

## Canopy Removal Restores Habitat Quality for an Endangered Snake in a Fire Suppressed Landscape

JONATHAN K. WEBB, RICHARD SHINE, AND ROBERT M. PRINGLE

In the last two centuries, European fire suppression practices have produced increases in vegetation density and canopy cover in many landscapes. Potentially, increases in canopy cover could negatively affect small populations of nocturnal reptiles that use sun-exposed shelters for diurnal thermoregulation. We hypothesized that vegetation encroachment over rock outcrops might partly explain the recent decline of Australia's most endangered snake, the Broad-headed Snake *Hoplocephalus bungaroides*. To test this hypothesis, we carried out a field study in Morton National Park, southeastern Australia. We removed overhanging vegetation from above shaded rocks and compared their subsequent usage by reptiles to control (shaded) rocks. In spring, one year after canopy removal, experimental rocks were 10.3 C hotter than control rocks and were used as diurnal retreat sites by three species of reptiles, including the endangered Broad-headed Snake and its prey (Velvet Gecko, *Oedura lesueurii*). By contrast, no reptiles use control rocks as diurnal retreat sites. Our results show that modest canopy removal (~15% increase in canopy openness) can restore habitat quality for nocturnal reptiles. Future studies are needed to examine whether controlled burns can maintain an open canopy above sandstone rock outcrops. However, until effective fire management measures are in place, sapling removal from overgrown rock outcrops could help to protect small populations of endangered reptiles.

THE impact of landscape-level vegetation dynamics over decadal time scales is an important issue for conservation biologists and restoration ecologists (Bowman, 2001). In many cases, the success of restoration projects depends on understanding how ecosystems have responded to past environmental changes (Duncan et al., 1999; Gillson and Willis, 2004). In the last two centuries, anthropogenic fire suppression and agricultural practices have caused widespread increases in tree densities and canopy cover in several North American vegetation assemblages (Myers and White, 1987; Fralish et al., 1991; Rhemtulla et al., 2002; Wright and Agee, 2004). In eastern Australia, Europeans have suppressed fire since intense bushfires in 1939 (Flannery, 1994), and increases in tree density have occurred in savannas and woodlands (Lunt, 1998; Fenham and Fairfax, 2003).

Changes in vegetation density can influence a suite of habitat attributes (perch height, canopy cover, litter depth, food availability) and environmental factors (light intensity, ground temperatures, moisture content) that in turn may influence the suitability of such habitats for animals (Huey, 1991). For this reason, changes in vegetation structure may cause some animal populations to migrate or go extinct (Pease et al., 1989). For example, several studies have implicated vegetation succession in the local extinction of reptile (Ballinger and Watts, 1995; Fitch,

1999; Jäggi and Baur, 1999) and bird populations (Holmes and Sherry, 2001). Clearly, understanding how species respond to changes in vegetation structure is crucial to understanding how and why populations persist, decline, and disperse, and for predicting responses to future changes in climate and vegetation (Hannah et al., 2002).

Because the physiology and behavior of reptiles is influenced by temperature (Huey, 1982), vegetation thickening may seriously affect nocturnal reptiles that use diurnal shelters for thermoregulation. For example, in southeast Australia, reptile species richness and abundance is much lower on heavily shaded rock outcrops than on more open sites. Over relatively short spatial scales (<100 m), nocturnal reptiles showed strong responses to vegetation structure and were absent from shaded rock outcrops (Pringle et al., 2003). Potentially, increases in tree densities and canopy cover might explain the widespread decline of the endangered Broad-headed Snake *Hoplocephalus bungaroides* from "pristine" national parks in the last 60 years (Shine et al., 1998). In Morton National Park, the population of *H. bungaroides* has declined by 30% since 1992 (Webb et al., 2002). In concert with this decline, small shrubs and trees have grown above rocks that the snakes once used as diurnal shelters. We hypothesized that snakes no longer use rocks on overgrown sites because they are too cold for thermoregulation. To test this

hypothesis we removed canopy cover from half of our samples of snake retreat sites and left the vegetation over control rocks untouched. We then monitored the usage of control versus canopy removal rocks by reptiles one year later.

