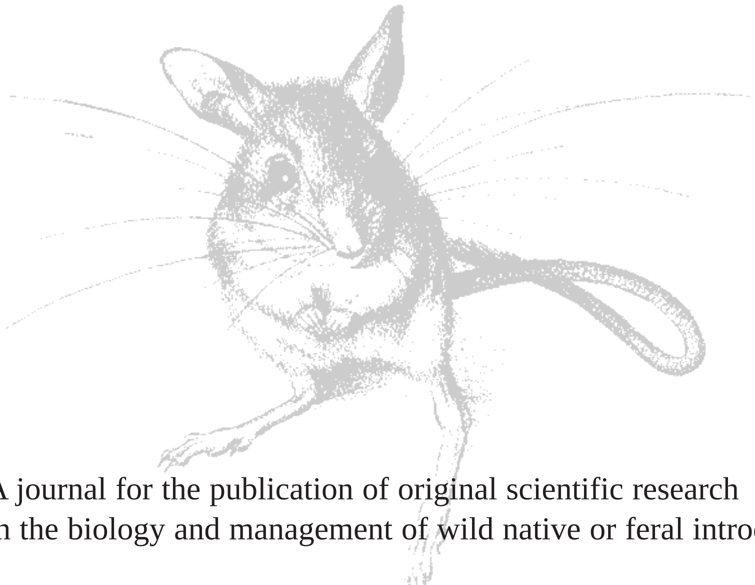
CSIRO PUBLISHING

Wildlife Research

Volume 25, 1998



A journal for the publication of original scientific research
in the biology and management of wild native or feral introduced vertebrates

www.publish.csiro.au/journals/wr

All enquiries and manuscripts should be directed to
Wildlife Research
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood
Vic. 3066
Australia
Telephone: 61 3 9662 7622
Facsimile: 61 3 9662 7611
Email: david.morton@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO and the
Australian Academy of Science

© CSIRO 1998 *Wildlife Research*, 1998, **25**, 285–295

The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides* (Serpentes : Elapidae)

Richard Shine[A], *Jonathan K. Webb, Mark Fitzgerald and Joanna Sumner*

School of Biological Sciences A08, The University of Sydney, NSW 2006, Australia.
[A]To whom correspondence should be addressed. email: rics@bio.usyd.edu.au

Abstract

We examined the impact of habitat degradation (removal of surface rocks) on an endangered snake species (*Hoplocephalus bungaroides*, Elapidae) at 23 sites in south-eastern Australia, by quantifying the impact of rock removal on (i) the availability of suitable shelter-sites for the snakes and their major prey species (the velvet gecko, *Oedura lesueurii*), and (ii) the numbers of snakes and geckos. Our survey showed that both the snakes and the geckos prefer rocks lying on other rocks, rather than on soil, and select rocks of particular sizes. The rocks removed by bush-rock collectors overlap considerably in size (diameter and thickness) and substrate (rock on rock) with those used by broad-headed snakes and velvet geckos. Multivariate path analysis suggests that population densities of broad-headed snakes (as measured by capture rates) may be determined primarily by gecko numbers, which in turn depend upon availability of suitable rocks. In some sites, rock numbers were substantially reduced by anthropogenic disturbance. Thus, our survey data suggest that bush-rock removal has contributed to the endangerment of *H. bungaroides*.

Introduction

The essential first step in halting the decline of an endangered species towards extinction is to identify the reasons for that decline. Natural habitats in south-eastern Australia have been profoundly modified since the invasion by Europeans 200 years ago. In this study, we focus on one such modification: the removal of surface rocks from bushland, to be used primarily for ornamentation of suburban gardens. Rock removal has been implicated as a significant contributor to the decline of the broad-headed snake (*Hoplocephalus bungaroides*) (Krefft 1869; Hersey 1980; Shine and Fitzgerald 1989). This small, brightly coloured nocturnal elapid snake is restricted to sandstone habitats within a 150-km radius from Sydney. It was once common in the Sydney area, but significant range reductions have prompted its inclusion on the NSW National Parks and Wildlife Service's list of 'threatened species' (Lunney and Ayers 1993).

The evidence that bush-rock removal has been a causal factor in the decline of *H. bungaroides* is weak, however. This inference is based only on the putative reliance of broad-headed snakes on sandstone rocks for shelter-sites. Logic suggests that the impact of rock removal may be relatively unimportant if the snakes are able to use alternative shelter-sites (e.g. tree-hollows and deep crevices in rock outcrops: Webb and Shine 1997*a*, 1997*b*). Hence, processes other than rock removal may be the actual cause of decline of *H. bungaroides*. For example, these small snakes may be vulnerable to predation by feral animals such as cats and foxes, which have been identified as major factors in the extinction of native mammals (Dickman 1994). Collection of snakes by amateur herpetologists might also contribute to endangerment of this species (Burbidge and Jenkins 1984; Cogger *et al*. 1993). Over a considerable period from the 1950s to the 1970s, these brightly-coloured snakes were collected in large numbers to be kept as pets (H. G. Cogger, pers. comm.). Occasional seizures of illegally collected specimens by wildlife authorities confirm that the practice has continued throughout the 1980s and 1990s, albeit to a lesser degree (L. Lewellyn, personal communication). Other threatening processes possibly involved in the decline of *H. bungaroides* include habitat clearance and urban development (Hoser 1991; Cogger *et al*. 1993).

