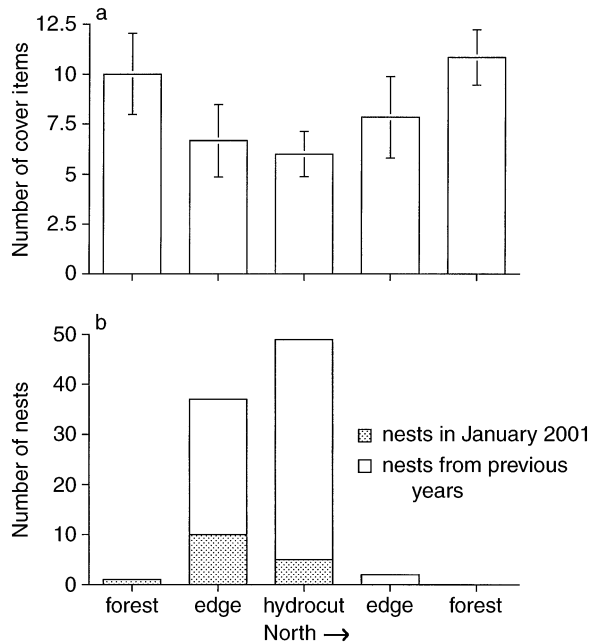


FIG. 5. Number of nest sites as a function of their location relative to a hydrocut at Picadilly Circus in the Brindabella Range, Australia. (a) Potential nest sites. The available cover items were counted during surveys in January 2001; histograms show means \pm 1 SE. (b) Lizard (*Bassiana duperreyi*) nests found under cover items; also counted during January 2001. The histograms also show total counts of nests in these areas as recorded over a longer period (1994–2001).

illumination, $F_{5,49} = 16.79$, $P < 0.0001$; for total radiation, $F_{5,49} = 22.48$, $P < 0.0001$). In both cases, Tukey-Kramer post-hoc tests showed that the characteristics of natural nests did not differ significantly from those of potential nest sites either in the middle or on the southern edge of the hydrocut ($P > 0.05$) but were higher than values recorded in the forest or on the northern edge of the clearing (all $P < 0.05$).

DISCUSSION

At our study site (Brindabella Range, Southeastern Australia), forest clearing for hydroelectric power lines (hydrocuts) has substantially modified the thermal regimes available in potential nest sites of oviparous lizards. Although the type and thickness of a cover item affect the incubation regime available beneath it, the duration and intensity of solar radiation onto the site are even more important. Clearing for the hydrocut greatly increased the amount of radiation reaching the ground, but did so in an asymmetric manner (Fig. 2). Because our study area lies well south of the equator, the sun is to the north throughout the year, and hence the southern edge of the clearing receives more radiant heating than does the northern edge (Fig. 3). Despite potential nest-site cover items (logs, rocks) being slightly more abundant in the forest, lizards actively selected sites in the middle and southern edge of the

hydrocut where warmer nests were available (Fig. 5). These data support an earlier study showing that temperatures under cover items selected by nesting *Bassiana* were higher and more variable than under a random collection of potential cover items in the same area (Shine and Harlow 1996).

Incubation trials in the laboratory and in the field indicate that the thermal minimum for effective nests (i.e., successful hatching) in *Bassiana duperreyi* is $\sim 18^\circ\text{C}$ (Shine and Harlow 1996). Embryos of this species cease to develop at temperatures $< 16.5^\circ\text{C}$ (Shine and Harlow 1996, Shine et al. 1997), close to the mean temperatures that we recorded under cover items in the forest (Fig. 4). The present study was conducted in the warmest part of the incubation period, and in the hottest summer for many years (mean incubation temperature higher than in any of the preceding seven years; R. Shine, unpublished data). Thus, in most years the temperatures available in forest nests would certainly average too low for successful hatching of this species. We conclude that nest-site availability for *Bassiana* in this area has been increased by forest clearing. Whether or not this process actually extends the species' elevational range will depend on the availability of other sites for nesting, such as might be produced by open areas from natural tree falls. However, most natural clearings would be too small to generate the kinds of thermal effects seen in the Picadilly hydrocut. Our data show that sites within 15–20 m of the north edge of the clearing were cool, and rarely used as nesting sites (Figs. 4 and 5). Thus, a gap in the canopy of < 20 m has only a minor impact on the thermal regimes underneath cover items.

Female reptiles of many taxa select nest sites based on physical cues (thermal, hydric) that relate to incubation success (Bull et al. 1988, Janzen and Paukstis 1991, Bragg et al. 2000). Because human activities may frequently modify thermal regimes of natural habitats, we suspect that nest-site availability for many taxa has been modified by anthropogenic factors. For example, the introduction of exotic vegetation can shade previously exposed sites and render them unsuitable for nesting (Congdon and Gatten 1989). Similarly, the northern latitudinal distribution of the European grass snake (*Natrix natrix*) is apparently determined by the availability of manure piles on farms, because these provide warm nest sites (Madsen 1984). Regulations requiring such piles to be enclosed (to reduce groundwater contamination) resulted in a decline of the northernmost grass-snake populations (Zuiderwijk et al. 1993).

The construction of corridors of cleared land in forested montane areas may have diverse consequences. For example, allowing oviparous taxa to reproduce successfully in high-elevation sites may indirectly affect populations of invertebrate prey, of predators, or of sympatric viviparous lizards (if these species compete with the oviparous forms). Such corridors may also

have more subtle effects on the oviparous taxa, apart from extending their range. For example, the population structure of such animals in natural areas is likely to be fragmented, centered around natural clearings that offer the only available nest sites with high enough temperatures. Corridors of continuous open habitat disrupt this metapopulation structure, and provide stronger genetic connectivity to lowland conspecifics. In turn, such connectivity may reduce opportunities for local adaptations to high-elevation conditions, and facilitate the transmission of diseases and parasites (Caughley and Sinclair 1994).

Our study also identifies two attributes of corridor design that are readily manipulated, and could substantially reduce the effects of forest clearing on thermal regimes for oviparous reptiles. The first such attribute is the width of the clearing; for example, a road divided lengthways by a vegetated median strip will have less impact on microclimate than an undivided equivalent. Second, orientation is crucial also; a narrow corridor oriented east-west would generate very different thermal profiles than would a similar corridor in a north-south orientation (Fig. 4).

Last, the effects of hydrocuts may provide a logistically feasible model system with which to predict the results of broader shifts in climate variables, as would occur with global climate shifts. Although many human activities modify thermal attributes of natural environments, they often do not mimic the kinds of processes at work during overall climate change. For example, industry-generated heating of waters can strongly modify downstream water temperatures and hence the aquatic biota (Fischer et al. 1998, Gibbons et al. 2000, Martinez-Arroyo et al. 2000), but involves an "artificial" source of heat and has little effect on adjacent terrestrial systems. In contrast, clearing for hydrocuts will modify natural determinants of thermal regimes and hence offers a better model system for detecting and interpreting small-scale effects of climate change. For example, predicted increases in solar radiation can be translated directly into predicted shifts in mean nest temperatures. From incubation temperature we can predict developmental rates, incubation periods, and hatchling phenotypes (e.g., Shine et al. 1997). Species differences in thermal optima for incubation (e.g., Shine 1999) allow calculations to be conducted separately for different taxa, and thus permit comparisons of their sensitivity to climate change. Because the ability of oviparous montane reptiles to reproduce successfully depends upon temperatures at discrete and readily identifiable nest sites, these animals may provide an unusually powerful opportunity to examine the ways in which climate factors constrain species' distributions.

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