#### MATERIALS AND METHODS

*Site description and study species.*—Three study sites were located on a sandstone plateau (400 m above sea level) in Morton National Park, approximately 160 km south of Sydney, in southeast Australia. During eight months of the year (April–November), Velvet Geckos, Broad-headed Snakes, and Small-eyed Snakes (*Cryptophis nigrescens*) shelter in crevices and under small stones in exposed locations on a narrow (<50 m wide) band of outcropping rock adjacent to the 30–50 m high cliffs that dissect the park from south to north (Webb and Shine, 1998). Both snake species use thin, exposed rocks for diurnal retreat sites, but conspecific males and heterospecifics are seldom found together under the same rocks (Webb et al., 2004). The vegetation on the study sites consists of an evergreen mixed eucalypt forest dominated by *Eucalyptus piperita*, *E. gummifera*, *E. agglomerata*, and *Syncarpia glomulifera*. Each spring since 1992, JKW and several herpetologists have surveyed the study sites for reptiles. During each field trip, all loose surface rocks were carefully turned, and all snakes under rocks were briefly held, measured, weighed, permanently marked with miniature PIT tags (Biomark, USA), and released at the site of capture. Each “snake rock” was given a unique number (underneath, with a paint pen) and its location recorded with a GPS. Full descriptions of the study sites, field methods, and the dates of field trips are provided elsewhere (Webb et al., 2002, 2003).

*Canopy removal experiment.*—Because our study sites were located within a “wilderness area,” we were not permitted to carry out a large-scale tree removal study. Instead, we trimmed canopy from above individual rocks to test the critical assumption that “hot rocks” are a limiting resource for reptiles. We selected 16 rocks of similar size and thickness that were shaded by emerging shrubs (*Acacia* spp. and *Banksia* spp.) and saplings (*Eucalyptus piperita* and *Syncarpia glomulifera*) and were located <5 m from the cliffs. Six of these rocks were used as retreat sites by *H. bungaroides* in 1992 and 1993, but were not used by snakes during the period 1994–2001 after emergent vegetation shaded the rocks (JKW, unpubl. data). In May 2002 we allocated three “snake rocks” and five randomly chosen rocks to

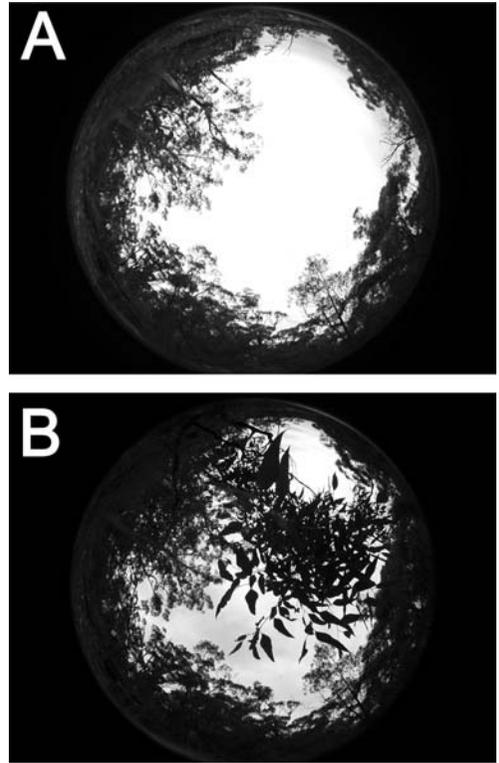


Fig. 1. Hemispherical photographs taken directly above a snake retreat-site (A) after and (B) before overhanging tree branches were removed.

control ( $n = 8$ ) and experimental ( $n = 8$ ) groups and measured their canopy cover using hemispherical photography and gap analysis (see Pringle et al., 2003 for full details). We then trimmed branches from above the experimental rocks but left the vegetation above control rocks unchanged. Analysis of hemispherical photos taken before and after canopy removal (Fig. 1) confirmed that tree trimming increased the mean canopy openness of experimental rocks by 15% (Pringle et al., 2003).