1035-3712/98/030285

In order to identify the processes that actually contribute to the decline of an endangered taxon via habitat degradation, we need to look in detail at (i) the ways in which the endangered taxon uses the habitat, (ii) the ways in which the anthropogenic process modifies the habitat, and (iii) the relationship between the intensity of that 'threatening' process and the abundance of the endangered species. Information on the first of these issues is available from our detailed studies of habitat use by *H. bungaroides* in Morton National Park, south of Sydney (Webb 1996, Webb and Shine 1997*a*, 1997*b*). This paper focuses on the two latter issues: the degree of habitat degradation caused by bush-rock removal, and the response of broad-headed snakes and their prey to this disturbance. To clarify these topics, we surveyed habitat and herpetofaunal characteristics of most of the sites from which *H. bungaroides* has been reliably recorded to occur.

Methods

Our survey was designed to provide quantitative information on the availability of habitat suitable for *H. bungaroides* at each site, on the nature and degree of anthropogenic disturbance to that habitat, and on the abundance of reptiles (including broad-headed snakes and their prey) at each site. We surveyed 23 sites over the period from May to October 1994 (Table 1). Survey areas were chosen to cover the known range of the species, based on locality records of all preserved specimens in the Australian Museum, except for those that now are completely transformed by urban development (e.g. 'on the shores of Middle Harbour, and of the Lane Cove and Parramatta inlets, many specimens occur': Krefft 1869, p. 57). The choice of specific

Table 1. Sites surveyed for broad-headed snakes

Each site was less than 1 km2 in area. Precise locations of sites are not given because this endangered species is vulnerable to collection; thus, we provide only the name of the 1:25 000 topographic map in which each site is located. Each transect was 30 m long; see text for description of survey methods

Site name	Date	Map name	Number of transects	Person-hours spent searching	Number of broad-headed snakes found
Stoney Creek	31.v.94	Wirraba	2	2	1
Jacobs Hollow	1.vi.94	Putty	2	3	0
Stoney Swamp	1.vi.94	Wirraba	2	3	0
Kings Water Hole	1.vi.94	Wirraba	3	6	1
Robertson's Knoll	6.vi.94	Port Hacking	2	2	0
Wise's Ridge Road	6.vi.94	Otford	4	2	0
Flat Rock Creek	5.x.94	Port Hacking	3	2	0
Castle Rock	28.vi.94	Corang	unsuitable	–	–
Yarramunmun Fire Trail	21.ix.94	Sassafras	2	1	4
Monkey Gum Road, site 1	29.vi.94	Sassafrass	4	2	0
Monkey Gum Road, site 2	29.vi.94	Sassafrass	4	2	1
Thomas Point	30.vi.94	Yalwal	2	3	0
Bass-wood Trail	30.vi.94	Yalwal	unsuitable	–	–
Wanganderry Lookout	5.vii.94	Hilltop	4	4	0
Linden Reservoir	2.ix.94	Katoomba	4	2	1
Evans Lookout	4.ix.94	Katoomba	unsuitable	–	–
Double Hill	6.ix.94	Jamison	2	2	0
Newnes State Forest	5.ix.94	Cullen Bullen	3	3	2
O'Hares Creek, site 1	8–9.ix.94	Appin	3	7.5	0
O'Hares Creek, site 2	10.ix.94	Appin	1	4	1
Mt Wiadgon	11.ix.94	Wattle Flat	unsuitable	–	–
Wollemi National Park	13.ix.94	Coricudgy	2	4	0
Bare Rock Bluff	13.ix.94	Coricudgy	unsuitable	–	–

sites was based on topographical features (e.g. cliffs or rock outcrops) from 1:25 000 topographic maps, or from information supplied by amateur herpetologists.

Despite historical records of the occurrence of this species, five of the sites were clearly unsuitable for broad-headed snakes. They either lacked suitable exfoliating rocks due to their geology, or were too highly degraded by human activities, or were so overgrown by vegetation that they were too cool and damp for *H. bungaroides*. After searching unsuccessfully for snakes at these sites, we excluded the areas from further analyses. At each of the remaining 18 sites, we randomly selected one or two areas of exposed ridge-top and marked out 30-m-long transects with a measuring tape. The total number of transects (100 m apart) depended on the area of the outcrop. In all, 49 transects were set out.

All rocks lying under the tape measure along each transect were measured for the following characteristics: length, width, thickness, substrate type (rock, soil or both), percentage vegetative cover over the rock, and whether the rock had been disturbed or removed. Where possible, we also estimated dimensions of removed rocks. This was often practicable for rock diameters (because a measurable 'scar' remains on the substrate after the rock is removed), but often impossible for rock thicknesses. All rocks on transects were lifted (unless they were too large) and any vertebrates found were recorded and identified to species level.

Once transect surveys were completed, an opportunistic survey for reptiles was carried out in the immediate vicinity of the transect by two people. The overall time spent looking for reptiles varied among sites (see Table 1). Opportunistic surveys involved lifting rocks and searching in crevices, although active reptiles were also recorded. The transects provided information on physical characteristics of the habitat but, because they were unlikely to reveal rare animals such as broad-headed snakes, we needed to search over a larger area than the transects alone in order to quantify snake abundance.

Analysis

These data were analysed to answer the following questions:

What are the characteristics of rocks used by reptiles, compared with those removed by rock-collectors?

The degree of overlap in characteristics of the rocks used by the snakes and their prey, compared with those removed by rock-collectors, may affect the impact of rock removal on the reptiles. Thus, we compared the characteristics of removed rocks with those of the rocks used by broad-headed snakes and velvet geckos, using one-factor analysis of variance.

Given that broad-headed snakes occur on an outcrop (or have been previously recorded to occur there), does bush-rock removal affect the abundance of the snakes on the outcrop?

The abundance of snakes at a given site is likely to be influenced by a number of factors. For example, we might expect snakes to be more numerous where there are many rocks (especially, rocks of the correct size and type), abundant prey (geckos), and little disturbance by humans. These factors are themselves intercorrelated – geckos are likely to be more abundant where rocks are common, and rock-collectors are also likely to be attracted to sites with many rocks.

Multivariate path analysis is well-suited to addressing the problem of intercorrelated data (e.g. Kingsolver and Schemske 1991; King 1993). The analysis uses the underlying covariance matrix in the data to try to tease apart correlations due to direct causation from those that arise secondarily as consequences of other correlations among variables. The technique relies upon an *a priori* hypothesis, the path diagram. Variables in the path diagram are linked by path coefficients, which are standardised partial regression coefficients. The path coefficient linking two variables expresses the strength of the association between the two variables after effects of the other relevant variables have been removed. Because all variables are standardised (to a mean of zero and a standard deviation of 1.0) prior to analysis, the magnitude of the path coefficient indicates the expected change in the dependent variable for an increment of one standard deviation in the independent variable (e.g., a path coefficient of –0.50 means that we would expect a decrease of half an s.d. in the dependent variable for an increment of one s.d. in the independent variable). We view path analysis as an exploration of the degree to which the data fit particular causal hypotheses, rather than a statistically rigorous attempt to discriminate among alternative pathways (Kingsolver and Schemske 1991).

For each site, raw transect data were used to calculate:

(a) the mean number of rocks per metre of transect;
(b) the mean number of ‘snake rocks’ per metre of transect [‘snake rocks’ were rocks that we classified as being highly suitable for broad-headed snakes (Webb and Shine 1997*a*, 1997*b*), namely rocks that lay on rock substrates, were <15 cm thick, and had <30 % vegetated cover over them];
(c) the mean percent of such rocks that had been removed by rock-collectors or other persons; and
(d) the mean percent of such rocks that had been disturbed (i.e. moved, but not removed), presumably by reptile collectors.

Data from the opportunistic surveys were used to calculate the number of broad-headed snakes, velvet geckos and all lizards (geckos plus other lizards) found at each site per person-hour of searching. Collectively, these two data sets formed the basis of the path analysis (see Table 2).

Results

Characteristics of rocks used by humans and reptiles

We have data on 92 rocks under which velvet geckos were found (during opportunistic surveys), 90 rocks under which broad-headed snakes were found (combining data from this survey with those from Webb and Shine, unpublished), and 74 rocks that had been removed by bush-rock collectors. This latter sample included 11 rocks that had been removed from their original position and then placed in a pile (at one site) by the rock-collectors, and 63 rocks (at other sites) that had been physically removed. The diameters of the 63 removed rocks were estimated from the ‘scars’ they had left on the substrate. We were able to estimate the thicknesses of 54 of these rocks, plus those of the 11 rocks that were displaced but not removed. These data were analysed to compare the attributes of rocks used by reptiles to those taken by humans:

Substrate upon which the rock is lying

All of the rocks under which we found broad-headed snakes and velvet geckos were lying at least partly on rock substrates, although 26% of rocks sheltering velvet geckos lay on soil as well as rock. Rocks lying on soil were abundant at all of the sites we visited, but these rocks were not used by snakes and geckos. At least 85% of our sample of the rocks taken by humans had been lifted from rock substrates. Because the remaining 15% were found stacked in a pile, we do not know their original locations. Rocks lying on soil may be less attractive to bush-rock collectors, because they are difficult to remove. Unfortunately, rocks collected from soil do not leave long-term obvious scars, so we do not know whether such rocks have been collected in the past. Nevertheless, it is clear that many of the rocks that had been removed by humans had substrates suitable for both broad-headed snakes and velvet geckos.