*Surveys.*—We resurveyed all control and experimental rocks in late June and August 2003, one year after canopy removal. All reptiles using rocks as shelters were captured, measured (snout-vent length, SVL), and sexed. We marked lizards with a paint pen (on the ventral surface) and injected snakes with miniature PIT tags. All reptiles were released under their rocks within 5 min of capture. To measure temperatures under rocks, we glued a miniature data logger (thermochron i-button, Dallas Semiconductor) on the underside of each rock. To ensure that each rock sat flush on the rock substrate below (with no change to crevice size) we placed each data

logger in a depression or hole on the rock's surface. Temperatures were recorded at 15-min intervals over five days in winter (25–30 June) and early spring (27–31 August) 2003.

## RESULTS

*Thermal effects of canopy removal.*—In mid-winter (June) 2003, thermal regimes underneath control and canopy removal rocks were similar (Fig. 2), and diurnal maxima and mean (24 h) temperatures did not differ between the two groups (repeated measures ANOVAs,  $P > 0.05$ ). By contrast, in early spring (August), daytime temperatures of canopy removal rocks were 10.3 C higher than those of control rocks (Fig. 2, repeated measures ANOVA, treatment  $F_{1,4} = 11.47$ ,  $P = 0.03$ , time  $F_{4,16} = 14.40$ ,  $P < 0.0001$ , time  $\times$  treatment  $F_{4,16} = 6.97$ ,  $P = 0.002$ ). However, because night time temperatures were slightly higher under control rocks (Fig. 2), mean temperatures did not differ between the two groups (repeated measures ANOVA, treatment  $F_{1,4} = 0.59$ ,  $P = 0.48$ , time  $F_{4,16} = 102.39$ ,  $P < 0.0001$ , time  $\times$  treatment  $F_{4,16} = 2.86$ ,  $P = 0.06$ ).

*Effects of canopy removal on rock usage by reptiles.*—In winter (June), reptiles used similar numbers of control and de-shaded rocks as diurnal shelters (contingency table analysis,  $\chi^2 = 0.33$ ,  $P = 0.55$ , corrected for small sample sizes). One control rock contained a Velvet Gecko (*Oedura lesueurii*), and three of eight canopy-removal rocks each contained a single gecko (two juveniles, SVLs = 29 mm, one adult male, SVL = 64 mm). By contrast, in spring (August), reptiles had colonized significantly more experimental rocks than control rocks (contingency table analysis  $\chi^2 = 9.14$ ,  $P = 0.003$ , corrected for small sample sizes; see Fig. 3). No reptiles were found under control rocks, but three species of reptiles (*Hoplocephalus bungaroides*, *Oedura lesueurii*, and *Bassiana platyotum*) had colonized seven of eight canopy removal rocks. Six rocks each contained a single reptile (adult male *O. lesueurii*, SVLs 61 and 55 mm; juvenile female *H. bungaroides*, SVLs 297 and 395 mm; juvenile *B. platyotum*, SVL 45 mm), while the seventh rock contained two juvenile *O. lesueurii* (SVLs 29 mm). One marked juvenile gecko was found under the same canopy removal rock where it was initially captured in June.

## DISCUSSION

Several studies have implicated vegetation overgrowth in the local extinction of reptile

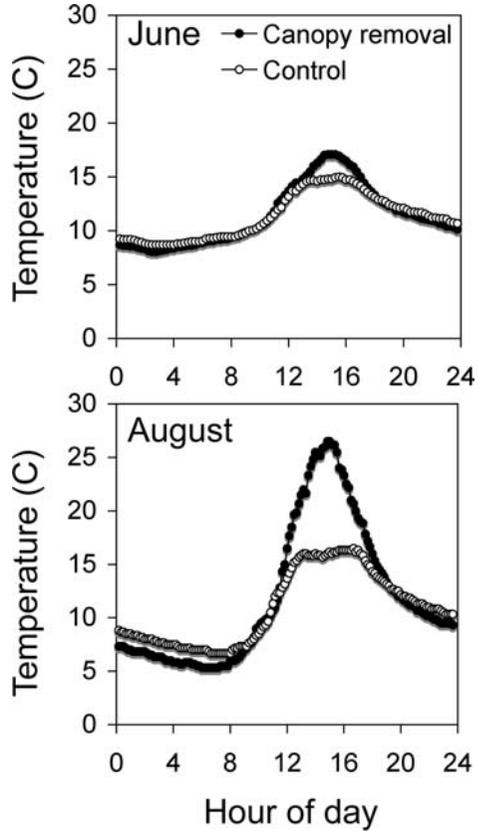


Fig. 2. Temperature profiles under control (open circles) and canopy removal rocks (solid circles) on sunny days in (upper) winter and (lower) spring 2003, one year after overhanging branches were removed from above experimental rocks.

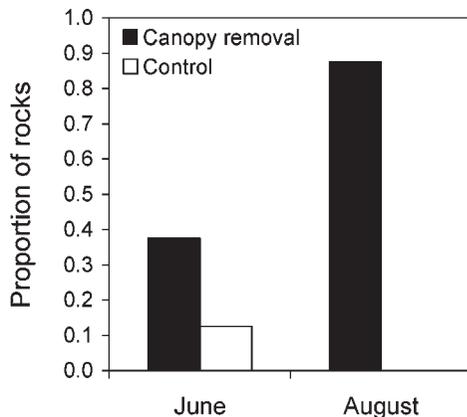


Fig. 3. Proportion of control (open bars) and canopy removal rocks (solid bars) used by reptiles during June and August 2003, one year after canopy was removed from above experimental rocks.

populations (Ballinger and Watts, 1995; Fitch, 1999; Jäggi and Baur, 1999), but the exact mechanisms responsible for these extinctions are unclear. Vegetation overgrowth could change both prey abundance and the habitat's thermal or structural quality. Our field experiment showed that canopy removal increased the thermal suitability of refugia for reptiles (Fig. 2). On sunny days in spring, experimental rocks were 10.3 C hotter than control rocks, but presumably because they lacked insulating canopy cover, experimental rocks cooled faster in the evening than control rocks and were 1.7 C colder at night (Fig. 2). During spring, significantly more reptile species (and individuals) used canopy removal rocks than control rocks as diurnal retreat-sites (Fig. 3). More importantly, juvenile Broad-headed Snakes used two rocks that were last used by snakes of this species in 1993 (according to our annual surveys) after we removed saplings from above the rocks. Thus, although nocturnal reptiles are active at night when ambient temperatures are low, they selected "hot rocks" that conferred the greatest physiological benefits during the day (e.g., increased digestive efficiency; Huey, 1991). Selection of rocks that were hotter by day but colder at night may also allow ambush foragers like *H. bungaroides* to conserve energy at night (Regal, 1967). Collectively, these results show that overgrowing forest decreases diurnal rock temperatures, which directly influences habitat suitability for nocturnal reptiles. Importantly, we confirmed that "hot rocks" are a limiting resource for nocturnal reptiles on our study sites.