Rock diameter

The diameters of rocks taken by bush-rock collectors were similar to those of the rocks used by velvet geckos and broad-headed snakes (Fig. 1). Nonetheless, analysis of variance revealed that the mean diameters of rocks from the three groups were significantly different (one-factor ANOVA, $F_{2,253} = 7.684$, $P < 0.001$). *Post hoc* tests showed that the mean diameters of rocks used by broad-headed snakes were significantly greater than diameters of rocks used by velvet geckos (Scheffé *F*-tests, mean difference = 8.29, $P < 0.001$), but that the diameters of rocks taken by humans were not significantly different from the diameters of rocks used by either broad-headed snakes or velvet geckos ($P > 0.05$).

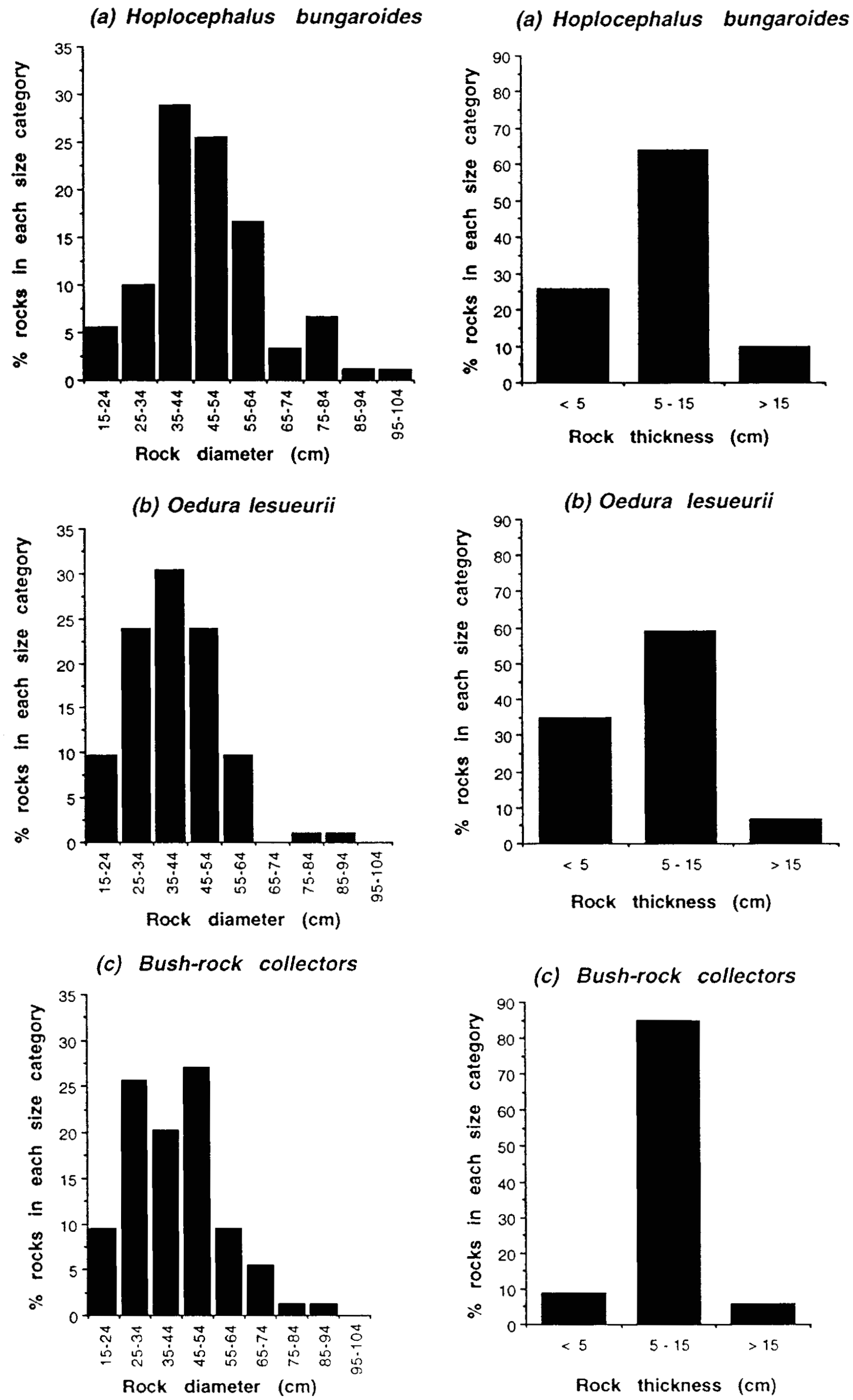


Fig. 1. Distribution of rock dimensions used by (a) broad-headed snakes, (b) velvet geckos, and (c) those removed by bush-rock collectors. Graphs on left show rock diameter, and graphs on right show rock thickness.

Rock thickness

Most of the rocks (85%) removed by bush-rock collectors appear to be of moderate thickness (5–15 cm: Fig. 1), whereas broad-headed snakes and velvet geckos used thin (<5 cm thick) as well as moderately thick (5–15 cm) rocks (Fig. 1). The mean diameters of rocks from the three groups were not significantly different (one-factor ANOVA, $F_{2,253} = 2.208$, $P > 0.05$).

Collectively, these results show that rock-collectors remove rocks that lie on other rocks, and that are similar in size (diameter and thickness) to those used by broad-headed snakes and velvet geckos. Hence, bush-rock removal may have a negative effect on broad-headed snakes and/or their prey. This possibility was further investigated using multivariate path analysis.

Path analysis of factors that influence snake abundance

A multivariate path diagram was constructed to incorporate hypotheses regarding the determinants of distribution and abundance of geckos and broad-headed snakes (Fig. 2). This analysis allowed us to address the following questions:

What determines the degree of human interference at a site (removal and disturbance of rocks)?

The intensity of activities of bush-rock collectors (as assessed by the proportion of rocks removed from the site) was only weakly correlated with the number of rocks originally present on the outcrop (path coefficient = 0.02). This result, although counter-intuitive at first sight, is consistent with an earlier study showing that other factors (such as size of rocks, and the proximity of the outcrop to vehicle access) are important influences on bush-rock removal (Schlesinger and Shine 1994*a*). Most rocks are too small for commercial use. Thus, the total number of rocks gives only a weak indication of the area’s vulnerability to bush-rock removal.

Interestingly, the analysis also reveals a negative correlation between the intensity of bush-rock removal activities and the intensity of other disturbance to rocks on the site. Undoubtedly, a significant contributor to rock displacement (without removal) is the activity of people looking for reptiles. The data suggest that such disturbance tends to be focussed on areas that have not been subject to prior removal of rocks (path coefficient = –0.22), and where there are many rocks still available to turn (path coefficient for number of rocks = 0.37).

What determines habitat suitability for broad-headed snakes?

The overall number of rocks, regardless of their size, was a poor predictor of the number of rocks suitable for broad-headed snakes (path coefficient = 0.05). That is, an increase of 1 s.d. in the total number of rocks in an outcrop corresponded to an increase of only 0.05 s.d.s in the number of rocks suitable for use by broad-headed snakes. Instead, spatial variation in the number of ‘suitable’ rocks in an area was largely explained by the operation of two factors: the number of suitable rocks originally present (path coefficient = 1.01) discounted by the number of rocks removed by humans (–0.53), with little unexplained residual variance (U = 0.34).

What determines prey abundance?

Lizards are the main prey of broad-headed snakes (Webb and Shine 1997*a*). Velvet geckos (*Oedura lesueurii*) are the most abundant lizards in these sandstone outcrops, and are by far the most important prey type for juvenile broad-headed snakes (Webb 1996; Webb and Shine 1998). The number of large rocks in sunny positions, lying on other rocks (i.e. ‘snake rocks’) in an outcrop was a strong predictor of the numbers of both geckos (path coefficient = 1.04) and other lizards (0.70). As might be expected *a priori*, the number of lizards was also negatively affected by disturbance (–0.36 for geckos, –0.21 for other lizards). That is, sites that had suffered more disturbance tended to have fewer lizards, independent of the numbers of rocks actually removed. Some of this reduction in lizard numbers may reflect actual capture and removal of specimens, whereas another component may be due to habitat degradation or emigration of lizards following disturbance.

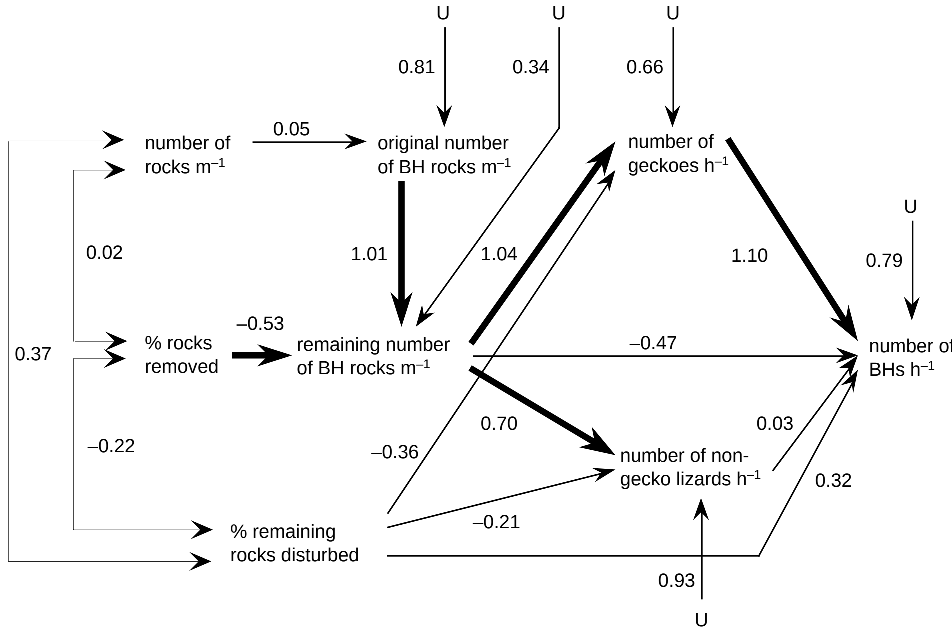


Fig. 2. Path diagram for multivariate analysis of determinants of abundance of broad-headed snakes. 'BH' = broad-headed snake; 'BH rocks' = rocks with characteristics similar to those frequently used by broad-headed snakes; see text for other definitions, for explanation of techniques used, and for interpretation of results. Thick arrows show path coefficents >0.50. Double-headed arrows represent correlation without causation; unidirectional arrows depict causal influences; and the component 'U' gives a measure of the amount of variation in the dependent variable that is not explained by the combination of independent variables (Kingsolver and Schemske 1991; King 1993).