Our results suggest that if vegetation encroachment continues unchecked, the abundance of thermally suitable rocks available to reptiles will decrease. Based on previous field studies, decreases in rock availability will cause populations of the Broad-headed Snake and its prey, the Velvet Gecko, to decline (Schlesinger and Shine, 1994; Shine et al., 1998). The widespread disappearance of *H. bungaroides* from "pristine" national parks and the recent decline of our study population supports this prediction. However, there is currently debate about the magnitude of vegetation change in eastern Australia, and additional studies on this topic are sorely needed (Griffiths, 2002). Nonetheless, preliminary analyses of historical photographs show that both tree density and canopy cover have increased on rock outcrops in Morton National Park over the last 60 years (Fig. 4, Pringle, unpubl. data). Because our study population of *H. bungaroides* is small (<100 snakes, Webb et al., 2002), continued vegetation thickening could contribute to the local extinction of this species.

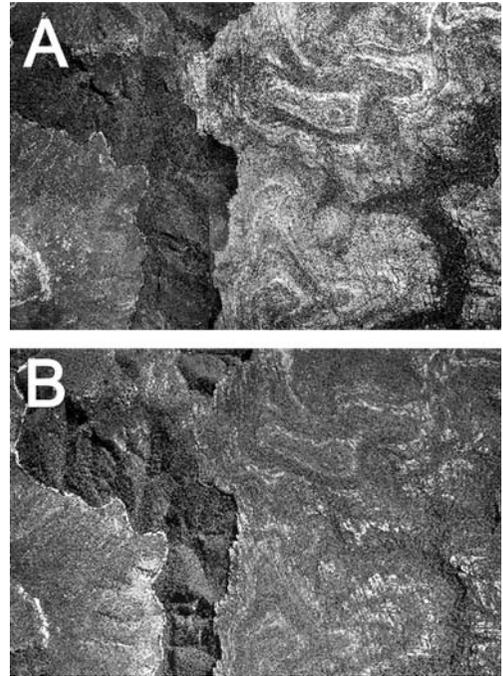


Fig. 4. Aerial photographs taken in (A) 1941 and (B) 2002 of the same sandstone plateau in Morton National Park, New South Wales, southeast Australia. Preliminary analyses of these photographs suggest that vegetation canopy cover over rock outcrops has increased during the 60-year period. However, further analyses are required to establish conclusively that vegetation thickening has occurred throughout Morton National Park over the last 60 years.

Clearly, management strategies to create open rock outcrops are urgently needed to conserve this endangered species.

The recruitment of juvenile Broad-headed Snakes and their prey (Velvet Geckos) to canopy removal rocks suggests that habitat management could be used to increase *H. bungaroides* numbers on rock outcrops where vegetation thickening has occurred. Our study demonstrates that accessible rock outcrops could be partially restored by manually removing saplings and tree branches from above shaded rocks. However, because loose surface rocks can take hundreds of years to weather from the rock substrate below, they are essentially a non-renewable resource that requires careful management (Porembski and Barthlott, 2000). Rock outcrops are also vulnerable to physical disturbance, and field studies show that outcrops damaged by humans support fewer reptiles than undamaged outcrops (Shine et al., 1998; Goode et al., 2004). Thus, mechanized techniques that are used to remove vegetation in other systems (e.g., the Florida sand

hills, Provencher et al., 2000) are unsuitable for restoring rock outcrops, because heavy vehicles and falling trees would permanently damage fragile rocks. Manual tree pruning and sapling removal is less destructive, but due to logistical difficulties, it is not suitable for restoring isolated rock outcrops.