What factors determine the abundance of broad-headed snakes?

By far the best predictor of the abundance of broad-headed snakes on a site was the abundance of velvet geckos (Fig. 2: path coefficient = 1.10): that is, an increase of 1 s.d. in gecko abundance was associated with a similar increase in the numbers of broad-headed snakes. In contrast, the numbers of other lizard species had little effect on numbers of snakes (path coefficient = 0.03).

If the path analysis is repeated without incorporating lizard abundances (i.e. looking only at physical characteristics of the habitat), there is a strong positive effect of rock numbers on abundance of broad-headed snakes (coefficient = 0.66). The proportion of 'snake rocks' removed from the site has a negative effect on numbers of broad-headed snakes (coefficient = –0.40) whereas the level of habitat disturbance has a minor impact (–0.03). The more inclusive analysis in the above paragraph suggests, however, that the positive effect of rock availability on snake numbers (more habitat = more snakes) is due primarily to an indirect pathway (more habitat = more geckos = more snakes) rather than to a simple direct relationship.

The lesser importance of disturbance than of rock removal suggests that the viability of populations of broad-headed snakes is less affected by disturbance (overturning or breaking of rocks) than by the actual removal of rock. The dichotomy between 'rock disturbance' and 'rock removal' may coincide largely with 'people searching for snakes' *v.* 'people removing bush-rock', but the correspondence is not exact. The best rocks for broad-headed snakes are typically very close to steep cliffs (because these sites receive greater sun exposure: Webb 1996), and vandals (including, perhaps, unscrupulous reptile collectors) sometimes push the rocks over the

Table 2. Characteristics of habitats and reptile abundances of the sites surveyed

'Snake rocks' are defined as rocks that lay on other rocks, had <30% vegetated cover over them, and were <15 cm in thickness. Numbers of broad-headed snakes, geckos (*Oedura lesueurii*) and total numbers of all lizards are expressed as numbers per person-hours of searching

Site name	Rocks/m currently present	'Snake rocks'/m originally present	% 'snake rocks' removed	% rocks disturbed but not removed	Snakes per hour	Geckos per hour	Total lizards per hour
Stoney Creek	0.52	0.27	23	3	0.5	2.50	3.00
Jacobs Hollow	0.01	0.01	0	0	0	0.67	0.67
Stoney Swamp	0.13	0.33	61	3	0	0	0
Kings Water Hole	0.20	0.24	30	1	0.17	1.00	1.00
Robertson's Knoll	0.04	0	0	0	0	0.50	0.50
Wise's Ridge Road	0.13	0.06	4	3	0	1.00	2.00
Flat Rock Creek	0.30	0.26	0	77	0	2.50	3.00
Yarramunmun Fire Trail	0.42	0.42	0	61	4.0	10.00	13.00
Monkey Gum Road 1	0.17	0.14	0	4	0	1.50	5.00
Monkey Gum Road 2	0.12	0.10	0	3	0.5	1.00	2.00
Thomas Point	0.08	0.09	25	13	0	0.67	1.00
Wanganderry	0.09	0.09	0	9	0	3.00	4.00
Linden Reservoir	0.14	0.14	0	6	0.5	3.50	4.00
Double Hill	0.28	0.28	0	0	0	5.00	7.00
Newnes State Forest	0.14	0.14	0	2	1.5	3.50	6.50
O'Hares Creek 1	0.20	0.19	0	78	0	0.40	2.67
O'Hares Creek 2	0.23	0.23	0	0	0.25	5.25	8.25
Wollemi National Park	0.10	0.10	17	14	0	1.00	1.00

cliff-edges. Under the more usual circumstance where rocks are displaced and sometimes broken, but not actually removed, the consequences to broad-headed snakes are less severe.

The overall conclusion from this path analysis is that broad-headed snakes are likely to be extirpated from outcrops that are subject to intensive bush-rock removal (Table 1). In some cases, the degree of habitat degradation is very high. We surveyed six sites where more than 15% of rocks lying on other rocks had been removed (see Table 2). At one site, >60% of rocks lying on other rocks had been removed by humans (Table 2). The Stoney Creek site offered a poignant example of the impact of bush-rock removal on habitat suitability for broad-headed snakes. At this site, only *one* ‘suitable’ rock remained (indeed, only half a rock, because the rock had been chiselled in half, and the other half removed). An adult female broad-headed snake was found under that rock. The long-term persistence of broad-headed snakes at this site seems unlikely.

Discussion

For more than 100 years, scientists have speculated that bush-rock removal reduces the abundance of broad-headed snakes (Krefft 1869; Shine and Fitzgerald 1989); our study provides the first empirical support for this hypothesis. Our analysis suggests that large sandstone rocks lying on other rocks are important habitat requirements both for the snakes and for their prey; that the rocks removed by bush-rock collectors are of the same general size and have the same general features as the rocks used as diurnal shelter-sites by broad-headed snakes and velvet geckos; that the number of geckos depends primarily on the availability of suitable rocks, and hence is substantially reduced by removal or (to a lesser degree) disturbance of rocks; that the number of broad-headed snakes in an area of apparently suitable habitat is primarily a function of the number of potential prey items, especially velvet geckos; and that the number of broad-headed snakes in an area is significantly reduced by bush-rock removal.

The survey encompassed most of the sites for which there are reliable records of the occurrence of *H. bungaroides*. Australian museums contain a total of only 63 preserved specimens of *H. bungaroides* accompanied by locality data. Twenty-three of these animals came from areas now destroyed by urban development (metropolitan regions of Sydney and Wollongong). A further 26 came from a single small area within the Royal National Park, south of Sydney. Thus, despite the low sample sizes (an almost inevitable aspect of work on endangered taxa), our conclusions are based on data for a high proportion of all known occurrences of the species (including, several populations not known to science prior to this study).

Recent studies on one population of broad-headed snakes (Webb 1996; Webb and Shine 1997*a*, 1997*b*) have shown that the snakes select thin rocks in sunny positions, and that these rocks offer thermally distinctive microhabitats where the snakes lie in wait to ambush their saurian prey. Because both the snakes and the lizards (Schlesinger and Shine 1994*a*, 1994*b*) are highly selective with respect to rock characteristics, any given area contains only a relatively small number of ‘suitable’ rocks, that are used by a high proportion of the reptiles in the area (Webb and Shine 1997*b*). This habitat specialisation makes the reptiles especially vulnerable to removal of these particular rocks.

We do not know if the apparent reliance of the snakes on these rocks is a direct effect, or an indirect effect mediated through the dependence of their prey upon the rocks. Our path analysis suggests that the most important proximate factor determining population densities of broad-headed snakes is gecko abundance rather than habitat availability (Fig. 2). In practice, the implications for conservation of *H. bungaroides* are the same. Gecko populations are sensitive to habitat disturbance, and especially to removal of bush-rock (Schlesinger and Shine 1994*a*, 1994*b*). The most important measure to conserve *H. bungaroides* is thus to conserve its habitat.

Alternative conservation measures (such as prosecution of individuals illegally collecting and holding broad-headed snakes) should also be enforced, but they are likely to be less effective. For example, our path analysis suggests that rock disturbance has less impact than does rock removal. This difference may relate to the fact that the snakes shelter under rocks for only part of the year, and are relatively inaccessible to collectors during other times (when they are widely scattered in tall trees in the woodland, or ensconced deep within crevices on the sheer cliff-face: Webb and Shine 1997*b*). Thus, collectors could, at best, find only a small proportion of the snake population at most times of year. This result from the path analysis is consistent with the fact that our main study area on the Yalwal Plateau supports many broad-headed snakes, despite considerable disturbance by reptile enthusiasts over many years.

Broad-headed snakes are not the only taxon likely to be affected by rock removal. Many invertebrates and other vertebrates also shelter under rocks, and may depend on the same kinds of thermal characteristics (and thus, rock sizes and locations) as do *H. bungaroides* and *O. lesueurii*. For example, several other reptile and amphibian species that are listed as 'vulnerable' in New South Wales legislation (Lunney and Ayers 1993) are found primarily under surface rocks. This category includes species that are sympatric with *H. bungaroides* (e.g. the myobatrachid frog, *Pseudophryne australis*), as well as reptile taxa from drier inland grassland habitats (e.g. the elapid snake, *Suta flagellum*, and the pygopodid lizards *Aprasia parapulchella* and *Delma impar*: Coulson 1990; Osborne *et al*. 1991, 1993; Jones 1992). All of these taxa are likely to be at risk from rock removal.

Undoubtedly, the removal of surface rock is not the only process threatening *H. bungaroides*. The determinants of vulnerability to endangerment are complex, and part of the reason for the decline of this species is to be found in its unusual life-history characteristics (e.g. delayed maturation, low reproductive output, low dispersal: Webb and Shine 1998) as well as in forms of habitat degradation unrelated to bush-rock removal. From the early account by Krefft (1869), it is clear that *H. bungaroides* was once common in many places that are now incorporated within the suburbs of Sydney, with consequent massive modification of habitats. Other, more widespread processes such as increasing vegetation density over the last 200 years, in response to less frequent fires (Kohen 1996), may also have disadvantaged *H. bungaroides* by reducing the availability of rocks offering the appropriate thermal conditions.

Despite these caveats, evidence points to bush-rock removal as one of the factors responsible for the decline of the broad-headed snake. Given that bush-rock collectors remove the same types of rocks (in terms of substrate, thickness and diameter) as those used by the snakes and their primary prey, and that snake and lizard densities are apparently controlled by rock availability, the implications are clear. Unless the activities of bush-rock collectors can be curtailed, the considerable range reduction experienced by the broad-headed snake is likely to continue.