Prescribed fire is currently used to conserve fire-suppressed habitats (Duncan et al., 1999), and could be used to restore overgrown rock outcrops or other important snake habitats (e.g., over wintering dens). In Australia, low intensity burns may not increase canopy openness on sites with high densities of larger stems because most trees are fire adapted (Gill et al., 1981). In such cases, thinning (removal of stems) and controlled burns of higher intensity are needed to maintain an open canopy. The efficacy of burning in keeping understory open will also depend on the size and location of burnt patches. In southeast Australia, eastern grey kangaroos preferentially graze recently burnt patches and at moderate densities they can prevent sapling and shrub regeneration (Meers and Adams, 2003). By burning small patches around target rock outcrops and leaving adjacent forests untouched, managers could promote kangaroo grazing near rock outcrops, thereby preventing vegetation encroachment, while still maintaining refuges for species that require dense understory vegetation (e.g., eastern bristle bird, Baker, 2000). Before fire can be used to restore rock outcrops, land managers should use predictive models to determine the optimal fire regime (frequency, intensity and season) for conserving biodiversity of target rock outcrops. For example, low intensity fires are currently used to reduce fuel loads in the Sydney region, but their frequency (5 years) is incompatible for conserving plant biodiversity (Morrison et al., 1996; Bradstock et al., 1998). At present, very little is known about the effects of prescribed burns on reptile diversity and abundance (Whelan, 2002). Obviously, to conserve both plants and animals on rock outcrops, we urgently need field studies to determine how fire intensity, season, and return interval influences reptile assemblages.

Finally, we note that many other plants and animals may face extirpation as a result of vegetation encroachment. For example, some of Morton National Park's endangered plants could suffer from light exclusion or competition that accompanies canopy closure (e.g., Carlsen et al., 2000; Munk et al., 2002). The endangered Brush-tailed Rock Wallaby (*Petrogale penicillata*) may also be threatened by vegetation thickening. Previous discussions of the conservation of the

charismatic rock wallabies have focused on predator control (chiefly foxes, *Vulpes vulpes*, Hone, 1999), but multiple causes for the Brush-tailed Rock Wallaby decline are more likely. *Petrogale penicillata* favors sunny north-facing cliff aspects and basks during winter, and it may require a mosaic of open grassy areas for basking, foraging, and for detecting predators. Prior to European settlement, several Aboriginal tribes used our study plateau as a major traveling route between the coast and western ranges (Sneddon, 1988), and they probably burnt the plateau both to facilitate travel and to create open grassy habitats suitable for macropod prey (Flannery, 1994). If foxes are wholly to blame for the extinction of *P. penicillata*, why did rock wallabies persist on our study sites until 1995 (Webb, pers. obs.), more than 150 years after fox introduction?

In conclusion, we suggest that canopy removal is an effective tool for conserving reptile habitats on accessible rock outcrops where vegetation overgrowth is a serious problem. Prescribed burns should be used to maintain an open canopy above rock outcrops in more remote areas. Sandstone rock outcrops contain many endemic species and have a high conservation value, yet scientists have studied only a handful of species (Recher et al., 1993; Goldsbrough et al., 2003). Future experimental studies are urgently needed to investigate the efficacy of various management tools (fire, understory clearing, canopy removal) for conserving the flora and fauna of these important and understudied ecosystems.

#### ACKNOWLEDGMENTS

We thank J. Thomas and M. Wall for their assistance in the field, and the University of Sydney and the Australian Research Council for financial assistance. This study was carried out in accordance with the University of Sydney Animal Care and Ethics Committee (Approval LO4/5-2003/2/3753 to J. Webb) and under a scientific license from the New South Wales National Parks and Wildlife Service (license S10029 to J. Webb).

#### LITERATURE CITED

- BAKER, J. R. 2000. The eastern bristlebird: cover dependent and fire sensitive. *Emu* 100:286–298.
- BALLINGER, R. E., AND K. S. WATTS. 1995. Path to extinction: impact of vegetational change on lizard populations on Arapaho Prairie in the Nebraska Sandhills. *Am. Midl. Nat.* 134:413–417.
- BOWMAN, D. M. J. S. 2001. Future eating and country keeping: what role has environmental history in the management of biodiversity? *J. Biogeogr.* 28:549–564.