Acknowledgments

We thank the Australian Nature Conservation Agency, the NSW National Parks and Wildlife Service, and the Australian Research Council for financial support. Information on localities for our survey was provided by M. Black, N. Burns, P. Harlow, G. Hollis, and G. White.

References

Burbidge, A. A., and Jenkins, R. W. G. (1984). 'Endangered Vertebrates of Australia and its Island Territories'. (Report of the Working Group on Endangered Fauna of the Standing Committee of the Council of Nature Conservation Ministers: Canberra.)

Cogger, H. G., Cameron, E. E., Sadlier, R. A., and Eggler, P. (1993). 'The Action Plan for Australian Reptiles'. (Australian Nature Conservation Agency: Canberra.)

Coulson, G. (1990). Conservation biology of the striped legless lizard *Delma impar*: an initial investigation. Arthur Rylah Institute Technical Report Series No. 106. (Department of Conservation and Environment: Victoria.)

Dickman, C. R. (1994). Native mammals of western New South Wales: past neglect, future rehabilitation. In 'Future of the Fauna of Western New South Wales'. (Eds D. Lunney, S. Hand, P. Reed and D. Butcher.) pp. 81–91. (Royal Zoological Society of NSW: Sydney.)

Hersey, F. (1980). Broad-headed snake *Hoplocephalus bungaroides*. In 'Endangered Animals of New South Wales'. (Ed. C. Haigh.) pp. 38–40. (NSW National Parks and Wildlife Service: Sydney.)

Hoser, R. T. (1991). 'Endangered Animals of Australia.' (Pierson and Co.: Sydney.)

Jones, S. J. (1992). Habitat relationships, diet and abundance of the endangered pygopodid *Aprasia parapulchella* in the Australian Capital Territory and surrounding New South Wales. B.App.Sc. (Hons) Thesis, University of Canberra.

King, R. B. (1993). Determinants of offspring number and size in the brown snake, *Storeria dekayi*. *Journal of Herpetology* **27**, 175–185.

Kingsolver, J. G., and Schemske, D. W. (1991). Path analyses of selection. *Trends in Ecology and Evolution* **6**, 276–280.

Kohen, J. L. (1996). Aboriginal use of fire in southeastern Australia. *Proceedings of the Linnean Society of New South Wales* **116**, 19–26.

Krefft, G. (1869). 'The Snakes of Australia.' (Thomas Richards, Government Printer: Sydney.)

Lunney, D., and Ayers, D. (1993). The official status of frogs and reptiles in New South Wales. In 'Herpetology in Australia'. (Eds D. Lunney and D. Y. Ayers.) pp. 404–408. (Transactions of the Royal Zoological Society of NSW: Sydney.)

Osborne, W. S., Lintermans, M., and Williams, K. D. (1991). Distribution and conservation status of the endangered pink-tailed legless lizard *Aprasia parapulchella* (Kluge). ACT Parks and Conservation Service Research Report No. 5. (36 pp.)

Osborne, W. S., Kukolic, K., and Williams, K. D. (1993). Conservation of reptiles in lowland native grasslands in the Southern Tablelands of New South Wales and the Australian Capital Territory. In 'Herpetology in Australia'. (Eds D. Lunney and D. Y. Ayers.) pp. 151–158. (Transactions of the Royal Zoological Society of NSW: Sydney.)

Schlesinger, C. A., and Shine, R. (1994*a*). Choosing a rock: perspectives of a bush-rock collector and a saxicolous lizard. *Biological Conservation* **67**, 49–56.

Schlesinger, C. A., and Shine, R. (1994*b*). Selection of diurnal retreat sites by the nocturnal gekkonid lizard *Oedura lesueurii*. *Herpetologica* **50**, 156–163.

Shine, R. (1983). Arboreality in snakes: ecology of the Australian elapid genus *Hoplocephalus.* *Copeia* **1983**, 198–205.

Shine, R., and Fitzgerald, M. (1989). Conservation and reproduction of an endangered species: the broad-headed snake, *Hoplocephalus bungaroides* (Elapidae). *Australian Zoologist* **25**, 65–67.

Southwood, T. R. E. (1978). 'Ecological Methods.' (Methuen: London.)

Webb, J. K. (1996). Ecology and conservation of the threatened broad-headed snake, *Hoplocephalus bungaroides*. Ph.D. Thesis, University of Sydney.

Webb, J. K., and Shine, R. (1997*a*). Out on a limb: conservation implications of tree-hollow use by a threatened snake species (*Hoplocephalus bungaroides*: Serpentes, Elapidae). *Biological Conservation* **81**, 21–33.

Webb, J. K., and Shine, R. (1997*b*). A field study of spatial ecology and movements by a threatened snake species *Hoplocephalus bungaroides* (Serpentes, Elapidae). *Biological Conservation* 82:203–217.

Webb, J. K., and Shine, R. (1998). Ecological characteristics of a threatened snake species, *Hoplocephalus bungaroides* (Serpentes, Elapidae). *Animal Conservation*, in press.

Manuscript received 19 February 1997; accepted 11 November 1997