- BRADSTOCK, R. A., M. BEDWARD, B. J. KENNY, AND J. SCOTT. 1998. Spatially explicit simulation of the effect of prescribed burning on fire regimes and plant extinctions in shrublands typical of south-eastern Australia. *Biol. Conserv.* 86:83–95.
- CARLSEN, T. M., J. W. MENKE, AND B. M. PAVLIK. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restor. Ecol.* 8:18–29.
- DUNCAN, B. W., V. L. LARSON, D. L. BREININGER, AND P. A. SCHMALZER. 1999. Coupling past management practice and historic landscape change on John F. Kennedy Space Center. *Landscape Ecol.* 14: 291–309.
- FENSHAM, R. J., AND R. J. FAIRFAX. 2003. Assessing woody vegetation cover change in north-west Australian savanna using aerial photography. *Int. J. Wildland Fire* 12:359–367.
- FITCH, H. S. 1999. A Kansas Snake Community: Composition and Change over Fifty Years. Krieger, Malabar, Florida.
- FLANNERY, T. F. 1994. *The Future Eaters: An Ecological History of the Australasian Lands and People*. Reed Books, Chatswood, New South Wales, Australia.
- FRALISH, J. S., F. B. CROOKS, J. L. CHAMBERS, AND F. M. HARTY. 1991. Comparison of pre-settlement, second-growth and old-growth forest on six site types in the Illinois Shawnee Hills. *Am. Midl. Nat.* 125:294–309.
- GILL, A. M., R. H. GROVES, AND I. R. NOBLE. 1981. Fire and the Australian Biota. Australian Academy of Science, Canberra, Australia.
- GILLSON, L., AND K. J. WILLIS. 2004. As earth's testimonies tell: wilderness conservation in a changing world. *Ecol. Lett.* 7:990–998.
- GOLDSBROUGH, C. L., D. F. HOCHULI, AND R. SHINE. 2003. Invertebrate biodiversity under hot rocks: habitat use by the fauna of sandstone outcrops in the Sydney region. *Biol. Conserv.* 109:85–103.
- GOODE, M. J., D. E. SWANN, AND C. R. SCHWALBE. 2004. Effects of destructive collecting practices on reptiles: a field experiment. *J. Wildl. Manage.* 68:427–432.
- GRIFFITHS, T. 2002. How many trees make a forest? Cultural debates about vegetation change in Australia. *Aust. J. Bot.* 50:375–389.
- HANNAH, I., G. F. MIDGLEY, AND D. MILLAR. 2002. Climate change-integrated conservation strategies. *Global Ecol. Biogeogr.* 11:485–495.
- HOLMES, R. T., AND T. W. SHERRY. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk* 118:589–609.
- HONE, J. 1999. Fox control and rock-wallaby population dynamics: assumptions and hypotheses. *Wildl. Res.* 26:671–673.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles, p. 25–91. *In: Biology of the Reptilia. Physiology C. Physiological ecology.* Vol. 12. C. Gans and F. H. Pough (eds.). Academic Press, New York.
- . 1991. Physiological consequences of habitat selection. *Am. Nat.* 137:S91–S115.
- JÄGGI, C., AND B. BAUR. 1999. Overgrowing forest as a possible cause for the local extinction of *Vipera aspis* in the northern Swiss Jura Mountains. *Amphibia-Reptilia* 20:25–34.
- LUNT, I. D. 1998. Two hundred years of land use and vegetation change in a remnant coastal woodland in southern Australia. *Aust. Ecol.* 46:629–647.
- MEERS, T., AND R. ADAMS. 2003. The impact of grazing by eastern grey kangaroos (*Macropus giganteus*) on vegetation recovery after fire at Reef Hills Regional Park, Victoria. *Ecol. Manage. Restor.* 4:126–132.
- MORRISON, D. A., R. T. BUCKNEY, B. J. BEWICK, AND C. J. CARY. 1996. Conservation conflicts over burning brush in south-eastern Australia. *Biol. Conserv.* 76:167–175.
- MUNK, L. M., A. L. HILD, AND T. D. WHITSON. 2002. Rosette recruitment of a rare endemic forb (*Gaura neomexicana* Subsp. *coloradensis*) with canopy removal of associated species. *Restor. Ecol.* 10:122–128.
- MYERS, R. L., AND D. L. WHITE. 1987. Landscape history and changes in sandhill vegetation in North-Central and South-Central Florida. *Bull. Torrey Bot. Club* 114:21–32.
- PEASE, C. M., R. LANDE, AND J. J. BULL. 1989. A model of population growth, dispersal and evolution in a changing environment. *Ecology* 70:1657–1664.
- POREMBSKI, S., AND W. BARTHOLOTT. 2000. Inselbergs: Biotic Diversity of Isolated Rock Outcrops in Tropical and Temperate Regions. Springer, Berlin.
- PRINGLE, R. M., J. K. WEBB, AND R. SHINE. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84:2668–2679.
- PROVENCHER, L., B. J. HERRING, D. R. GORDON, H. L. RODGERS, G. W. TANNER, L. A. BRENNAN, AND J. L. HARDESTY. 2000. Restoration of northwest Florida sandhills through harvest of invasive *Pinus clausa*. *Restor. Ecol.* 8:175–185.
- RECHER, H. F., P. A. HUTCHINGS, AND S. ROSEN. 1993. The biota of the Hawkesbury-Nepean catchment: reconstruction and restoration. *Aust. Zool.* 29: 3–41.
- REGAL, P. J. 1967. Voluntary hypothermia in reptiles. *Science* 155:1551–1553.
- RHEMTULLA, J. M., R. J. HALL, E. S. HIGGS, AND S. E. MACDONALD. 2002. Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada. *Can. J. For. Res.* 32:2010–2021.
- SCHLESINGER, C. A., AND R. SHINE. 1994. Choosing a rock: perspectives of a bush-rock collector and a saxicolous lizard. *Biol. Conserv.* 67:49–56.
- SHINE, R., J. K. WEBB, M. FITZGERALD, AND J. SUMNER. 1998. The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides*. *Wildl. Res.* 25:285–295.
- SNEDDON, R. 1988. The Aborigines and the landscape, p. 48–63. *In: Fitzroy Falls and Beyond: a Guide to the Fitzroy Falls, Bundanoon Shoalhaven, Ettrema Wilderness, Northern Morton National Park and Bungonia State Recreation Area.* Budawang Committee (eds.). 1988, Budawang Committee, Eastwood, New South Wales, Australia.

- WEBB, J. K., AND R. SHINE. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biol. Conserv.* 86: 233–242.
- , B. W. BROOK, AND R. SHINE. 2002. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecol. Res.* 17:59–67.
- , ———, AND ———. 2003. Does foraging mode influence life history traits? A comparative study of growth, maturation and survival of two species of sympatric snakes from southeastern Australia. *Austr. Ecol.* 28:601–610.
- , R. M. PRINGLE, AND R. SHINE. 2004. How do nocturnal snakes select diurnal retreat-sites? *Copeia* 2004:919–925.
- WHELAN, R. J. 2002. Managing fire regimes for conservation and property protection: an Australian response. *Conserv. Biol.* 16:1659–1661.
- WRIGHT, C. S., AND J. K. AGEE. 2004. Fire and vegetation history in the eastern cascade mountains, Washington. *Ecol. Appl.* 14:443–459.

(JKW, RS) SCHOOL OF BIOLOGICAL SCIENCES, THE UNIVERSITY OF SYDNEY, NEW SOUTH WALES 2006, AUSTRALIA; AND (RMP) DEPARTMENT OF BIOLOGICAL SCIENCES, STANFORD UNIVERSITY, STANFORD, CALIFORNIA 94305. E-mail: (JKW) jwebb@bio.usyd.edu.au. Send reprint requests to JKW. Submitted: 13 Feb. 2005. Accepted: 4 May 2005. Section editor: M. J. Lannoo.